

SEASONAL VARIATION IN THERMOGENIC CAPACITY OF MIGRATORY WARBLING VIREOS

DAVID L. SWANSON

Department of Biology, University of South Dakota, 414 E. Clark St., Vermillion, South Dakota 57069, USA

ABSTRACT.—Seasonal physiological adjustments are similar for migration and winter acclimatization in passerine birds, as both involve endurance muscular activity. Consequently, migratory disposition should elevate maximal thermogenic capacity ($\dot{V}O_{2sum}$) under cold stress, as winter acclimatization does for most temperate-wintering passerines. This hypothesis was tested with a Neotropical migrant, the Warbling Vireo (*Vireo gilvus*), during migration and summer residency in southeastern South Dakota. Vireos were subjected to cold stress in an atmosphere of 79% He/21% O₂ (helox), with concurrent measurement of oxygen consumption during spring, summer and fall. In the spring, vireos had a significantly higher $\dot{V}O_{2sum}$ (17.7%) and tolerated colder temperatures in helox than either summer or fall birds. Standard metabolic rate was $0.643 \pm$ SD of 0.133 ml O₂ min⁻¹ ($n = 6$) in summer, but could not be measured in spring and fall as vireos were nocturnally active and failed to attain steady-state conditions, presumably as a result of Zugunruhe. The increment of $\dot{V}O_{2sum}$ in spring, apparently, was not a function of higher body mass in spring, given that mass did not vary significantly between seasons. Elevated thermogenic capacity in spring may be adaptive as chances of encountering cold weather during spring migration in the north-central United States are greater than at other seasons. Alternatively, enhanced thermogenic capacity in spring may be related to differential migratory speeds between spring and fall, which might select for increased endurance (with thermogenic capacity increasing as a by-product) in spring birds. The ubiquity of this pattern among migratory passerines is unknown. Received 12 May 1994, accepted 27 January 1995.

SHIVERING THERMOGENESIS in cold temperatures and long-distance migration are energetically expensive endeavors for small birds. Since both sustained shivering and long-distance flight represent forms of endurance muscular activity, adaptation for flight might be expected to influence thermogenic performance, or vice-versa. Indeed, such coupled changes in maximal capacity for thermogenesis and exercise (locomotion) have been detected for some mammals (Hayes and Chappell 1986), although this apparently is not universal (Conley et al. 1985). Similar studies have not been performed on birds, probably because convincing measurements for maximal metabolism during flight are nonexistent (Marsh and Dawson 1989). An indirect test for such coupled changes in maximal metabolism associated with flight and thermogenesis is to measure thermogenic capacity in birds in migratory disposition. These birds are presumably adapted for sustained flight, but are not exposed to the cold-temperature extremes faced by Temperate Zone residents during winter. Nevertheless, a number of physiological and biochemical adjustments associated with improved cold tolerance and migratory disposition are similar.

Fat is the major fuel for shivering (Marsh and Dawson 1989) and winter-acclimatized passerines often show increased levels of stored fat relative to summer-acclimatized birds (Blem 1990), especially in species exploiting unpredictable winter food resources (Rogers and Smith 1993). Stored fat also increases markedly before migration in most small migrants, especially in those migrating long distances (Blem 1990), and fat serves as the major fuel for migration (Dawson et al. 1983).

Winter-acclimatized passerines exhibit elevated pectoralis-muscle activities of enzymes involved in lipid and carbohydrate catabolism, particularly the former (Marsh and Dawson 1982, Yacoe and Dawson 1983), suggesting an increased reliance on fat during shivering thermogenesis relative to summer birds. An increase in activities of enzymes involved in fatty acid oxidation is also a component of migratory disposition in several migrants (Marsh 1981, Lundgren and Kiessling 1985, 1986, Driedzic et al. 1993). In addition, plasma-free fatty acids and triglycerides, as well as pectoralis lipids, increase during premigratory fattening in some migrants (Driedzic et al. 1993); plasma-free fatty acids, glycerol and triglycerides, in addition to

pectoralis muscle β -hydroxyacyl Co-A dehydrogenase activity, increase during periods of migratory flight in several migratory passerines, relative to resting periods between flights (Jenni-Eiermann and Jenni 1991, 1992, Jenni and Jenni-Eiermann 1992). These adjustments suggest an increased reliance on fat relative to substrate use during activity in nonmigratory periods.

