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SEASONAL ADJUSTMENTS IN METABOLISM AND INSULATION IN THE DARK-EYED JUNCO[1]

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Abstract. Trends during summer and winter in body mass and composition, insulation, body temperature, and metabolism were investigated in seasonally acclimatized Dark-eyed Juncos (*Junco hyemalis*) from western Oregon to determine if patterns of acclimatization were similar to those of passerines inhabiting harsher winter habitats. Body mass was significantly increased in winter (19.4 ± 0.2 g) compared to summer (17.8 ± 0.1 g), primarily because of elevated stored fat. Lean dry mass was seasonally constant. Dry mass of contour plumage was measured as an index of insulation and increased by 31.7% in winter birds. Little seasonal variation in body temperature was apparent and there was no evidence of torpor and only a very mild regulated nocturnal hypothermia at either season. Standard metabolic rate was significantly elevated in winter-acclimatized juncos (1.02 ml O_2/min, 3.45 ml $O_2 \cdot g^{-1} \cdot hr^{-1}$) relative to summer-acclimatized birds (0.87 ml O_2/min, 3.16 ml $O_2 \cdot g^{-1} \cdot hr^{-1}$). In addition, winter juncos demonstrated an ability to decrease thermal conductance below thermoneutrality. Insofar as winter increments in insulation do not offset increased thermogenic requirements at temperatures characteristic of this season, winter-acclimatization in Dark-eyed Juncos from western Oregon is similar to that for passerines from more severe winter climates in that it is primarily a metabolic process.

Key words: Dark-eyed Junco; Junco hyemalis; *seasonal adjustments; metabolism; insulation.*

INTRODUCTION

Small passerine birds wintering in cold regions of temperate zones undergo seasonal acclimatization which facilitates maintenance of thermoregulatory homeostasis under winter conditions. Insulatory adjustments assist in winter improvement of cold tolerance in some passerines, but it appears that acclimatization is primarily metabolic in those birds inhabiting regions with relatively harsh winters (Pohl and West 1973, Dawson and Carey 1976, Dawson et al. 1983a). The primary feature of metabolic acclimatization in these birds is an enhanced ability to maintain greatly elevated metabolism to support shivering thermogenesis (Dawson and Carey 1976, Dawson and Smith 1986).

Seasonal patterns of cold tolerance in passerines have been investigated primarily in species subject to extreme winter cold [e.g., Evening Grosbeaks (*Coccothraustes vespertinus*), European Starlings (*Sturnus vulgaris*), and House Sparrows (*Passer domesticus*) from Ottawa, Canada (Hart 1962), Gray Jays (*Perisoreus canadensis*) from Alaska (Veghte 1964), House Sparrows (*P. domesticus*) from Illinois (Barnett 1970), Bramblings (*Fringilla montifringilla*) from Scandinavia (Pohl 1971), Common Redpolls (*Carduelis flammea*) from Alaska (West 1972, Pohl and West 1973), American Goldfinches (*Carduelis tristis*) from Michigan (Dawson and Carey 1976, Dawson and Smith 1986), and House Finches (*Carpodacus mexicanus*) from Colorado (Dawson et al. 1983a)]. However, the small size and high energy requirements of many passerines might require seasonal cold adjustments in species inhabiting less stressful temperate regions (Dawson et al. 1983a). Geographic variation in cold tolerance associated with severity of winter climate has been demonstrated for some passerines (Blem 1973, Dawson et al. 1983a). Perhaps the relative roles of metabolic and insulative contributions to acclimatization also vary with climate. Characterization of metabolic and insulatory contributions to seasonal acclimatization in birds inhabiting regions with relatively mild winters will demonstrate the ubiquity of the acclimatization pattern documented for passerines wintering in harsh climates. The present study was undertaken to determine patterns of metabolic and insulatory cold-acclimatization in Dark-eyed Juncos (*Junco hyemalis*) which inhabit

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western Oregon, a region of relatively mild winter climate. Variables investigated here include body mass and composition, body temperature (T_b), standard metabolic rate (SMR), and the relation of metabolic rate ($\dot{V}O_2$) to ambient temperature (T_a).

