SEASONAL VARIATION IN COLD HARDINESS AND PEAK RATES OF COLD-INDUCED THERMOGENESIS IN THE DARK-EYED JUNCO (*JUNCO HYEMALIS*)

DAVID L. SWANSON

Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA

ABSTRACT.—I used helium-oxygen (heliox) gas mixtures (approximately 79.5% He : 20.5% O_2) to study seasonal variation in cold resistance and peak rates of thermogenesis ($\dot{V}O_{2\,max}$ = maximum oxygen consumption maintained over a 10-min period) in Dark-eyed Juncos (*Junco hyemalis*). Cold tolerance increased markedly in winter-acclimatized juncos. Heliox temperatures required to induce hypothermia within 90 min in more than 50% of the birds tested were 4°C in summer and −9°C in winter. In winter, $\dot{V}O_{2\,max}$ increased significantly on both a per-bird and mass-specific basis. In summer, $\dot{V}O_{2\,max}$ was 5.78 ml O_2/min (20.75 ml $O_2 \cdot g^{-1} \cdot h^{-1}$), and 7.39 ml O_2/min (23.42 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) in winter. $\dot{V}O_{2\,max}$ exceeded standard metabolic rate by 6.6 times, and by 6.7–7.2 times in winter. Maximal instantaneous oxygen consumption ($\dot{V}O_{2\,i}$ = maximal 1-min $\dot{V}O_2$) under cold stress did not vary seasonally on either a per-bird or mass-specific basis. Mass loss rates during cold stress did not vary seasonally. Winter increases in $\dot{V}O_{2\,max}$ and cold tolerance characterize metabolic acclimatization in Dark-eyed Juncos. *Received 2 May 1989, accepted 29 January 1990.*

SMALL birds that overwinter in temperate climates show marked seasonal changes in cold tolerance (Hart 1962, Barnett 1970, Pohl and West 1973, Dawson and Carey 1976, Dawson et al. 1983). Seasonal variation in peak rates of cold-induced thermogenesis ($\dot{V}O_{2\,max}$, defined here as maximal $\dot{V}O_2$ maintained over 10 min) in these birds has received little attention, mostly because of problems associated with generating experimental temperatures low enough to elicit maximum metabolism. High specific heat helium-oxygen gas mixtures (*heliox*) facilitate heat loss, and induce $\dot{V}O_{2\,max}$ at less extreme temperatures (Rosenmann and Morrison 1974).

Consequently, heliox gas mixtures have been used to document winter increases in maximal thermogenic capacity in several mammals, including snowshoe hares (*Lepus americanus*; Feist and Rosenmann 1975), red-backed voles (*Clethrionomys rutilus*; Rosenmann et al. 1975), and white-footed mice (*Peromyscus leucopus*; Wickler 1980). In birds, Dawson and Smith (1986) documented an increased $\dot{V}O_{2\,max}$ in winter-acclimatized American Goldfinches (*Carduelis tristis*) from Michigan compared with those acclimatized to spring conditions. Higher $\dot{V}O_{2\,max}$ in winter may indicate changes in the metabolic machinery involved in thermogenesis that increase thermogenic capacity and enable small birds to prolong cold resistance. However, it remains unclear whether seasonal variation in maximal thermogenic capacity is widespread among small birds wintering in temperate climates.

I examined seasonal variation in cold resistance and $\dot{V}O_{2\,max}$ in Dark-eyed Juncos (*Junco hyemalis*) from western Oregon. These juncos appear to be local migrants wintering at low elevations throughout the breeding range (AOU Check-list 1957, Bent 1968). I measured $\dot{V}O_{2\,max}$ and cold resistance under heliox cold stress to determine if thermogenic capacity varies seasonally in this species.

METHODS

Dark-eyed Juncos were captured by mist net near Corvallis, Benton County, Oregon, during June to August 1987 and December 1987 to February 1988. Birds were trapped in the morning, transported to the laboratory, and caged at room temperature (20–25°C). Food and water were provided *ad libitum*. Birds were allowed to feed for at least 2 h before testing on the day of capture. Cold stress tests were conducted between 1100 and 1930. Juncos tested from June through August were designated *summer birds*. Those tested from December through February were designated *winter birds*. Both males and females were used and male to female (sexed by plumage) ratios were 20:15 in winter and 15:13 in summer. All birds tested were adults.