Passerines demonstrating marked winter improvement of cold tolerance exhibit muscle-glycogen sparing coupled with increased utilization of fat to support shivering thermogenesis (Marsh and Dawson 1982, Swanson 1991). However, increased enzyme activities for both lipid and carbohydrate catabolism were not correlated with an increase in the ability of isolated mitochondria or crude pectoralis-muscle homogenates to oxidize these substrates (Yacoe and Dawson 1983). This suggests a lack of seasonal variability in the mass-specific aerobic capacity of flight muscles as a result of winter acclimatization, even though the pectoralis is prominently involved in shivering thermogenesis (Marsh and Dawson 1989). Glycolytic enzymes do not exhibit a common directional change associated with migration in small birds (Marsh 1981, Lundgren and Kiessling 1985, 1986, Driedzic et al. 1993), which suggests a relatively minor role for carbohydrates as a migratory fuel. Key aerobic enzymes (citrate synthase and/or cytochrome c oxidase) exhibit an increment in activity during migration in some migrants (Lundgren and Kiessling 1985, 1986), but not in others (Marsh 1981, Driedzic et al. 1993). This indicates that an increase in mass-specific aerobic capacity of flight muscles with migratory disposition may not be a feature common among migrants, which is similar to the absence of seasonal changes in mass-specific aerobic capacity reported for seasonal acclimatization.

Hypertrophy of pectoralis muscle is associated with winter acclimatization in at least some passerines (Swanson 1991), and this hypertrophy is correlated with winter increases in maximal capacity for thermogenesis. Premigratory and migratory hypertrophy of the pectoralis muscle, presumably leading to increased total aerobic capacity and power output, is also a general feature among small, long-distance migrants (Dawson et al. 1983).

Since both migration and winter acclimatization exhibit similar physiological and biochemical adjustments, and these adjustments are

associated with increases in cold tolerance and maximal thermogenic capacity in winter-acclimatized passerines (Dawson and Smith 1986, Swanson 1990, O'Connor 1993, Cooper and Swanson 1994), it might be expected that long-distance migrant passerines in a migratory disposition also would exhibit elevated maximal thermogenic capacity and cold tolerance relative to nonmigratory individuals. In this study, I test this hypothesis by measuring thermogenic capacity and cold tolerance in migratory and summer-resident Warbling Vireos (*Vireo gilvus*), a long-distance Neotropical migrant, in southeastern South Dakota.

METHODS AND MATERIALS

Vireos were captured with mist nets near Vermillion, Clay County, South Dakota in 1992 and 1993. Mass, unflattened wing chord and visible fat scores (Helms and Drury 1960) were determined at capture. Birds tested between 5 and 13 May were designated "spring migrants," those from 29 May through 1 August were considered "summer residents," and those from 24 August through 21 September were designated "fall migrants." The bulk of the migratory passage of Warbling Vireos through South Dakota occurs during the second half of May in the spring and throughout August in the fall (South Dakota Ornithologists' Union 1991), although banding returns indicate return breeders on previous breeding territories by 12 May (pers. obs.). The dates for the vireos that I have designated for spring migrants are near or before the early end of the main movement in the spring and those for fall migrants are near or beyond the late end of the major movement in the fall. Birds captured during the designated migratory dates had elevated visible fat scores relative to summer birds (pers. obs.), presumably indicative of migratory disposition. Given the conservative dates of the migratory designations and the elevated fat scores, it is almost certain that the birds tested as "migrants" were indeed in migratory disposition. Vireos were tested without regard to sex because no reliable methods exist for sexing Warbling Vireos by plumage (Pyle et al. 1987). The fall sample included both adult and hatching-year (HY) birds, since HY birds were fully grown by this time and exhibited metabolic rates similar to those of adults. Spring and summer samples consisted solely of adults.