METHODS AND MATERIALS

BIRDS

Dark-eyed Juncos were captured before 10:00 hr, near Corvallis, Benton County, Oregon in 1987 and 1988 by mist-nets or live-traps. Birds captured from 15 May–30 Sept. were designated "summer birds"; those captured 1 Dec.–28 Feb. were designated "winter birds." Body mass to the nearest 0.2 g was determined immediately upon capture with a Pesola spring balance (0–50 g with 0.5 g gradations). Visible fat depots in furcular and abdominal regions were also scored immediately upon capture using a scale of 0–5 (Helms and Drury 1960). All tests were conducted on the day of capture.

BODY CONSTITUENTS

For determination of body constituents, juncos were killed by cervical dislocation immediately upon return from the field and stored frozen at −20°C for later measurement. Plumage mass was measured by plucking and drying contour feathers to a constant mass in an open-ended vial at 80°C. Carcass, remiges, and retrices were homogenized, lyophilized, and weighed to the nearest 0.01 g. Neutral lipid was extracted from the lyophilized carcass by Soxhlet extraction for 4 hr in diethyl ether (Oregon State University Agricultural Chemistry). Extractable neutral lipid was considered as fat content. Lean dry mass was calculated as lyophilized carcass weight minus fat content.

BODY TEMPERATURE

Juncos were housed individually, or in a few cases in pairs, in 25 cm × 30 cm × 38 cm cages that were placed in a constant temperature-controlled room. The temperature of the room was maintained within ±2°C of the desired values, 30°C, 15°C, 5°C, and −10°C (winter only, as summer birds became hypothermic at this temperature). Food and water were provided ad libitum. Every four hours, from 12:00 to 24:00 hr, birds were quickly removed from the cages and T_b was measured cloacally with a 20 gauge copper-constantan thermocouple connected to a Cole-Parmer thermocouple thermometer (Model 8500-40) with an accuracy of ±0.1°C. The thermometer was calibrated with a standard thermometer traceable to the U.S. Bureau of Standards. Data from birds that showed signs of undue stress (e.g., panting) or that were difficult to capture were omitted.

METABOLIC RATE AND AMBIENT TEMPERATURE

Juncos were weighed, placed in a metabolic chamber (3.8 l) at 30°C, and fasted for at least five hours prior to metabolic tests to ensure postabsorptive conditions. Tests were conducted from 20:00 to 03:00 hr in winter and from 21:00 to 03:00 hr in summer. Oxygen consumption ($\dot{V}O_2$) was measured by open-circuit respirometry with a Beckman Model E2 oxygen analyzer according to Swanson (1990). $\dot{V}O_2$ was calculated as mean steady state $\dot{V}O_2$ for the test period (DePocas and Hart 1957, Hill 1972, Equation 2) from values recorded every 60 sec. Flow rates of dry, CO_2-free air through the metabolic chamber were maintained at 230–290 ml/min with a Cole-Parmer precision rotameter (Model FM082-03ST) calibrated to ±1% accuracy and positioned upstream from the metabolic chamber (Swanson 1990). These rates yielded changes in O_2 content between influx and efflux air of 0.3 to 0.5%, and maintained O_2 content of dry, CO_2-free efflux air above 20.3%. Temperature within the metabolic chamber was controlled by immersion of the chamber into a water/ethylene glycol bath capable of regulating temperature within ±0.5°C. Chamber temperature was monitored continuously with a thermocouple thermometer.