I measured the rate of oxygen consumption ($\dot{V}O_2$) during heliox cold stress in an open-circuit metabolism system. Metabolic chambers were fabricated from 1-gal (3.8 l) paint cans with a black inner surface. Birds were weighed to the nearest 0.1 g with a Pesola spring

balance (50 g) and placed in the metabolism chamber which was then lowered into a water/ethylene glycol bath capable of regulating chamber temperature to ±0.5°C. Chamber temperature was monitored by a Cole-Parmer thermocouple thermometer, previously calibrated to ±0.1°C with a thermometer traceable to the U.S. Bureau of Standards. Gas flow (premixed gas mixtures ca. 20.5% He : 79.5% O_2) into the chamber was initiated upon submersion into the water/ethylene glycol bath. Flow rates through the chamber were controlled by Cole-Parmer Precision rotameters (Model FM082-03ST), which were calibrated by timing water displacement by air and heliox from a 6-l spirometer. Flow rates were corrected for water vapor pressure within the spirometer, which was measured with an Extech (Model 5070) humidity meter. This procedure allowed calibration of flow rates to ±1% accuracy. Flow rates varied from 900–1,025 ml/min, which provided approximately 0.5% difference between influx and efflux oxygen concentrations and kept efflux oxygen concentrations above 19.75%. A Beckman Model E2 paramagnetic oxygen analyzer measured the fractional concentration of oxygen in the respiratory gas. Measurements of dry, CO_2-free efflux gas were recorded every 60 seconds. Oxygen-consumption values were calculated as instantaneous rates (Bartholomew et al. 1981). The initial 10 min of $\dot{V}O_2$ measurements were deleted from calculations.

Procedures utilized to measure standard metabolic rate (SMR) were similar to those for $\dot{V}O_2$ under cold stress. Standard metabolic rate measurements were conducted at night after at least a 5-h fast within the metabolic chamber. Chamber temperature was maintained within the thermal neutral zone for the junco (Swanson unpubl. data). Flow rates of dry, CO_2-free air were maintained at 225–290 ml/min for SMR measurement. Standard metabolic rate was determined as the mean $\dot{V}O_2$ over a 60-min period. Oxygen consumption was calculated both by steady state (Depocas and Hart 1957) and instantaneous (Bartholomew et al. 1981) methods. Mean $\dot{V}O_2$ calculated by the two methods differed by ≤4%, so gas mixing within the chamber was considered satisfactory. I used steady state SMR values for metabolic expansibility determinations.

Juncos were exposed to a series of decreasing temperatures in heliox until $\dot{V}O_{2\,max}$ was attained and hypothermia was induced in a majority of the birds. Exposure temperatures were 8°C, 4°C, 2°C, and 0°C in summer, and 0°C, −3°C, −6°C, and −9°C in winter. Individual birds were exposed to a single temperature within the series for 90 min, or until they experienced *hypothermia* (indicated by a steady decline in $\dot{V}O_2$ over several minutes). At the end of the test, birds were quickly removed from the chamber. Cloacal temperature (±0.1°C) was recorded with a Cole-Parmer thermocouple thermometer and 20-gauge copper-constantan wire thermocouple probe inserted to approximately 1 cm depth. Birds with a cloacal temperature >36°C were considered *normothermic*. Following cloacal temperature measurement, birds were reweighed.

I analyzed $\dot{V}O_{2\,max}$ data by averaging instantaneous $\dot{V}O_2$ measurements over successive 10-min intervals. The highest average $\dot{V}O_2$ of these intervals was designated as $\dot{V}O_{2\,max}$ *at the test temperature*. The highest 1-min $\dot{V}O_2$ over the test period was considered *maximal instantaneous metabolic rate* ($\dot{V}O_{2\,i}$). All values for $\dot{V}O_2$ were corrected to STP.