Following capture, birds were transported to the laboratory and given free access to food (*Tenebrio* larvae) and water for at least 2 h prior to metabolic tests. Oxygen consumption ($\dot{V}O_2$) was determined by open-circuit respirometry according to Swanson (1993). Metabolic chambers for $\dot{V}O_2$ measurement were 3.8-L paint cans filled approximately half-full with solid paraffin. The inside of the chamber was painted flat

black to provide an emissivity near 1.0. The effective volume (calculated according to Bartholomew et al. 1981) of the chamber, when equipped with a perch, was 2,354 ml. Chamber temperature was regulated to $\pm 0.2^\circ\text{C}$ by immersing the chamber into a bath of water/ethylene glycol. Chamber temperature was monitored continuously with a Cole-Parmer (Model 8500-40) thermocouple thermometer and copper-constantan thermocouple previously calibrated to $\pm 0.1^\circ\text{C}$ against a thermometer traceable to the U.S. Bureau of Standards. Cold-stress tests were conducted in an atmosphere of approximately 79% helium/21% oxygen (helox) to elicit peak rates of cold-induced oxygen consumption (i.e. maximal thermogenic capacity, or summit metabolism, $\dot{V}\text{O}_{2\text{sum}}$) at relatively moderate temperatures (Rosenmann and Morrison 1974). Cold-stress temperatures in helox were -1° to 4°C in the spring, 6°C in the summer, and -1° to 9°C in fall. Temperatures at the low end of these ranges produced hypothermia in a majority of the vireos tested.

Individual vireos were exposed to a single temperature in helox for 60 min or until they became hypothermic (indicated by a steady decline in $\dot{V}\text{O}_2$ over several minutes). Cold-stress tests were conducted between 1220 and 1920 CST at all seasons. Flow rates of dry, CO_2 -free helox through the chamber were maintained between 1,000 and 1,020 ml/min by a Cole-Parmer precision rotameter (Model FM082-03ST) calibrated to $\pm 1\%$ accuracy (Swanson 1990). Prior to immersion of the chamber into the water/ethylene glycol bath, the chamber was flushed with helox for 5 to 6 min at these flow rates. Oxygen consumption was measured every 60 s during metabolic tests with an Ametek S-3A oxygen analyzer, and was calculated as instantaneous $\dot{V}\text{O}_2$ according to Bartholomew et al. (1981). The highest 10-min mean $\dot{V}\text{O}_2$ (excluding first 10 min of measurements) over the test period was designated as the $\dot{V}\text{O}_2$ for an individual bird at a particular test temperature for subsequent statistical analyses (Dawson and Smith 1986).

Standard metabolic rate (SMR) also was measured by open-circuit respirometry for summer residents. Measurement of SMR differed from that of $\dot{V}\text{O}_{2\text{sum}}$ because dry, CO_2 -free air was used as the respiratory medium (rather than helox), metabolic tests were conducted at night (from 1945–0130), flow rates of air into the chamber were maintained at 280 to 300 ml/min, and birds were fasted for at least 5 h prior to metabolic tests to ensure postabsorptive conditions. Chamber temperature was maintained at $30.0 \pm 0.3^\circ\text{C}$ during SMR measurement, which is well within the predicted thermoneutral zone for a passerine bird the size of a Warbling Vireo (Weathers and van Riper 1982).

Oxygen consumption during SMR measurement was calculated according to steady-state equations (Hill 1972: eq. 2) from readings taken every 60 s. The lowest 10-min mean $\dot{V}\text{O}_2$ over an 1-h test period following at least an 1-h equilibration within the metabolic

chamber was considered SMR. SMR was not measured during migratory periods as vireos were active during nocturnal metabolic tests, presumably as a result of Zugunruhe, and failed to attain steady-state metabolic rates. All values for $\dot{V}\text{O}_2$ were corrected to STP.

