

EXERCISE-GENERATED HEAT CONTRIBUTES TO THERMOREGULATION BY GAMBEL'S QUAIL IN THE COLD

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Summary

The purpose of this study was to investigate the relationship between the allocation of exercise-generated heat and resting metabolic heat production during cold exposure. We tested the hypothesis that, during cold exposure, exercise-generated heat contributes to the fulfillment of the thermostatic requirement. Our assumption was that the thermostatic requirement is higher for exercising than for resting birds in still air because of the disruption of boundary and plumage insulation layers. We predicted that, during moderate exercise, the metabolic heat production of exercising birds would be higher than that for resting birds in still air but would not differ significantly from the metabolic heat generated by resting birds exposed to similar convective conditions. To test our hypothesis we measured whole-animal oxygen consumption of Gambel's quail (*Callipepla gambelii* Gambel) running in a circular metabolic chamber and at rest in still air at ambient temperatures below the animal's lower critical temperature. We compared these data to previous data for Gambel's quail at rest exposed to wind at a speed equal to the running speed used in our experiments. In addition to oxygen consumption measurements, we measured body temperatures of exercising and resting birds. The data supported our assumption and predictions. (1) Whole-body thermal resistance for exercising birds was lower than that for resting birds in still air, indicating that the thermostatic requirement was higher for exercising birds because of the disruption of boundary and plumage insulation layers. (2) Heat productions of exercising birds were significantly higher than those of resting birds in still air but were not significantly different from the heat productions of resting birds exposed to similar convective conditions. (3) Body temperatures were not significantly different between resting birds in still air and exercising birds. The mean body temperature of exercising birds, however, was 2°C higher than that of resting birds exposed to wind. We concluded that an exercising animal probably does not incur an energetic cost associated with locomotor activity at low ambient temperatures in comparison to an inactive animal exposed to a similar convective regime.

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Introduction

Endothermic animals are commonly active at cold ambient temperatures that require an increase in energy metabolism to maintain body temperature. Consequently, energy must be allocated to meet both thermostatic demands and energy requirements for locomotor activity. The thermostatic demands for small birds can constitute as much as 20–40 % of their daily energy needs (Weathers *et al.* 1984). It is well established that thermostatic requirements vary with air temperature but only recently have convective effects on metabolic heat production been considered. Studies of oxygen consumption of resting birds in wind tunnels have provided evidence that metabolic rate increases significantly with increased wind speed (Goldstein, 1983; Biesel and Nachtigall, 1987; Rothe *et al.* 1987; Webster and Weathers, 1988). It is apparent that wind coupled with cold temperatures can impose high thermoregulatory requirements (Webster and Weathers, 1988).

For exercising birds, convective effects on heat balance are presumably greater than for resting birds. During exercise, the aerodynamic boundary layer and plumage insulation layer are disrupted by both wind and the movement of the bird's body through the air (Walsberg *et al.* 1978; Walsberg, 1988). Although thermal conductance is obviously increased under these circumstances, during whole-body locomotion, muscle contraction clearly produces additional heat (Hill, 1938). The purpose of this study was to investigate the allocation of exercise-generated heat and thermoregulatory heat production during cold exposure. We tested the hypothesis that, during cold exposure, exercise-generated heat contributes to the thermostatic requirement and in some cases completely substitutes for regulatory thermogenesis.

The relationship between exercise-generated heat produced by terrestrial locomotion and thermostatic heat production has been studied for both small mammals (Hart and Jansky, 1963; Hart, 1971) and birds (Pohl and West, 1973; Paladino and King, 1984; Webster and Weathers, 1990). The interpretations of the results do not always support the hypothesis that exercise-generated heat substitutes for regulatory thermogenesis. In some investigations, partial or complete substitution was observed, but only at ambient temperatures well below lower critical temperatures (Pohl, 1969; Pohl and West, 1973; Paladino and King, 1984). At more moderate cold ambient temperatures, exercise-generated heat and thermoregulatory heat were considered to be additive (Hart and Jansky, 1963; Pohl, 1969; Hart, 1971; Pohl and West, 1973; Nomoto *et al.* 1983; Brackenbury, 1984; Paladino and King, 1984). In these studies, exercise-generated heat may have appeared to be additive more often than substitutive to regulatory thermogenesis, because heat productions of resting animals in still air were compared to those of exercising animals with presumably higher thermostatic requirements.