All values are presented as $\bar{x} \pm$ SD. Mean $\dot{V}O_2$ at each temperature, body mass, and mass loss were compared by Student's *t*-test, or by Mann-Whitney *U*-test, when variances of mean values were unequal. Birds that became hypothermic in <30 min in summer or <60 min in winter had substantially lower $\dot{V}O_{2\,max}$ than birds that remained normothermic for longer periods and were omitted from calculation of mean $\dot{V}O_{2\,max}$. The effect of heliox ambient temperature (T_a) on body temperature (T_b) was analyzed by one-way ANOVA. Statistical significance was accepted at $P < 0.05$.

RESULTS

Cold tolerance in winter-acclimatized juncos increased markedly compared with summer-acclimatized juncos (Fig. 1). At 0°C in heliox in summer, 11 of 12 juncos tested became hypothermic before 90 minutes. In winter, all birds tested at 0°C remained normothermic ($T_b >$ 36°C). A temperature of −9°C in heliox was required in winter to induce hypothermia in >50% of the birds tested. To elicit hypothermia in >50% of summer birds required only 4°C in heliox. At temperatures below 0°C in summer and −9°C in winter, all birds tested rapidly became hypothermic.

Mean T_b of normothermic birds after cold stress was 39.5 ± 0.9°C in summer and 39.6 ± 0.4°C in winter. For normothermic birds, T_b was not dependent on T_a in heliox in either summer or winter.

Mean mass at the initiation of cold stress tests was significantly greater ($P < 0.01$) in winter (18.2 ± 1.5 g, $n = 35$) than in summer (16.9 ± 1.1 g, $n = 28$). Mass-specific $\dot{V}O_2$ is commonly assumed to account for variation in $\dot{V}O_2$ as a function of body mass. Hence, I report all $\dot{V}O_2$ on both a per-bird and a mass-specific basis.

Standard metabolic rate was 0.87 ± 0.09 ml O_2/min (3.16 ± 0.30 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) in summer and 1.03 ± 0.14 ml O_2/min (3.49 ± 0.48 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) in winter. Standard metabolic rate in winter was significantly greater than in summer on a per-bird basis ($P < 0.01$), but not on a mass-specific basis.
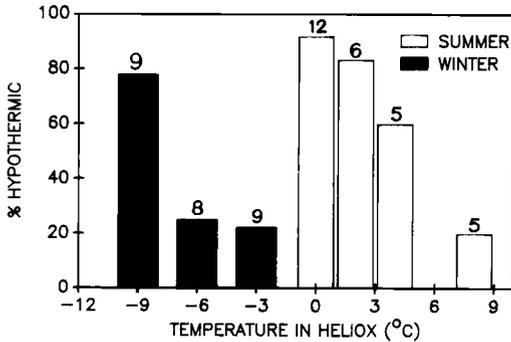
Fig. 1. Cold tolerance in seasonally acclimatized juncos over the 90-min test period. The numbers over the bars indicate sample size. In winter at 0°C all birds tested ($n = 9$) remained normothermic.

TABLE 1. Maximal $\dot{V}O_2$ sustained over a 10-min period ($\bar{x} \pm$ SD) at heliox test temperatures in summer and winter juncos. Body masses are means for the treatment group. Birds that became hypothermic in <60 min in winter and <30 min in summer had substantially lower $\dot{V}O_2$ and were excluded from calculations.

Season/ Temp.	n	Mass (g)	$\dot{V}O_2$ (ml/min)	×SMR
Summer				
8°C	5	17.8	5.28 ± 0.23	6.1
4°C	5	17.3	5.67 ± 0.42	6.5
2°C	6	17.0	5.93 ± 0.22	6.8
0°C	9	17.1	5.75 ± 0.46	6.6
Winter				
0°C	9	18.7	6.21 ± 0.68	6.0
−3°C	7	18.7	6.51 ± 0.46	6.3
−6°C	8	18.2	6.95 ± 0.25	6.7
−9°C	6	18.6	7.39 ± 0.35	7.2