Body mass was measured to the nearest 0.1 g on a Sartorius (Model 3704) top-loading balance before and after $\dot{V}\text{O}_2$ tests, and mass loss over the test period was assumed to be constant. Body temperature (T_b) was measured immediately on removal from the chamber with a thermocouple inserted to a depth (10–12 mm) where further insertion did not alter temperature readings. Birds with a T_b of less than 36.0°C were considered hypothermic.

Data are presented as means \pm SD. Differences between mean $\dot{V}\text{O}_2$ at different test temperatures within a single season were evaluated using an one-way ANOVA, or by a Kruskal-Wallis test if variances among means were unequal (*F*-test). Seasonal comparisons of mass, wing chord, visible fat scores, and $\dot{V}\text{O}_{2\text{sum}}$ also were done using a one-way ANOVA or Kruskal-Wallis test. If the ANOVA indicated significant differences, differing means were detected by a Fisher's least-significant-difference test. Metabolic rates and masses of normothermic and hypothermic birds were compared by Student's *t*-test or by Mann-Whitney *U*-test when sample variances were not equal. Comparisons of the percentages of birds becoming hypothermic at the same helox temperature in different seasons were made using a chi-squared test for goodness of fit. Statistical significance was accepted at $P < 0.05$.

RESULTS

Mass at the initiation of cold stress tests was 14.4 ± 1.5 g ($n = 10$) in spring, 13.6 ± 0.8 g ($n = 7$) in summer, and 14.1 ± 1.3 g ($n = 26$) in fall; it did not differ significantly among seasons. Mass at capture also did not differ significantly among seasons, although spring vireos had significantly longer wings than summer or fall vireos, and visible-fat scores were significantly lower in summer than in either spring or fall (Table 1).

For spring birds, $\dot{V}\text{O}_2$ was not significantly different from -1° to 4°C and, for fall birds, $\dot{V}\text{O}_2$ did not differ significantly between -1° and 9°C . Values for $\dot{V}\text{O}_{2\text{sum}}$ in spring and fall represent pooled mean $\dot{V}\text{O}_2$ over these temperature ranges. Spring $\dot{V}\text{O}_{2\text{sum}}$ was significantly greater than both fall and summer $\dot{V}\text{O}_{2\text{sum}}$ ($P < 0.001$) on both total and mass-specific bases (Table 2). Fall and summer $\dot{V}\text{O}_{2\text{sum}}$ were not significantly different.

In addition, spring vireos required colder

TABLE 1. Mass, unflattened wing chord, and visible-fat scores ($\bar{x} \pm SD$) at capture in Warbling Vireos from spring ($n = 15$), summer ($n = 35$), and fall ($n = 93$) in southeastern South Dakota.

	Spring	Summer	Fall
Mass (g)	14.6 \pm 1.5	14.0 \pm 0.8	14.4 \pm 1.2
Wing (mm)	70.1 \pm 2.2**	68.0 \pm 2.1	68.1 \pm 2.0
Furcular fat	2.1 \pm 1.2	0.8 \pm 0.6***	2.0 \pm 1.1
Abdominal fat	2.2 \pm 1.1	0.8 \pm 0.6***	2.1 \pm 1.0

** $P < 0.01$ indicating significant differences from the other two seasons; *** $P < 0.001$.

temperatures in helox to induce hypothermia in a majority of individuals than either fall or summer birds (Fig. 1), which suggests improved cold tolerance in spring relative to other seasons. Furthermore, at 6°C in helox, only 7 of 12 vireos (58.3%) became hypothermic in fall, while 6 of 7 (85.7%) became hypothermic in summer (Fig. 1). These percentages were significantly different ($X^2 = 5.37, P = 0.02$), suggesting improved cold tolerance in fall relative to summer.

For summer residents, SMR was 0.643 ± 0.133 ml O_2 min^{-1} ($n = 6$), and mean mass was 12.2 ± 0.6 g. This value for SMR is 5.3% lower than allometrically predicted SMR for passerines (Aschoff and Pohl 1970). Metabolic expansibility ($\dot{V}O_{2sum}/SMR$) was 6.5 for summer residents, a value similar to those reported in other passerines (Marsh and Dawson 1989, Swanson 1990, Cooper and Swanson 1994).