Individual birds were exposed to a series of decreasing temperatures beginning with 30 ± 1.2°C. After equilibration, $\dot{V}O_2$ at 30°C was measured for 1 hr. Chamber temperature was then decreased until the desired test temperature was attained. Approximately 15 min equilibration was allowed at each new test temperature before $\dot{V}O_2$ measurements were initiated. $\dot{V}O_2$ at each test temperature below 30°C was measured for 45 min. This procedure was continued until $\dot{V}O_2$ measurement at the lowest T_a desired was completed, at which time the bird was removed from the chamber and weighed. $\dot{V}O_2$ of individual birds was measured at a maximum of four test temperatures. Total time for metabolic tests was approximately 5.5 hr. Mass loss over the experi-

TABLE 1. Seasonal values for body mass and constituents and plumage. Sample size is indicated in parentheses. The * indicates $P < 0.01$, ** indicates $P < 0.001$. Sex ratios (M:F), determined by plumage, were 3:2 in summer and 3:3 in winter for total body lipid, 2:2 in summer and 3:3 in winter for lean dry mass, and 7:7 in summer and 8:6 in winter for plumage mass.

Measurement	Summer	Winter
Total body mass	17.8 ± 0.1 g (59)	19.4 ± 0.2 g (56)**
Total body lipid	0.49 ± 0.03 g (5)	1.16 ± 0.27 g (6)
Visible fat-furcular	1.0 ± 0.1 (57)	3.1 ± 0.1 (57)**
-abdominal	1.2 ± 0.1 (57)	3.3 ± 0.1 (57)**
Lean dry mass	4.28 ± 0.13 g (4)	4.50 ± 0.19 g (6)
Plumage mass	0.60 ± 0.03 g (14)	0.79 ± 0.02 g (14)*

ment was determined as initial mass upon introduction into the metabolic chamber minus final mass after removal from the chamber. A constant rate of mass loss throughout the test period was assumed. Mass-specific $\dot{V}O_2$ calculations used mass values corrected for time in the chamber.

STATISTICS

Data are reported as means ± SE, unless otherwise indicated. Means were compared by student's *t* test or by Mann-Whitney *U* test when sample variances were not equal. Regression lines were fit by the method of least squares. Comparison of slopes and intercepts of regression lines was by analysis of covariance. Significance was accepted at $P < 0.05$.

RESULTS

BODY MASS AND COMPOSITION

Dark-eyed Juncos were significantly heavier in winter than in summer (Table 1). Mean body mass in winter exceeded the summer value by 9.0%. This increase was largely due to increased fat stores, as indicated by the significant increase in visible fat depots in furcular and abdominal regions (Table 1). Total body lipid increased in winter birds, although not significantly ($P = 0.07$) due to large sample variance in winter (Table 1). Total body lipid and visible fat scores were measured on birds caught in the morning, so fat stores were presumably at or near a daily minimum. Fat stores prior to nightly roosting probably show even greater seasonal differences. In contrast to stored fat, lean dry mass does not appear to vary seasonally (Table 1). Plumage mass increased significantly in winter (Table 1), exceeding summer values by 31.7%.

BODY TEMPERATURE

Cloacal temperature (T_b) showed a weak dependence on T_a at both seasons during the day and during winter nights. For summer nights, T_b was independent of T_a over the range of T_as tested (Fig. 1). The only significant seasonal differences in T_b occurred at 5°C and 15°C T_a during winter days and at 30°C T_a during winter nights, where mean values were significantly elevated over summer values (Table 2). The mean fluctuation in T_b between resting and active daily periods was 2.3°C in summer and 2.5°C in winter. These values were not significantly different.

METABOLIC RATE AND AMBIENT TEMPERATURE

Standard metabolic rates (SMR) were 3.16 ± 0.07 ml $O_2 \cdot g^{-1} \cdot hr^{-1}$ (0.87 ± 0.02 ml O_2/min, $n = 11$) during summer and 3.45 ± 0.13 ml $O_2 \cdot g^{-1} \cdot hr^{-1}$ (1.02 ± 0.04 ml O_2/min, $n = 8$) during winter. These values were significantly different

TABLE 2. Body temperatures of juncos housed at different temperatures in winter and summer. Sample sizes are indicated in parentheses. The * indicates $P < 0.05$, ** indicates $P < 0.001$ for corresponding values at the opposite season.