In winter, $\dot{V}O_{2\,max}$ was significantly greater than it was in summer on both a per-bird and a mass-specific basis (Table 1). In summer, $\dot{V}O_{2\,max}$ occurred at 2°C, but mean $\dot{V}O_2$ at 2°C was not significantly different from 0°C or 4°C on a per-bird basis (combined $\dot{V}O_2 = 5.78 \pm 0.39$ ml O_2/min, $n = 20$), or from 4°C on a mass-specific basis (combined $\dot{V}O_2 = 20.75 \pm 1.64$ ml $O_2 \cdot g^{-1} \cdot h^{-1}$, $n = 11$). In winter, $\dot{V}O_{2\,max}$ occurred at −9°C. On a per-bird basis, $\dot{V}O_2$ at −9°C was significantly greater than at other temperatures. However, on a mass-specific basis, $\dot{V}O_2$ at −9°C was not significantly different from −6°C (combined $\dot{V}O_2 = 23.42 \pm 1.25$ ml $O_2 \cdot g^{-1} \cdot h^{-1}$, $n = 14$). In summer, $\dot{V}O_{2\,max}$ represents an increment of 6.6 times SMR in both total and mass-specific $\dot{V}O_2$. In winter, $\dot{V}O_{2\,max}$ increased to 7.2 times SMR on a per-bird basis and to 6.7 times on a mass-specific basis.

Maximal instantaneous oxygen consumption ($\dot{V}O_{2\,i}$) did not vary seasonally on either a per-bird or mass-specific basis (Table 2). In summer, $\dot{V}O_{2\,i}$ at 2°C and at 4°C were not significantly different (combined $\dot{V}O_2 = 9.30 \pm 2.01$ ml O_2/min, 33.40 ± 6.69 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, $n = 11$). Winter $\dot{V}O_{2\,i}$ at −9°C, −6°C, and −3°C were not significantly different (combined $\dot{V}O_2 = 9.73 \pm 1.42$ ml O_2/min, 32.35 ± 4.97 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, $n = 26$). Summer $\dot{V}O_{2\,i}$ exceeded SMR by 10.9 times and 10.8 times on a per-bird and mass-specific basis, respectively. In winter, $\dot{V}O_{2\,i}$ was 9.8 times SMR on a per-bird basis, and 9.6 times SMR on a mass-specific basis.

Cold exposure-induced maximal rates of mass loss did not vary seasonally at any temperatures (Fig. 2). Mean mass loss values were -0.6 ± 0.3

g per hour in summer ($n = 28$) and -0.6 ± 0.4 g per hour in winter ($n = 35$). Absolute values for mass loss in terms of percent wet mass were −3.6% per hour in summer, and −3.3% per hour in winter. Smaller individuals exhibited slightly decreased capacities for cold tolerance at both seasons (Table 3).

DISCUSSION

Increased thermogenic capacity in winter, indicated by augmented $\dot{V}O_{2\,max}$, appears to be a feature of metabolic acclimatization in the Dark-eyed Junco. In addition, winter-acclimatized juncos exhibited a marked increase in cold tolerance over summer-acclimatized juncos. Other small passerines exposed to severe cold also showed increased metabolic rates and improved cold tolerance at colder times of the year (Hart 1962, Pohl and West 1973, Southwick 1980, Dawson and Smith 1986). However, House Finches (*Carpodacus mexicanus*) in Colorado showed no seasonal differences in $\dot{V}O_{2max}$ (Dawson et al. 1983), and Gray Jays (*Perisoreus canadensis*) from Alaska had higher metabolic rates at −50°C in spring than in winter, although summer rates were lower (Veghte 1964). A winter increment of $\dot{V}O_{2\,max}$ elicited by cold stress implies augmented thermogenic capacity and seems to be associated with increased shivering endurance. Enhanced shivering endurance is primarily responsible for increased cold tolerance in other passerines (Dawson and Carey 1976, Dawson et al. 1983).

TABLE 2. Maximal instantaneous oxygen consumption ($\dot{V}O_{2_i}$) at heliox test temperatures in summer and winter juncos.