Mass-specific minimal thermal conductance (C) in helox was calculated for individual birds according to

$$C = \dot{V}O_2 / (T_b - T_a), \quad (1)$$

where T_b is body temperature and T_a is chamber temperature. Calculation of C under helox cold stress was performed twice: for all birds (hypothermic and normothermic) using a T_b of 37.9°C (pooled mean T_b for normothermic birds from all seasons); and for only normothermic

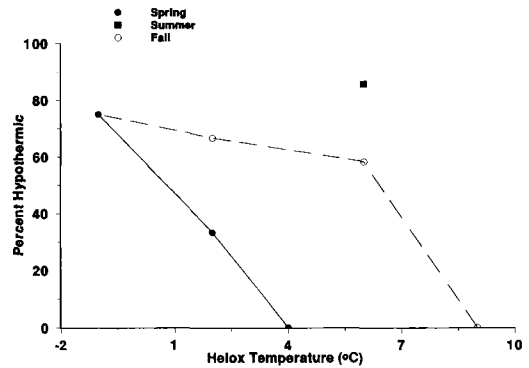


Fig. 1. Cold tolerance in Warbling Vireos from spring, summer, and fall. Solid and dashed lines connect values for spring and fall birds, respectively, at different helox temperatures. Sample sizes were: Spring, 4°C ($n = 4$), 2°C ($n = 3$), -1°C ($n = 4$); Summer, 6°C ($n = 7$); and Fall, 9°C ($n = 6$), 6°C ($n = 12$), 2°C ($n = 6$), -1°C ($n = 4$).

birds. I calculated C by both methods because the calculation for "all birds" assumes that $\dot{V}O_{2sum}$ was attained while birds were normothermic. However, since many birds became hypothermic, this assumption may not be valid in all cases. Consequently, I also calculated C only for birds that were normothermic ($T_b > 36.0^\circ C$) at the termination of the cold-stress test. For both calculations a caloric equivalent of 4.8 cal/ml O_2 was assumed. Minimum conductance for all birds in fall occurred from -1° to 2°C and was 2.83 ± 0.21 mW $g^{-1}C^{-1}$ ($n = 10$). This was significantly lower ($P = 0.004$) than values for C in spring (-1° to 4°C, 3.24 ± 0.30 mW $g^{-1}C^{-1}$, $n = 10$) and summer (3.23 ± 0.29 mW $g^{-1}C^{-1}$, $n = 7$). This difference was not apparent for normothermic vireos, where C was 3.30 ± 0.34 mW $g^{-1}C^{-1}$ (-1° to 9°C, $n = 14$) in fall, 3.26 ± 0.30 mW $g^{-1}C^{-1}$ (0° to 4°C, $n = 7$) in spring, and 3.58 mW $g^{-1}C^{-1}$ ($n = 1$) in summer.

DISCUSSION

Maximal thermogenic capacity was higher in spring-migrant vireos than in either their fall-

TABLE 2. Maximal thermogenic capacity ($\dot{V}O_{2sum}$) in Warbling Vireos in spring, summer and fall.

Season	n	Mass (g)	$\dot{V}O_{2sum}$ (ml O_2 min^{-1})	$\dot{V}O_{2sum}$ (ml O_2 $g^{-1} h^{-1}$)
Spring	10	14.4 \pm 1.5	5.00 \pm 0.34***	21.0 \pm 1.8***
Summer	7	13.6 \pm 0.8	4.19 \pm 0.34	18.5 \pm 1.7
Fall	26	14.1 \pm 1.3	4.26 \pm 0.45	18.3 \pm 1.7