T_a (°C)	Winter		Summer	
	Day	Night	Day	Night
30	42.5 ± 0.3 (12)	40.6 ± 0.2* (8)	42.3 ± 0.1 (18)	39.6 ± 0.4 (6)
15	42.6 ± 0.2 (12)	39.8 ± 0.3 (12)	41.7 ± 0.1** (18)	39.2 ± 0.5 (6)
5	42.4 ± 0.3 (12)	39.9 ± 0.2 (12)	41.5 ± 0.3** (14)	39.6 ± 0.8 (4)
−10	41.8 ± 0.3 (12)	39.1 ± 0.3 (12)	—	—

on both a total metabolism basis ($P < 0.01$) and a mass-specific basis ($P = 0.05$). [Note: SMR data from Swanson (1990) were reanalyzed to reduce rounding errors. SMR for winter-acclimatized juncos was slightly lower than previously reported values (Swanson 1990).] Factorial increment of SMR in winter was 1.17 for total metabolism SMR and 1.09 for mass-specific SMR. SMR for summer-acclimatized juncos was within 3% of predicted values (Aschoff and Pohl 1970) for passerines of equal mass, whereas SMR for winter-acclimatized juncos exceeded predicted values by 14.6%.

Below thermoneutrality, the relationship between mass-specific $\dot{V}o_2$ (ml $O_2 \cdot g^{-1} \cdot hr^{-1}$) and ambient temperature (Fig. 2) was best described by:

$$\text{Summer: } \dot{V}o_2 = 7.32 - 0.19T_a$$

$$(n = 23, R^2 = 0.93, P < 0.001) \quad (1)$$

$$\text{Winter: } \dot{V}o_2 = 6.80 - 0.13T_a$$

$$(n = 21, R^2 = 0.80, P < 0.001) \quad (2)$$

The intercepts of the two regression lines were not significantly different. However, the slope of the data for the summer-acclimatized juncos was significantly steeper than the slope for winter-acclimatized juncos ($P < 0.001$). Lower critical temperature (LCT) was determined as the intersection of the regression line below thermoneutrality with a horizontal line through the mean $\dot{V}o_2$ at 30°C. LCT was 21.8°C in the summer and 25.8°C in the winter.

Thermal conductance [ml $O_2 \cdot g^{-1} \cdot hr^{-1} \cdot {}^{\circ}C^{-1}$] is equivalent to the slope of the line relating $\dot{V}o_2$ to ambient temperature only if the curve extrapolates to body temperature at zero metabolism. Only the equation for summer-acclimatized juncos conformed closely to the Newton-Scholander cooling model (Scholander et al. 1950). The regression line for summer-acclimatized birds extrapolated to 38.5°C at zero metabolism. The mean nocturnal T_b below thermoneutrality was 39.6°C. Consequently, conductance for summer juncos was relatively constant at 0.19 ml $O_2 \cdot g^{-1} \cdot hr^{-1} \cdot {}^{\circ}C^{-1}$ below thermoneutrality. This value exceeds that allometrically predicted for passerines (Aschoff 1981) by 20.2%. The equation for the data from winter-acclimatized juncos extrapolated to 52.3°C at zero metabolism, which is more than 10°C higher than the nocturnal T_b and implies declining thermal conductance below thermoneutrality. If conductance is calculated as ml $O_2 \cdot g^{-1} \cdot hr^{-1} \cdot {}^{\circ}C^{-1}$ for winter birds, it decreases from 0.194 ml $O_2 \cdot g^{-1} \cdot hr^{-1} \cdot {}^{\circ}C^{-1}$ at 15°C to 0.162 ml $O_2 \cdot g^{-1} \cdot hr^{-1} \cdot {}^{\circ}C^{-1}$ at −10°C.