To clarify the contribution of exercise-generated heat to the thermostatic requirement in nature, we compared heat productions of resting and exercising birds exposed to similar convective conditions and therefore with similar thermostatic requirements. We measured heat productions of Gambel's quail (*Callipepla gambelii*) running in a circular metabolic chamber and at rest in still air, and

compared these data with those of Goldstein (1983) for the same species at rest exposed to a wind speed equal to the running speed used in our experiments. We predicted that the thermostatic requirement and metabolic heat productions of exercising birds would be higher than those of resting birds in still air but would not differ significantly from metabolic heat generated by resting birds exposed to similar convective conditions. In the latter case, exercise-generated heat would fulfill the thermostatic requirement and alleviate the need for regulatory thermogenesis.

The question of whether exercise-generated heat contributes to the fulfillment of the thermostatic requirement at low ambient temperatures has important implications for the thermal stress an animal experiences. The answer to the question partly determines the extent to which an animal is incurring an energetic cost associated with locomotor activity relative to an inactive animal (Walsberg, 1983). This concept has particular significance for time–energy budgets of animals living in cold environments. If the time to meet energetic demands is reduced, then more energy would be available for foraging or social interactions (Ketterson and King, 1977; Paladino and King, 1984). Whether an animal is inactive or forages actively in the cold could depend upon whether substitution occurs (Paladino and King, 1984; Webster and Weathers, 1988).

Materials and methods

Animal collection and maintenance

Gambel's quail were captured with funnel traps near Buckeye, Maricopa County, Arizona, in late September. This species was selected for study because it is cursorial and spends approximately 50 % of its active day engaged in terrestrial locomotion, 28 % of which includes foraging activities (Goldstein and Nagy, 1985). Foraging Gambel's quail may travel up to 3.5 km daily (Goldstein and Nagy, 1985). Also, although thermoregulatory adaptations are expected to involve mechanisms to reduce heat stress, Gambel's quail commonly experience winter ambient temperatures that can drop to near freezing in open areas of the desert. Low ambient temperatures coupled with wind and rain, and on rare occasion snow, can impose high thermoregulatory requirements. The thermoregulatory responses of these desert-adapted birds to low ambient temperatures could be primary determinants of their survival in winter.

All birds were color-banded for ease of identification and put in a large outdoor aviary on the Arizona State University campus. They were therefore exposed to temperatures and photoperiods similar to those for free-living birds. Birds were fed a mixture of wild bird seed mix and game bird feed. Water and food were given *ad libitum*. All birds used were adults and ranged in body mass from 142.8 to 177.3 g. The mean body mass for 20 birds was 162.8 ± 11.8 g. Individuals were chosen at random for each experimental treatment and were not deprived of food prior to oxygen consumption measurements.

Heat production measurements

Whole-animal oxygen consumption of Gambel's quail running in a circular metabolic chamber and at rest in still air was measured at 0, 10 and 20°C. The lower critical temperature (LCT) for resting Gambel's quail is 27°C (Goldstein, 1983). Twenty individual birds were used – 10 males and 10 females. Oxygen consumption of each bird at rest in still air and during locomotor activity was measured at all three test temperatures.