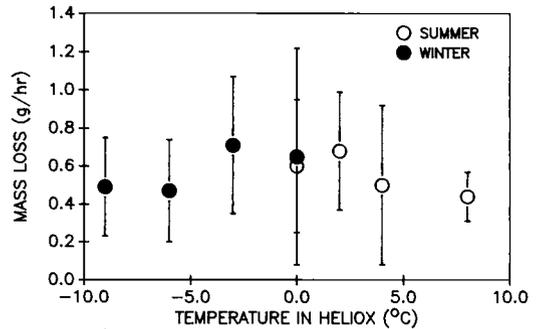| Season/ Temp.	n	$\dot{V}O_2$ (ml/min)	×SMR
Summer			
8°C	5	6.81 ± 0.63	7.8
4°C	5	8.41 ± 1.83	9.7
2°C	6	10.05 ± 1.98	11.6
0°C	12	8.13 ± 1.09	9.3
Winter			
0°C	9	8.26 ± 1.48	8.0
−3°C	9	9.03 ± 1.50	8.8
−6°C	8	9.72 ± 0.79	9.4
−9°C	9	10.44 ± 1.53	10.1

Fig. 2. Mass loss rates as a function of heliox test temperature in seasonally acclimatized juncos. All values were statistically indistinguishable.

Birds I studied exhibited a relatively wide seasonal fluctuation in heliox temperatures that elicited $\dot{V}O_{2\,max}$. In summer, $\dot{V}O_{2\,max}$ occurred at 0–4°C, and at −6°C to −9°C in winter. Heliox cold stress in seasonally acclimatized American Goldfinches from Michigan produced $\dot{V}O_{2\,max}$ from 0°C to 6°C in spring and 0°C to −6°C in winter (Dawson and Smith 1986).

Elevated winter $\dot{V}O_{2\,max}$ might be attributed to differential feeding before cold stress in winter-acclimatized and summer-acclimatized birds. Winter juncos might have eaten more before tests, which allowed them to maintain elevated $\dot{V}O_2$ longer. However, fasted winter juncos also had increased cold tolerance (Swanson unpubl. obs.). I suggest that the seasonal variation in $\dot{V}O_{2\,max}$ and cold tolerance can be attributed to metabolic changes.

Heavier Dark-eyed Juncos tolerated cold more effectively than small birds. For both seasons, only the smaller birds became hypothermic at higher test temperatures in heliox, while only the larger birds remained normothermic at lower test temperatures (Table 3). Increased cold tolerance could be due to increased substrate (fat or glycogen) reserves, enhanced mobilization of these reserves, or both, or to some size-dependent effect on thermogenic abilities.

I estimated air temperature equivalents to heliox test temperatures by extrapolation. Heliox $\dot{V}O_2$ values were inserted into equations that relate $\dot{V}O_2$ to T_a (Swanson unpubl. data) and solved for T_a. Estimated ambient temperatures at $\dot{V}O_{2\,max}$ were −69°C in summer and −125°C in winter. Actual air temperatures were probably not this low as thermal conductance often changes with T_a. Nevertheless, juncos tolerated

extreme cold stress (90 min maximum) far in excess of any temperatures experienced under natural climatic conditions. Extreme minimum temperatures are 0°C in June–August and −26°C in December–February in Corvallis, Oregon (Oregon State University Climatic Research Institute). Effective extreme minimum ambient temperatures are probably below these values because of environmental factors such as wind, humidity, or radiation. Cold tolerance data suggest that as long as food supplies are readily available, juncos probably face little danger from environmental cold stress.

However, these data may inaccurately predict environmental cold tolerance because experimental cold exposure was acute and severe. Chronic exposure to more moderate environmental cold stress (i.e. "normal" winter conditions) probably necessitates prolonged elevation of metabolic rates (although not to maximal levels). Wind, humidity, and radiation might further reduce effective ambient temperatures below actual values, and necessitate further metabolic enhancement. Environmental conditions most challenging to cold tolerance capabilities are overnight fasting and fasting induced by severe weather that limits foraging. Stuebe and Ketterson (1982) predicted survival of fasting winter-acclimatized juncos at 4°C through the night, and the following day and night, if the birds were near the peak of the daily fat cycle at the onset of fasting. Colder temperatures would probably decrease survival time. Fasting capacities of summer-acclimatized juncos are unknown. Nevertheless, it seems juncos have a considerable margin of safety when confronted with natural cold stress.