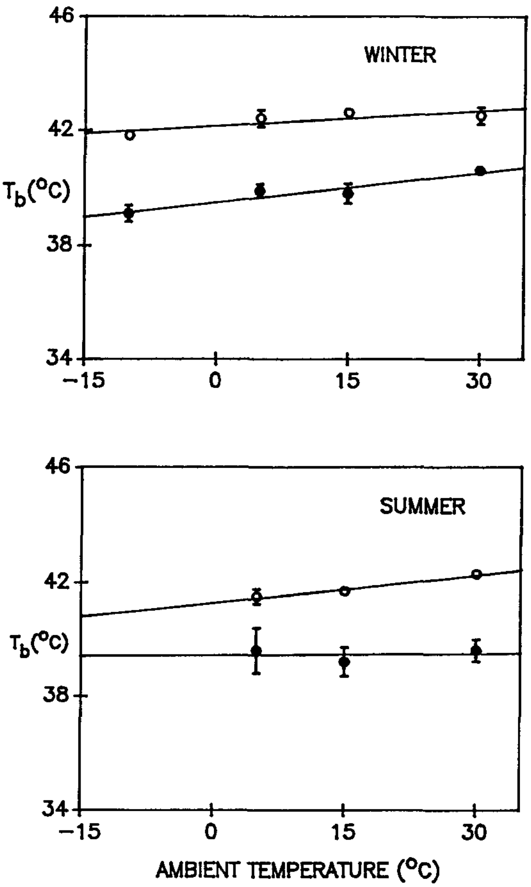

FIGURE 1: The relationship between T_b and T_a for winter- and summer-acclimatized juncos during day (○) and night (●). Error bars represent standard error. All regressions except that for summer nights were significantly different from zero slope. Equations were, Winter day: $T_b = 42.1 + 0.18\ (T_a)$ [$R^2 = 0.09$, $P = 0.04$], Winter night: $T_b = 39.5 + 0.04\ (T_a)$ [$R^2 = 0.23$, $P = 0.001$], and Summer day: $41.3 + 0.03\ (T_a)$ [$R^2 = 0.19$, $P = 0.002$].

DISCUSSION

For winter-acclimatized Dark-eyed Juncos, the significantly greater body mass compared to summer-acclimatized juncos was primarily due to increased stored fat rather than lean dry mass. This pattern of seasonal fat storage is similar to that for most other temperate-wintering passer-