Aerobic metabolism was determined by measuring oxygen consumption in an open-flow respirometry system using an Applied Electrochemistry oxygen analyzer (model S-3A). The entire metabolic chamber was placed in a Queue Systems temperature-controlled environmental chamber. Incurrent air from a tank of compressed air was desiccated and all CO₂ removed by a column of Drierite and Ascarite. Air flow into the chamber was controlled at 2 l min⁻¹ by a Brooks mass flow controller with a resolution of 1 ml min⁻¹. Incurrent air was equilibrated with chamber temperature by flowing it through copper coils upstream from the metabolic chamber. Air temperature within the metabolic chamber was measured with a thermocouple (26 gauge) connected to an Omega telethermometer accurate to ±0.15°C. Excurrent air from the metabolic chamber passed through (1) a dew point hygrometer (EG and G model 911), to measure water content of the sample air, (2) a tube containing Drierite and Ascarite, to remove all water and CO₂, and (3) the sensor of the oxygen analyzer.

Two tests were performed to check for leaks in the metabolic chamber. First, flow meters were placed before the inlet and after the outlet valve. Flow rates measured at both locations were within 2 ml min⁻¹ of each other. Second, the chamber was slightly pressurized and the change in pressure measured at 48 h. At this time, the pressure was 98 % of the initial value.

Instantaneous oxygen consumption was calculated using the equation of Bartholomew *et al.* (1981). The effective volume of the system was determined by introducing pure oxygen into the chamber, then drawing through room air and measuring the fractional concentration of oxygen in the excurrent air as it decreased towards the value of room air (20.94 %). All gas volumes were corrected to standard temperature and pressure. To calculate total heat production, we assumed a respiratory quotient of 0.74 and an energy equivalent of oxygen of 20.1 kJ l⁻¹. This seemed reasonable since these birds were not post-absorptive and were probably metabolizing primarily fats and carbohydrates (Kleiber, 1961). We also based our assumption on the few species of birds in which both oxygen consumption and carbon dioxide production during flight have been reported (Tucker, 1968; Berger and Hart, 1974).

The metabolic chamber containing a circular running path was constructed of aluminum walls to serve as heat exchangers and a Plexiglas top (Fig. 1). The walls were painted white and had a high emissivity. The circular path of the floor was 6 cm wide and had 334 cm of running length. This design differed from typical treadmills in that the hardware cloth floor used for the running path remained stationary. The movement of the bird across the floor simulated more closely the

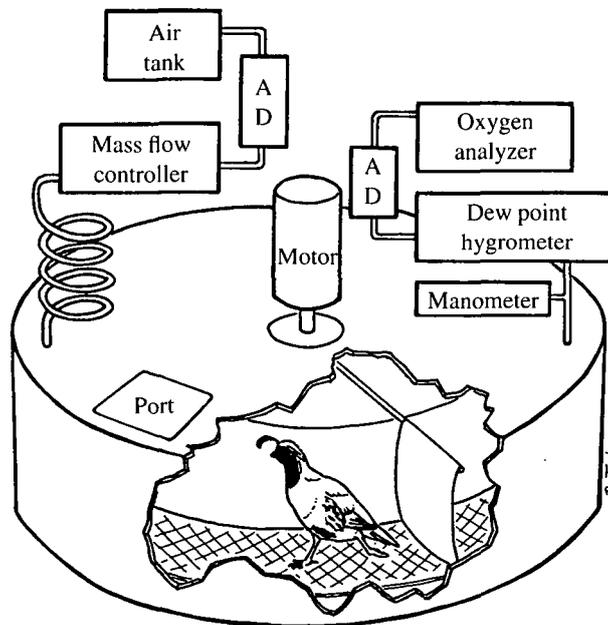


Fig. 1. Diagram of the metabolic chamber containing a circular running path. This design forced birds to move across the floor and simulated more closely natural convective heat transfer of an animal moving through air compared with one standing stationary on a conventional treadmill. The two boxes labeled A and D represent cylinders containing Ascarite (A) and Drierite (D) which remove CO_2 and water, respectively, from the sample air.

natural convective heat transfer of an animal moving through air compared with one standing stationary on a conventional treadmill. In using this design we were able to equate locomotor speed to the air velocity used in Goldstein's (1983) study.

Birds were placed in the metabolic chamber for 30–60 min before oxygen consumption measurements were made. For measurements of resting metabolism, an individual bird was placed within the metabolic chamber in a small cage that was approximately the length of its body and slightly wider than body width. This allowed vertical but no horizontal movement. All measurements of energy metabolism were performed during the bird's normal active period under moderate light conditions.