I calculated minimal thermal conductance

TABLE 3.   Cold tolerance of juncos according to body mass at the initiation of cold stress. Unequal numbers of birds in each mass class were exposed to each heliox test temperature. Data for 0°C in winter are excluded because birds remained normothermic. Hypothermic and normothermic temperatures are heliox temperatures that resulted in hypothermia or normothermia for birds in the specified mass class. Numbers in parentheses are the number of birds that remained normothermic or became hypothermic at the given temperature in heliox; $\bar{t}_H$ is the mean time to hypothermia for birds that became hypothermic.

Mass (g)	Normothermic/ Total	Hypothermic temps. (°C)	Normthermic temps. (°C)	$\bar{t}_H$ (min)
Summer				
<16	0/4	8, 2, 0 (2)	—	54.3
16–17	2/6	2 (2), 0 (2)	4, 8	52.3
17–18	1/7	4, 2, 0 (4)	4	52.3
>18	4/7	2, 0 (2)	8 (3), 0	62.0
Winter				
<17	0/1	−3	—	36.0
17–18	2/7	−3, −6, −9 (3)	−6 (2)	58.0
18–19	5/7	−6, −9	−3 (2), −6 (3)	61.5
>19	8/11	−9 (3)	−3 (5), −6, −9 (2)	72.7

from $\dot{V}O_2$ at heliox temperatures that elicited $\dot{V}O_{2\ max}$ (assuming $T_b = 39.5°C$ and 4.85 cal/ml O_2). For winter-acclimatized juncos minimal thermal conductance was 2.81 mW·g^{-1}·°C^{-1} and for summer-acclimatized juncos it was 3.21 mW·g^{-1}·°C^{-1}. This represents a 14.2% increase in conductance for summer birds and indicates that winter birds are somewhat better insulated. Values for minimal thermal conductance at equivalent air temperatures are 0.94 mW·g^{-1}·°C^{-1} in winter and 1.05 mW·g^{-1}·°C^{-1} in summer. Conductance in heliox exceeded that in air by 3.0 times in winter and by 3.1 times in summer. These values slightly exceed increments in heliox reported in Common Redpolls (*Carduelis flammea*; 2.6×, Rosenmann and Morrison 1974) and American Goldfinches (2.7×, Dawson and Smith 1986).

There was no seasonal variation in $\dot{V}O_{2\ i}$. Although $\dot{V}O_{2\ i}$ probably reflects activity, it may represent intense short-term shivering bouts. Either would increase heat production over the short term. Apparently, changes in the metabolic machinery that produce increased $\dot{V}O_{2\ i}$ are not important to cold tolerance in the junco, whereas those that elevate $\dot{V}O_{2\ max}$ are.

Metabolic expansibility ($\dot{V}O_{2\ max}$/SMR; Dawson and Carey 1976) for Dark-eyed Juncos—6.6× in summer and 7.2× in winter on a per-bird basis—is the highest yet reported for passerine birds (Rosenmann and Morrison 1974, Dawson and Carey 1976, Dawson and Smith 1986, Koteja 1986). Dawson (pers. comm.) found winter Dark-eyed Juncos from Michigan capable of $\dot{V}O_{2\ max}$ equal to 6.3 × SMR. The values for cold-induced metabolic expansibility in the juncos are surpassed by those from several winter-acclimatized small mammals, which equal or exceed 8 × BMR (Feist and Rosenmann 1975, Rosenmann et al. 1975, Wickler 1980).

Consideration of $\dot{V}O_2$ on a per-bird or mass-specific basis had some effect on metabolic expansibility determinations. In winter, $\dot{V}O_{2\ max}$ per bird was 7.2 × SMR, while mass-specific $\dot{V}O_{2\ max}$ was only 6.7 × SMR. In summer, this effect disappeared, as metabolic expansibility on both a per-bird and mass-specific basis was 6.6 × SMR. The increase in body mass in passerines in winter is due largely to an increase in fat which is relatively inert metabolically (Dawson and Smith 1986). This accounts for the difference in metabolic expansibility between per-bird and mass-specific $\dot{V}O_2$ in winter. Thus, per-bird $\dot{V}O_2$ may be more appropriate than mass-specific $\dot{V}O_2$ for seasonal comparisons (Dawson and Smith 1986).