*** $P < 0.001$ indicating a significant difference from the other two seasons.

migrant or summer counterparts. In addition, spring vireos were more cold tolerant than fall birds, which were, in turn, slightly more cold tolerant than summer residents. These increases in thermogenic capacity and cold tolerance apparently were not simple functions of body mass, for there were no significant differences among seasons in mass at the initiation of cold-stress tests or in mass at capture. However, mass tended to be higher among spring and fall vireos than in summer birds, but was more variable, which might mask any differences between groups. Spring and fall vireos carried significantly more visible fat than summer residents. In addition, spring vireos had significantly longer wings than fall or summer birds, which suggests larger body size (wing length is often considered indicative of body size in birds; James 1970, Nolan and Ketterson 1983), although this relationship may be confounded by feather wear in summer, and/or by suspended postbreeding molt and shorter primaries in juveniles than in adults in fall (Pyle et al. 1987). Wing-length differences also may reflect sampling from different populations at the different seasons, although some overlap among seasons (i.e. breeding birds attaining migratory disposition) probably occurred. Consequently, the relationship of wing length to body size of James (1970) and Nolan and Ketterson (1983) may not apply as effectively to this study of vireos at different seasons. Thus, there is little evidence for seasonal changes in mass affecting maximal thermogenic capacity and cold tolerance in Warbling Vireos.

Maximal thermogenic capacity in spring vireos was 19.2% greater than in summer, 17.3% greater than in fall, and 17.7% greater than pooled $\dot{V}O_{2sum}$ for summer and fall. These values are similar to increments of maximal thermogenic capacity in winter relative to summer for passerines wintering in cool/cold temperate regions, which range from 0 to 43% (Marsh and Dawson 1989, Swanson 1990, Cooper and Swanson 1994). This indicates that migratory passerines are capable of elevating thermogenic capacity on a seasonal basis to a similar degree as Temperate Zone residents, even though they do not experience similar extremes of temperature throughout the year.

The greater cold tolerance of spring vireos relative to fall and summer birds is not a result of superior insulation, in that there were no significant differences in thermal conductance

in helox for normothermic birds at any season, and fall vireos had lower conductance than spring or summer birds when conductance was calculated from all birds. The lower conductance in fall birds may be due, at least partially, to completion of postbreeding molt prior to migration when plumage mass is at maximal levels, although this molt regularly may be suspended until migration is completed in Warbling Vireos (Pyle et al. 1987). However, increased plumage mass may not account completely for decreased conductance in fall vireos, for helox markedly reduces the effectiveness of plumage insulation (Rosenmann and Morrison 1974).

Given that spring birds are more cold tolerant but do not have improved insulation, it is evident that metabolic alterations, indicated by augmented maximal thermogenic capacity, are responsible for seasonal changes in cold tolerance. These metabolic adjustments could be due to increased muscle mass devoted to shivering thermogenesis (muscular hypertrophy) and/or increased aerobic capacity of flight muscles. Current evidence suggests that both mechanisms may occur among migratory birds. However, since an increment of aerobic capacity associated with migration apparently is not a feature common to all migrants (Marsh 1981, Driedzic et al. 1993), and an increase in aerobic capacity is not associated with elevated maximal thermogenic capacity in winter-acclimatized passerines (Marsh and Dawson 1982, Yacoe and Dawson 1983), such an increment might not be expected for vireos. In addition, vireos in my study exhibited a lack of significant seasonal variation in body mass, so there is little evidence for muscular hypertrophy in these birds. Nevertheless, a direct assessment of flight-muscle mass at each season is necessary to discern whether seasonal variation in muscle mass contributes to increased maximal thermogenic capacity in spring birds.

Although seasonal trends in cold tolerance in vireos were evident, there was considerable individual variation in cold resistance (Fig. 1). Since elevated thermogenic capacity and increased shivering endurance are often correlated in birds (Marsh and Dawson 1989), differences in maximal thermogenic capacity may account for differences in cold tolerance in individuals. For summer vireos, the single bird remaining normothermic had the highest $\dot{V}O_{2sum}$ at that season. For fall birds at 6°C, normother-