A week before activity metabolism measurements were made, all birds were acclimated to the running chamber for 30 min at a time on three different days. Activity metabolism was measured as an individual bird ran across the circular running path of the metabolic chamber for 60 min. The birds were induced to run at a constant speed by a revolving gate within the metabolic chamber. A variable-speed motor located outside the metabolic chamber maintained the speed of the gate at 1.5 m s^{-1} . This was the average locomotor speed of birds observed in the field. The running speeds of 64 quail in the field were determined by timing a bird

as it moved from a given marker, usually a patch of cover to another marker, and then measuring the distance covered. In the running chamber, all birds ran approximately 20 cm in front of the gate and used a posture and gait similar to those of birds observed in the field. Individuals that were reluctant to run were replaced by another bird.

Thermal resistance

Whole-body thermal resistance is a measure of temperature-specific heat flux between the animal's core and its environment and is analogous to insulation. For birds, whole-body thermal resistance to heat transfer incorporates tissue, plumage and aerodynamic boundary layer resistances (Robinson *et al.* 1976; Campbell, 1977; Mahoney and King, 1977). We used the equation of Robinson *et al.* (1976) to calculate whole-body thermal resistance. This equation utilizes the equivalent black-body temperature (T_e), the temperature of a black-body enclosure that would produce the same net thermal load on an animal as its natural environment (Bakken, 1976; Robinson *et al.* 1976). We assumed that T_e was essentially equal to the metabolic chamber air temperature because, by design, there was probably no thermally significant short-wave radiation, and long-wave radiation originated from chamber walls with emissivity near 1.0 and at a temperature near that of the air. The external surface area of birds was estimated using the equation of Walsberg and King (1978).

Body temperature

The body temperature of each bird was measured immediately, within 30 s of removing the animal from the metabolic chamber, by inserting a catheter tube containing a 36 gauge thermocouple 4 cm into the cloaca. This method may slightly underestimate core body temperature. For white-crowned sparrows, intraperitoneal temperatures exceed cloacal temperature by an average of 1°C (Southwick, 1973). Thermocouple temperatures were read from an Omega telethermometer accurate to $\pm 0.15^\circ\text{C}$. All thermocouples were calibrated against a standard mercury thermometer with accuracy traceable to the National Bureau of Standards.

Statistical analyses

Means and standard errors were determined for all variables. Multifactor analysis of variance (ANOVA) was used to determine the effects of activity level, ambient temperature and sex on mean values of heat production and whole-body thermal resistance (Sokal and Rohlf, 1981). Tukey's test was used for *a posteriori* pairwise comparisons among means of experimental groups (Neter *et al.* 1985). We found no significant differences between males and females for any of the metabolic variables and so pooled the data for both sexes. Significance levels were set at $P=0.05$ for all statistical tests.

Results

Heat production of exercising and resting birds

During cold exposure, activity level and ambient temperature independently affected heat production. At 0, 10 and 20°C, the values for metabolic heat productions of exercising birds were significantly higher than those of resting birds in still air (ANOVA; $F=116.4$, $P=0.0001$, d.f.=1; Fig. 2). The ratios of activity/resting metabolism were 1.25, 1.40 and 1.76 at 0, 10 and 20°C, respectively. Heat productions of exercising and resting birds increased with decreasing ambient temperature (ANOVA; $F=75.45$, $P=0.0001$, d.f.=2; Fig. 2). For resting birds, mean values for heat productions differed significantly between the different temperatures. For exercising birds, contrasts of mean values for heat production at 0 and 10°C and 0 and 20°C differed significantly, whereas those for 10 and 20°C did not (Tukey's test; Fig. 2).

