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SEASONAL EFFECTS ON METABOLISM AND THERMOREGULATION IN NORTHERN BOBWHITE[1]

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Abstract. Seasonal differences in metabolism and cold hardiness are common among small passerine birds. However, seasonal adjustments of metabolism and insulation are less well studied in nonpasserines and in larger birds. We measured basal metabolic rate (BMR), metabolic response to temperature, and maximal capacity for thermogenesis (peak cold-induced oxygen consumption, $\dot{V}O_{2\,sum}$) in late spring/summer and winter in outdoor captive Northern Bobwhite (*Colinus virginianus*) near the northern boundary of their natural range, to determine whether seasonal adjustments in metabolism are a component of acclimatization in this species. Mass, BMR and regression equations describing diurnal and nocturnal metabolic response to temperature were not significantly different between seasons. After metabolic tests below thermoneutrality, cloacal temperature (T_b) was not dependent on ambient temperature (T_a) at either season, and nocturnal T_b did not differ significantly between seasons. However, after metabolic tests below thermoneutrality, diurnal T_b was significantly greater in summer (38.9 ± 1.1°C) than in winter (37.7 ± 1.1°C). Although body mass of winter birds was significantly greater than their body mass in late spring, maximal thermogenic capacity did not differ significantly on a seasonal basis, and winter bobwhite were only marginally more cold tolerant than late spring birds under severe cold stress. For individual birds tested in both winter and late spring, individual ranking of $\dot{V}O_{2\,sum}$ was not consistent between seasons (i.e., birds with a high $\dot{V}O_{2\,sum}$ in winter did not necessarily have a high $\dot{V}O_{2\,sum}$ in late spring). These data suggest little seasonal adjustment of metabolism or insulation in the Northern Bobwhite, a relatively large nonpasserine species native mainly to regions with relatively mild winter climates.

Key words: Northern Bobwhite, Colinus virginianus, *metabolism, thermoregulation, seasonal acclimatization, maximal thermogenic capacity.*

INTRODUCTION

Many small passerine birds are able to inhabit north temperate regions with relatively severe winter climates in spite of their high surface area to volume ratio, limited capacity for seasonally improving insulation and limited ability to store fat (Marsh and Dawson 1989). Winter acclimatization in these birds is primarily metabolic in nature. In small birds, basal metabolic rate (BMR) is often, although not always, higher in winter than in summer (Weathers 1980, Dawson et al. 1983a, Liknes and Swanson 1996). Maximal capacity for thermogenesis (peak, cold-induced oxygen consumption or summit metabolism, $\dot{V}O_{2sum}$) increases in winter relative to summer in birds showing marked seasonal changes in cold tolerance (Hart 1962, Dawson and Smith 1986, Cooper and Swanson 1994). A winter increment of shivering endurance is associated with this improved thermogenic capacity and is apparently the primary component of winter acclimatization in small passerines (Dawson and Carey 1976, Dawson et al. 1983b). The precise mechanistic basis for this improved shivering endurance in winter compared to summer remains uncertain (Marsh and Dawson 1989, Marsh et al. 1990). Seasonal adjustments in insulation in these small birds are less marked than metabolic adjustments and play only a minor role in seasonal acclimatization (Dawson and Carey 1976, Swanson 1991a, Cooper and Swanson 1994). These metabolic adjustments allow marked winter improvement in cold resistance relative to summer in passerines inhabiting relatively cold winter climates (Marsh and Dawson 1989, Swanson 1990, Cooper and Swanson 1994).

For large birds (> 100 g), insulation contributes to winter acclimatization to a greater degree than in small birds (West 1972, Stokkan 1992). Seasonal metabolic adjustments in large birds are less well studied, but appear to be less prominent than in small birds, and large birds fail to show consistent seasonal trends in metabolism (Bech 1980, Sherfy and Pekins 1994), although

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Weathers and Caccamise (1978) demonstrated that seasonal changes in BMR are inversely related to body mass, with several birds over 200 g actually exhibiting winter decreases in BMR relative to summer. Consequently, the degree to which seasonal metabolic adjustments contribute to acclimatization in larger birds is uncertain. We measured seasonal changes in BMR, metabolic response to temperature, and maximal thermogenic capacity to determine metabolic and insulatory contributions to winter acclimatization in captive Northern Bobwhite (*Colinus virginianus*), a relatively large (approx. 200–250 g) nonpasserine.