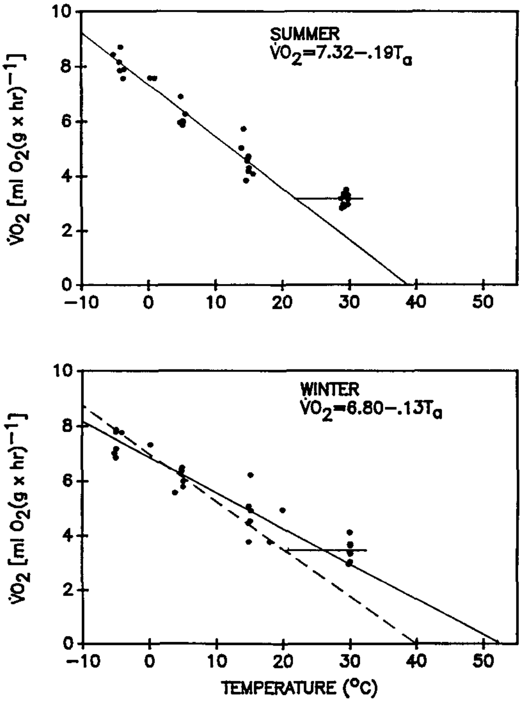

FIGURE 2: Relationship of mass-specific metabolism to ambient temperature in seasonally acclimatized Dark-eyed Juncos. Equations given describe the regression line below thermoneutrality. The horizontal lines represent SMR. The dashed line in winter was obtained by a forced fit of the mass-specific regression line below thermoneutrality through T_b at zero metabolism, which yields $\dot{V}o_2 = 6.95 - 0.17\ (T_a)$. On a total metabolism basis (ml O_2/min), equations below thermoneutrality were, Summer: $\dot{V}o_2 = 1.99 - 0.054\ (T_a)$ [$R^2 = 0.84$, $n = 23$, $P < 0.001$] and Winter: $\dot{V}o_2 = 1.95 - 0.036\ (T_a)$ [$R^2 = 0.73$, $n = 21$, $P < 0.001$]. These equations differed significantly in slope ($P < 0.001$), but not in intercept.

ines (see King 1972, Dawson et al. 1983b), although winter increments in non-fat body components usually accompany increased fat stores (Helms et al. 1967, Barnett 1970, Carey et al. 1978, Dawson et al. 1983a). The seasonal stability of lean dry mass in this study may be an artifact of small sample size. Wet masses of pectoralis muscle and liver are greater in winter than in summer for these juncos (Swanson, unpublished data).

The mean neutral lipid content for winter-acclimatized juncos that were captured in the morning soon after leaving their nightly roost was 1.16 g. If this were completely available for oxidation, at 39.3 kJ/g (Schmidt-Nielsen 1983), it would yield 45.6 kJ. This would support resting metabolism at 4°C (the mean daily temperature in January for Corvallis; Oregon State University Climatic Research Institute) for 19.1 hr. However, not all neutral lipid is available for oxidation. It appears that minimal fat content in birds amounts to 2–4% of body mass (Barnett 1970, Griminger 1986). Given 2% initial body mass as non-metabolizable fat, this decreases fat-supported metabolism to 12.7 hr. These calculations suggest that juncos could endure fasting through the winter night and the following day, but not through a second night. This implies that winter survival is dependent on daily food procurement in these birds. Since daily foraging is seldom prevented by inclement weather in the relatively mild winter climate of western Oregon food procurement likely is not a limiting factor.

In contrast, winter-acclimatized Dark-eyed Juncos from Indiana have an estimated fasting capacity of one day and two nights (Stuebe and Ketterson 1982), and winter-acclimatized juncos from Ohio exhibited a fasting endurance of 63.5 hr at 4°C (Ketterson and Nolan 1978). This suggests that fasting endurance in winter-acclimatized juncos may be adjusted to the relative severity of their resident winter climate.

Little seasonal variation in body temperature was apparent, and what variation was present indicated a higher T_b for winter birds. Apparently, winter-acclimatization in juncos does not involve either a reduced set point for thermoregulation or an increased circadian variation in T_b. No evidence of torpor and only a very mild regulated hypothermia were noted under the conditions of this study. However, these results do not rule out a more pronounced hypothermia as a result of food deprivation coupled with cold, as demonstrated for some passerines (Reinertsen 1986, Reinertsen and Haftorn 1986, Clemens 1989). Significantly, only winter-acclimatized juncos showed a decline in nocturnal T_b at colder temperatures (−0.8°C between 20°C and 0°C). This enhanced hypothermia at colder temperatures may contribute to the decreasing thermal conductance with decreasing T_a demonstrated by winter-acclimatized birds. At both seasons, cloacal temperature, T_b variation with T_a, and circadian variation in T_b were similar to those reported for other passerines (Dawson and Hudson 1970, Dawson and Carey 1976, Dawson et al. 1985).