The values we report for heat productions of resting and exercising birds were similar to those reported by Nomoto *et al.* (1983) for Japanese quail under similar experimental conditions. Our measures for heat productions of resting birds, however, were approximately 25% higher than those reported by Goldstein (1983) for Gambel's quail. Note that in Goldstein's (1983) study, the birds were post-absorptive and measurements were made in the dark. The birds used in our study were not deprived of food and measurements were made under moderate light and during active phases of the daily cycle. All these factors can elevate metabolic rate (Aschoff and Pohl, 1970; Calder and King, 1974). We attributed the difference between our values for heat production of resting birds and Goldstein's values to these factors and assumed that the effects were the same regardless of activity level or ambient temperature.

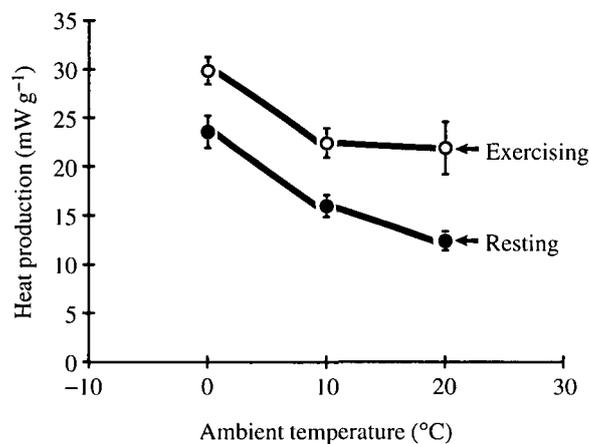


Fig. 2. Metabolic heat production as a function of ambient temperature of quail running at 1.5 m s^{-1} (open circles) and at rest in still air (filled circles). Values plotted are means with 95% confidence limits indicated by the error bars. The sample size was 20 in each case.

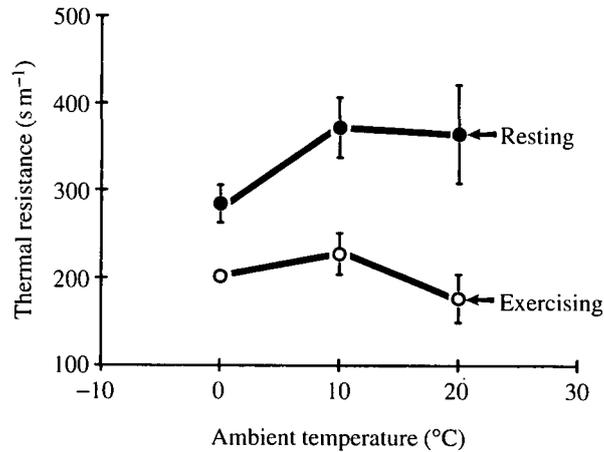


Fig. 3. Whole-body thermal resistance as a function of ambient temperature of quail running at 1.5 m s^{-1} (open circles) and at rest in still air (filled circles). Values plotted are means with 95% confidence limits indicated by the error bars. The value for exercising birds at 0°C shows no error bars because the error was so small that bars do not extend beyond the periphery of the circle. The sample size was 20 in each case.

Whole-body thermal resistance

Activity level and ambient temperature significantly affected whole-body thermal resistance (ANOVA; activity: $F=130.7$, $P=0.0001$, d.f.=1; temperature: $F=8.28$, $P=0.0005$, d.f.=2). Whole-body thermal resistance was significantly lower during running than at rest (Fig. 3). For both exercising and resting birds, from 0 to 10°C , whole-body thermal resistance increased. From 10 to 20°C , the thermal resistances for resting birds did not differ, whereas the values for exercising birds decreased (Tukey's test; Fig. 3).

Body temperatures

The body temperatures of exercising and resting birds ranged from 38.7 to 43.3°C . Ambient temperature but not activity level significantly affected body temperature (ANOVA; $F=8.11$, $P=0.0005$, d.f.=2; Fig. 4). Mean body temperatures of exercising and resting birds in still air were not significantly different. For exercising birds, mean body temperature decreased slightly with decreasing ambient temperatures from 10°C to 0°C . For resting birds in still air, body temperature was relatively constant and independent of ambient temperature (Fig. 4). In contrast, the body temperature of resting birds exposed to similar convective conditions as the exercising birds was 2°C lower than that of exercising birds at 10°C (Fig. 5; Goldstein, 1983).