Mass loss over the period of cold stress tests was consistent and independent of test temperature at both seasons. Seasonal stability of mass-loss rates in juncos during cold stress suggests that substrate mobilization is not a factor that limits $\dot{V}O_{2\ max}$ and cold tolerance. Decreased cold tolerance in smaller juncos in both seasons (assuming that low body mass indicates low fuel reserves) may suggest that depletion of fuel reserves beyond a certain critical level diminishes capacity to further mobilize metabolic substrates. However, the assumption that low body

mass indicates low fuel reserves is tenuous as birds were allowed to feed before cold stress. Mass-loss trends might also be explained by differences in feeding intensity before cold stress, differences in assimilation of digestive tract contents, or differences in respiratory water loss. In addition, hypothermia occurs in some passerines with substantial remaining fat stores (Carey et al. 1978), presumably above the putative critical level.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, fifth ed. Baltimore, Am. Ornithol. Union.

BARNETT, L. B. 1970. Seasonal changes in temperature acclimatization of the House Sparrow. Comp. Biochem. Physiol. 33: 559–578.

BARTHOLOMEW, G. A., D. VLECK, & C. M. VLECK. 1981. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in Sphingid and Saturnid moths. J. Exper. Biol. 90: 17–32.

BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, towhees, finches, sparrows, and allies, part 2. Pp. 1050–1071 in United States National Museum Bulletin 237 (O. L. Austin Jr., Ed.). Washington, D.C., Smithsonian Inst.

CAREY, C., W. R. DAWSON, L. C. MAXWELL, & J. A. FAULKNER. 1978. Seasonal acclimatization to temperature in Cardueline finches: II. Changes in body composition and mass in relation to season and acute cold stress. J. Comp. Physiol. 125: 101–113.

DAWSON, W. R., & C. CAREY. 1976. Seasonal acclimatization to temperature in Cardueline finches: I. Insulative and metabolic adjustments. J. Comp. Physiol. 112: 317–333.

———, & B. K. SMITH. 1986. Metabolic acclimatization in the American Goldfinch (Carduelis tristis). Pp. 427–434 in Living in the cold: physiological and biochemical adaptations (H. C. Heller, X. J. Musacchia, and L. C. H. Wang, Eds.). Elsevier.

———, R. L. MARSH, W. A. BUTTEMER, & C. CAREY. 1983. Seasonal and geographic variation of cold resistance in House Finches Carpodacus mexicanus. Physiol. Zool. 56: 353–369.

DEPOCAS, F. J., & J. S. HART. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption in open circuit systems and in a short-lag, closed circuit apparatus. J. Appl. Physiol. 10: 388–392.

FEIST, D. D., & M. ROSENMANN. 1975. Seasonal sympathoadrenal and metabolic responses to cold in the Alaskan snowshoe hare (Lepus americanus macfarlani). Comp. Biochem. Physiol. 51A: 449–455.

HART, J. S. 1962. Seasonal acclimatization in four species of small wild birds. Physiol. Zool. 35: 224–236.

KOTEJA, P. 1986. Maximum cold-induced oxygen consumption in the House Sparrow Passer domesticus L. Physiol. Zool. 59: 43–48.

POHL, H., & G. C. WEST. 1973. Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the Common Redpoll. Comp. Biochem. Physiol. 45A: 851–867.

ROSENMANN, M., & P. MORRISON. 1974. Maximum oxygen consumption and heat loss facilitation in small homeotherms by He-O_2. Am. J. Physiol. 226: 490–495.

———, ———, & D. FEIST. 1975. Seasonal changes in the metabolic capacity of red-backed voles. Physiol. Zool. 48: 303–310.

SOUTHWICK, E. E. 1980. Seasonal thermoregulatory adjustments in White-crowned Sparrows. Auk 97: 76–85.

STUEBE, M. M., & E. D. KETTERSON. 1982. A study of fasting in Tree Sparrows (Spizella arborea) and Dark-eyed Juncos (Junco hyemalis): ecological implications. Auk 99: 299–308.

VEGHTE, J. H. 1964. Thermal and metabolic responses of the Gray Jay to cold stress. Physiol. Zool. 37: 316–328.

WICKLER, S. J. 1980. Maximal thermogenic capacity and body temperatures of white-footed mice (Peromyscus) in summer and winter. Physiol. Zool. 53: 338–346.