The observation that SMR was elevated in winter-acclimatized juncos is contrary to the generalization that SMR is seasonally invariant in passerines (Dawson et al. 1985), but similar to results reported for some other small passerines (Pohl and West 1973, Kendeigh et al. 1977, Weathers and Caccamise 1978) and for some nonpasserines (Bech 1980, Rintimaki et al. 1983). The adaptive significance of seasonal variation in SMR in juncos is unclear. Increased SMR may be indicative of metabolic alterations providing augmented thermogenic capacity, although other passerines exhibiting seasonal variation in thermogenic capacity maintain seasonally static SMR (Dawson et al. 1985, Dawson and Smith 1986). The factorial increment in SMR found in this study (1.17) corresponds relatively closely to the factorial increment in maximal metabolic rate of 1.28 (Swanson 1990).

Lower critical temperature (LCT) in juncos varied little with acclimatization state and was similar to that recorded for other small passerines (Hart 1962, King 1964, Dawson and Carey 1976, Weathers et al. 1980, Dawson et al. 1985). LCT at both seasons was within 3°C of predicted values based on body mass (Weathers and van Riper 1982). However, lower critical temperature in winter may be artificially high due to nonconformity with Newtonian cooling. A forced fit of the data for winter-acclimatized juncos below thermoneutrality, so that the regression line passes through a point at zero metabolism corresponding to T_b, decreases lower critical temperature from 25.8°C to 20.1°C (Fig. 2). This is essentially the same as the summer value of 21.8°C. The slope of the line relating metabolic rate to ambient temperature below thermoneutrality was significantly steeper in summer. These slopes suggest slightly better insulation in winter, probably as a result of increased plumage mass, although changes in coat properties may also be involved (Walsberg et al. 1978, Walsberg and Schmidt 1989, Walsberg 1990).

The slope for the data from winter-acclimatized juncos does not conform to Newtonian cooling, indicating modulation of thermal conductance at temperatures below thermoneutrality. This pattern of nonconformity to Newtonian cooling has been noted in other passerines (West 1972, Dawson and Carey 1976). The slope for the data below thermoneutrality for summer-acclimatized juncos does conform to Newtonian predictions, suggesting an inability to modify conductance below thermoneutrality in summer birds. This implies that the ability to modify conductance below thermoneutrality, presumably through vasomotor changes and/or changes in T_b, although plumage or postural adjustments might also be involved, is a component of winter-acclimatization in juncos. This response provides additional energy conservation in winter birds at environmentally relevant temperatures.

Seasonal variation in insulation in passerines is not necessarily coincident with seasonal changes in cold tolerance (Hart 1962, Dawson and Carey 1976). Furthermore, increased insulation in winter juncos studied here did not obviate the requirement for elevation of metabolic rate to offset heat loss at lower winter temperatures. For example, the mean daily temperature for Corvallis is 4°C in January and 19°C in July/August (Oregon State University Climatic Research Institute). Rough estimates of thermoregulatory costs (disregarding convective and radiative effects and the substitution of heat produced as a by-product of physical activity for thermostatic costs) were derived by incorporation of these ambient temperatures into equations for $\dot{V}O_2$ below thermoneutrality, assuming a caloric equivalent of 20.1 kJ/l O_2 (Lasiewski and Dawson 1967). Estimated thermoregulatory costs above basal levels were 29.3 kJ/day in January and 6.7 kJ/day in July/August. Thus, estimated thermoregulatory costs are 4.4 times greater in winter than in summer. This demonstrates the primary importance of metabolic adjustments to seasonal acclimatization in the Dark-eyed Junco.

Overall, acclimatization in juncos from western Oregon appears primarily physiological, consisting of a capacity for maintenance of elevated metabolic rates in response to prolonged ambient cold. Insulation is increased in winter and heat conservation is further enhanced in winter-acclimatized juncos by an ability to decrease thermal conductance with decreasing T_a. However, improved capacity for heat conservation does not obviate the requirement for increased metabolic rates, even at moderate temperatures. This condition is similar to winter-acclimatization in passerines from more severe winter environments (Pohl and West 1973, Dawson and Carey 1976, Schwan and Williams 1978, Dawson et al. 1983a).

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