Discussion

In previous laboratory studies of the relationship between exercise-generated

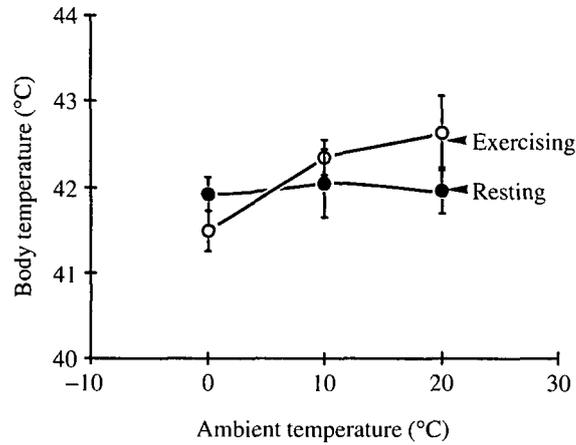


Fig. 4. Body temperature as a function of ambient temperature. Open circles represent data for exercising quail and filled circles are for quail at rest in still air. Values plotted are mean \pm s.e. The sample size is 20 in each case.

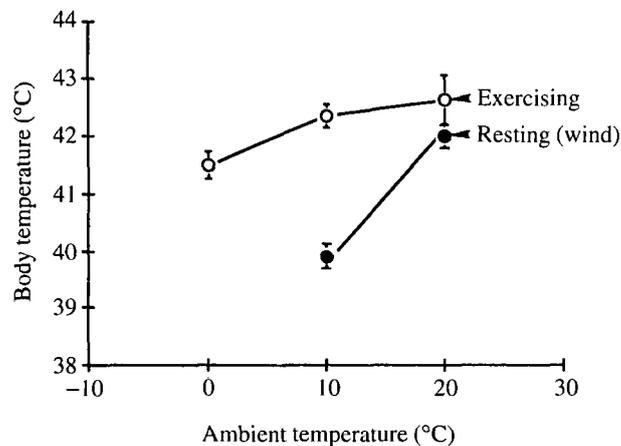


Fig. 5. Comparison of body temperatures of exercising (open circles) and resting (filled circles; from Goldstein, 1983) birds exposed to similar convective conditions. For exercising quail, the running speed was 1.5 m s^{-1} . Resting birds were exposed to a 1.5 m s^{-1} wind. Values plotted are mean \pm s.e. For exercising quail, the sample size is 20 in each case. For resting quail, the sample size is 11 in each case.

and thermostatic heat production, partial or complete substitution of exercise-generated heat for regulatory thermogenesis was observed but only at extremely low ambient temperatures (Pohl, 1969; Pohl and West, 1973; Paladino and King, 1984). In common redpolls, substitution was observed at ambient temperatures from -30 to -40°C , approximately 50°C below the LCT (Pohl and West, 1973), and in white-crowned sparrows at -10°C , approximately 20°C below the LCT