mic birds had significantly higher ($P = 0.01$) mean $\dot{V}O_{2sum}$ (4.57 ± 0.50 ml O_2 min^{-1} , $n = 5$) than did hypothermic birds (3.82 ± 0.36 ml O_2 min^{-1} , $n = 7$), although some overlap in $\dot{V}O_{2sum}$ between groups did occur. In general, this suggests that individuals with high thermogenic capacity tolerate cold better than those with lower thermogenic capacity. However, at colder temperatures (-1° to $2^\circ C$) in spring and fall, maximal thermogenic capacity did not differ significantly between normothermic and hypothermic vireos (Fall, normothermic $\dot{V}O_{2sum} = 4.43 \pm 0.55$ ml O_2 min^{-1} [$n = 3$], hypothermic $\dot{V}O_{2sum} = 4.39 \pm 0.38$ ml O_2 min^{-1} [$n = 7$]; Spring, normothermic $\dot{V}O_{2sum} = 5.14 \pm 0.20$ ml O_2 min^{-1} [$n = 3$], hypothermic $\dot{V}O_{2sum} = 4.52 \pm 0.74$ ml O_2 min^{-1} [$n = 4$]). In addition, there were no significant differences in mass between hypothermic and normothermic birds at any season. Thus, it is apparent that, while general positive correlations exist in birds between mass and thermogenic capacity (Hinds et al. 1993), and between thermogenic capacity and cold resistance (Marsh and Dawson 1989), the precise mechanisms by which cold resistance is established in birds are complex and incompletely understood.

Regardless of the mechanism promoting increased maximal thermogenic capacity in spring vireos relative to other seasons, the improved cold tolerance afforded by the metabolic adjustments underlying this response may be of significant benefit to spring migrants. Inclement weather conditions are more likely to be encountered during spring migration (May) in the north-central United States than during summer residency or fall migration (August-September). Consequently, an elevated capacity for heat production during spring migration may be selectively advantageous given the increased likelihood of encountering adverse climatic conditions where heat production becomes important. However, maximal thermogenic capacity in Warbling Vireos at all seasons undoubtedly far exceeds metabolic rates required to contend with cold weather during spring. Nevertheless, winter increment of maximal thermogenic capacity in temperate-wintering passerines is correlated with enhanced shivering endurance at more moderate temperatures (Marsh and Dawson 1989). Such improved shivering endurance also may be beneficial to spring vireos during inclement weather, although temperature extremes at this sea-

son do not approach those of Temperate Zone winters.

Alternatively, the spring increment of maximal thermogenic capacity simply may be a by-product of selection for heightened levels of endurance flight at this season. Spring migration in Palearctic passerine migrants proceeds at a faster rate than fall migration (Pearson and Lack 1992). In addition, Neotropical migrants tend to migrate later in the spring and in a more synchronous burst than Temperate Zone migrants (Francis and Cooke 1986, Hagan et al. 1991), which suggests greater urgency in reaching the breeding grounds for Neotropical migrants like the Warbling Vireo. Such an urgency may not be present in fall migrants proceeding southward after competition for breeding territories and mates has abated. Furthermore, the duration of the migratory passage is shorter in spring than in fall for most Neotropical migrants in the north-central United States (Winker et al. 1992, K. L. Dean and Swanson unpubl. data), which also suggests a more rapid rate of migration in spring. If spring vireos do migrate at faster rates than fall birds, this would favor enhanced adaptation for endurance flight in spring migrants. Since many physiological and biochemical adjustments for migratory flight and winter acclimatization are similar (Dawson et al. 1983), adaptation for increased endurance flight in spring could produce elevated capacity for thermogenesis and increased cold tolerance as corollaries. If it is assumed that spring vireos exhibit enhanced adaptation for endurance flight relative to other seasons, at least during the stages of migration measured in this study, then these data suggest that coupled changes in cold-induced and exercise-induced maximal metabolism occur in birds, as they do in some mammals (Hayes and Chappell 1986). However, until direct measurement of aerobic capacity and endurance during flight is accomplished, such a conclusion is not resolute.

Standard metabolic rate in summer was within 6% of allometrically predicted values for passerines (Aschoff and Pohl 1970). Measurement of SMR in migratory periods was not possible because birds exhibited nocturnal activity within the metabolic chamber, presumably associated with *Zugunruhe*. It is, therefore, unknown whether SMR changes with migratory state, as it often does with season in small, temperate-wintering species (Weathers 1980, Cooper and Swanson 1994).

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