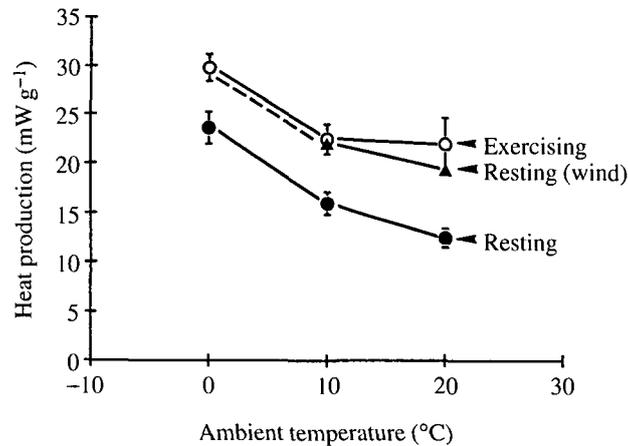


Fig. 6. Heat production as a function of ambient temperature for (1) birds at rest in still air (filled circles), (2) birds at rest exposed to a wind speed of 1.5 m s^{-1} (filled triangles, dashed line), and (3) exercising birds running in a circular metabolic chamber at 1.5 m s^{-1} (open circles). Data for cases 1 and 3 were re-plotted from Fig. 2. Values for resting heat production of birds exposed to wind at 10 and 20°C were calculated by adding the percentage increase in metabolic heat production due to forced convection to values in this study for resting heat production of birds in still air. This increase in heat production was determined by taking the percentage by which a resting bird at zero wind speed increases its metabolic rate when exposed to 1.5 m s^{-1} wind speed at the same ambient temperature (from Goldstein 1983, with permission). The fractional increase in heat production was used rather than absolute values because data from Goldstein (1983) for resting birds at zero wind speed were 25% lower than in the present study for resting birds in still air (see text). The dashed line indicates the predicted change in resting heat production from 10 to 0°C for birds exposed to wind.

(Paladino and King, 1984). In these studies, heat productions of resting birds in still air were compared to the heat productions of exercising birds with presumably higher thermostatic requirements (see below). Under these circumstances, it is difficult to discern whether exercise-generated heat substitutes for regulatory thermogenesis. In addition, when exercise-generated heat and thermoregulatory heat are considered to be additive (Hart and Jansky, 1963; Pohl, 1969; Hart, 1971; Pohl and West, 1973; Nomoto *et al.* 1983; Brackenbury, 1984; Paladino and King, 1984), it is unclear whether the higher heat productions of exercising birds are due to both regulatory thermogenesis and exercise-generated heat or to the metabolic increment associated with exercise alone. In our study, the comparison of animals with similar thermostatic requirements enabled us to identify the contribution of exercise-generated heat to the fulfillment of the thermostatic requirement in the cold. Under these circumstances we observed complete substitution of exercise-generated heat for regulatory thermogenesis at ambient temperatures from 0 to 20°C below the LCT (Fig. 6). Our results suggest that substitution of exercise-generated heat for regulatory thermogenesis may occur more frequently under natural environmental conditions than predicted by previous investigators. In

support of this concept, Webster and Weathers (1990) provided evidence for partial substitution of exercise thermogenesis for regulatory thermogenesis for free-ranging birds using labeled water techniques. Although our controlled laboratory study differs considerably from this field test of the hypothesis, the data are in close agreement. Our results and inferences are also consistent with those of Ketterson and King (1977), who inferred complete substitution by hyperactive birds exposed to daily ambient temperature cycles simulating natural winter conditions. They proposed thermostatic substitution as an explanation for the identical daytime oxygen consumption of hyperactive, fasted and normal fed control white-crowned sparrows, in spite of their eight- to ninefold difference in perch-hopping activity.

Our observation that exercise-generated heat substituted for thermostatic needs may also explain why, for exercising birds, whole-body resistance increased with declining ambient temperature from 20 to 10°C. This indicates that exercising birds increased the effectiveness of their insulation when exposed to temperatures below the LCT for resting Gambel's quail (27°C; Goldstein, 1983). It is possible that the LCT of active birds is lower than that of resting birds (Paladino and King, 1984). Based on the metabolic data we report for exercising birds, it appears that the thermoneutral zone for exercising quail may extend down to 10°C or lower (Fig. 2).

In some studies, the relationship between oxygen consumption and ambient temperature indicates that thermal conductance is similar in resting and active birds (Pohl and West, 1973). In contrast, our results for Gambel's quail indicate that whole-body thermal resistance was significantly higher for resting birds in still air than for exercising birds. One possible explanation for this is that thermostatic costs are increased during exercise owing to disruption of the aerodynamic boundary layer and plumage insulation layer. This explanation is consistent with the observation that wind increases thermal conductance at ambient temperatures below the LCT for resting Gambel's quail (Goldstein, 1983).

Although exercising birds have the potential for greater heat loss at a given ambient temperature compared to resting birds, they are able to maintain high body temperatures. When exercising and resting birds are exposed to similar convective conditions, the body temperature of exercising birds is significantly higher (Fig. 5). There is some evidence that birds regulate body temperature at a variety of set points depending upon activity and physiological conditions (Walsberg, 1983). Elevated body temperatures have been observed during flight (Torre-Bueno, 1976) and non-flight activities (Nomoto *et al.* 1983; Paladino and King, 1984) and during molt (Dolnik and Gavrilov, 1979). In at least some species, it appears that body temperature is electively elevated. For example, Paladino and King (1984) monitored core body temperature of white-crowned sparrows resting and hopping on a treadmill. Body temperature increased by an average of 1°C at the maximum hopping speed. This elevation of body temperature was independent of ambient temperature from 0 to 25°C. The elevation appears to be voluntary, since whole-body thermal resistance increased with declining ambient

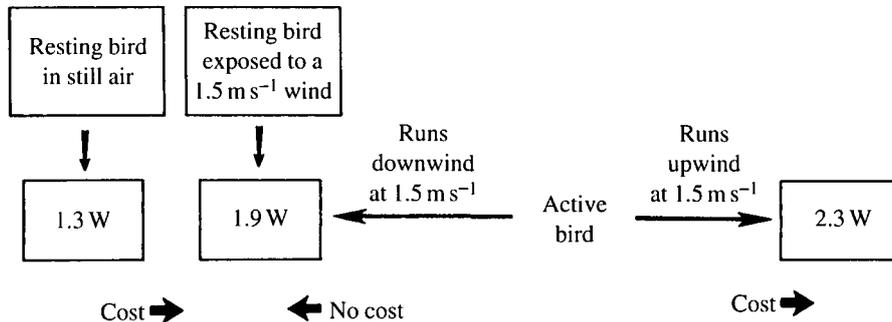


Fig. 7. Expected relationship of the energetic cost associated with locomotor activity and an animal's convective regime. The convective effect on the bird running upwind is assumed to equal a wind speed of 2.5 m s^{-1} .

temperature in exercised birds. The similar results we observed for Gambel's quail also suggest that body temperature may be electively regulated in this species.

The substitutive nature of activity metabolism and the elective elevation of body temperature have significant ecological implications concerning costs associated with an animal's locomotor activities and total energy expenditure in the cold. Under controlled laboratory conditions, our data for metabolic heat productions indicate that an exercising animal does not incur an energetic cost associated with locomotor activity at low temperatures in comparison to an inactive bird exposed to the same convective conditions. A resting bird exposed to a 1.5 m s^{-1} wind uses the same amount of energy to maintain body temperature as a bird running at 1.5 m s^{-1} (downwind or still air conditions assumed; Fig. 7). In nature, the thermostatic requirements vary with time of day and type of activity. The actual cost of natural locomotor activities in the cold is therefore more complicated. Convective conditions may be altered by changes in air temperature or directional changes in wind currents. For example, the convective effects on heat balance of a bird running upwind would be much greater than for a bird running downwind or in still air at same speed (Fig. 7). This would require a greater increase in heat production to maintain body temperature and to overcome the added resistance caused by the wind. Under these conditions, there would be a cost associated with the same level of locomotor activity as in the latter example in which no cost was evident (Fig. 7).

Our results support the concept that energy is conserved by exercising birds in the cold (Ketterson and King, 1977; Paladino and King, 1984; Webster and Weathers, 1990) and emphasize the importance of considering an animal's convective regime for interpreting metabolic data of active animals. We propose that substitution of exercise-generated heat for regulatory thermogenesis may provide a means by which some animals can minimize energy expenditures while engaging in activities such as foraging under environmentally stressful conditions such as cold exposure. These conclusions have particular significance for the

assignment of metabolic costs to terrestrial locomotion or to foraging in the construction of time–energy budgets of free-living birds (Goldstein, 1988).

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