The Northern Bobwhite is predominantly a species of the southern United States and northern Mexico where winters typically are rather mild (AOU 1983). However, the northern portion of their range encompasses regions with relatively severe winters, including southeastern South Dakota (SDOU 1991). In the northern reaches of the range of the bobwhite, populations fluctuate widely, and this fluctuation is correlated with severity of winter weather (Dinsmore et al. 1984, SDOU 1991). The role that temperature or other factors play in regulating the northern boundary of bobwhite distribution is uncertain. The northern boundary of bobwhite distribution in the Great Plains is associated with the approximate northern limit of the Central Great Plains Winter-Wheat and Rangeland Resource region (Root 1988a). However, the proximate role of vegetation in limiting the range of the bobwhite is uncertain because dietary composition varies geographically over the range of the bobwhite (Johnsgard 1973). The northern range boundary also is approximately coincident with the average minimum January temperature isotherm of −12°C (Root 1988a), which suggests that temperature may contribute to regulation of bobwhite distribution. Root (1988b) noted that average minimum January temperatures at the northern range boundaries for a number of passerine species produced resting metabolic rates of approximately 2.5 times BMR. Our measurements of seasonal variation in metabolic and insulatory parameters in a climate at the northern range boundary of the bobwhite help elucidate the role of temperature in limiting bobwhite distribution.

METHODS

BIRDS

Bobwhite (wild strain) were obtained from hatcheries in South Dakota, Nebraska and Minnesota where birds were maintained in unheated outdoor shelters. Quail were transported from hatcheries to Vermillion, Clay County, South Dakota (42° 47′N latitude) and housed in covered, unheated outdoor pens for at least two weeks prior to metabolic tests. Food (wild bird seed mix and rolled corn) and water were provided ad libitum. Metabolic tests were conducted in late spring/summer and winter from 1991–1996. For all seasonal metabolic comparisons, the same cohort of birds was tested in late spring/summer and winter, but separate cohorts of birds were used for measurement of diurnal metabolic response to temperature and BMR, nocturnal metabolic response to temperature, and maximal thermogenic capacity. Birds tested between 26 June and 11 September were considered "summer birds," whereas those tested between 8 January and 20 February were considered "winter birds." For maximal thermogenic capacity, birds were tested during the winter season and from 20–25 May, the latter group referred to as "late spring" birds. Bobwhite were tested without regard to sex because mean masses of males and females did not differ significantly for any of the cohorts tested, but male : female ratios for various metabolic parameters were: BMR, 6:3 (summer), 5:3 (winter); nocturnal metabolic response to temperature, 7:6 (summer), 5:3 (winter); diurnal metabolic response to temperature, 6:3 (summer), 5:3 (winter); and maximal thermogenic capacity, 6:6 (summer), 9:9 (winter). All birds were at least 8 months old at the time of testing and were considered adults.

BMR AND METABOLIC RESPONSE TO TEMPERATURE

Oxygen consumption ($\dot{V}O_2$) was measured by open-circuit respirometry with an Ametek S-3A Oxygen Analyzer according to Swanson (1993). Prior to measurement of $\dot{V}O_2$, birds were weighed to the nearest gram with a Fisher Model 2-116 balance. Birds were then introduced into a metabolic chamber fashioned from a 3.8 L paint can with the inner surface painted black to provide an emissivity near 1.0. The effective volume of the chamber, calculated according to Bartholomew et al. (1981), was 3,774 ml. Temperature within the chamber was controlled to ± 0.5°C by immersion of 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 a thermometer traceable to the U. S. Bureau of Standards. Flow of dry, CO_2-free air into the metabolic chamber was initiated prior to immersion, and flow rates over the test period were maintained from 610–755 ml min^{-1} for BMR, and from 915–1,425 ml min^{-1} for metabolic response to temperature. Flow rates were regulated with a Cole-Parmer precision rotameter (Model FM082-03ST) previously calibrated to ± 1% accuracy (Swanson 1990).

Metabolic tests were conducted during both day (12:40–19:00 CST in summer, 11:20–18:55 in winter) and night (21:00–03:40 in summer, 19:45–01:15 in winter) to discern circadian differences in metabolism. For measurement of BMR, birds were exposed to a chamber temperature of 30°C. Individual birds were exposed to a single temperature from −10 to 15°C for measurement of metabolic response to temperature; metabolism at only one temperature within this range was measured per day for any given individual. Over the course of a season, individual birds were tested at no more than three different temperatures within this range, with at least six days between measurements. BMR measurements were sometimes obtained on the same day as another temperature exposure (with at least 3.4 hr between measurements) or 3–16 days from another temperature exposure. BMR did not differ significantly between these two treatments so data were pooled. Nocturnal metabolism was measured after at least a 5 hr fast to ensure postabsorptive conditions. Birds also were fasted for at least 4 hr prior to daytime measurements. Nocturnal measurements were conducted for 1 hr, following a 1-hr equilibration period after introduction to the chamber. For diurnal metabolism, measurements were conducted for 30 min, following a 30-min equilibration period. These equilibration periods were sufficient to allow $\dot{V}O_2$ to reach steady-state conditions. The lowest 10-min mean $\dot{V}O_2$ over the test period was designated $\dot{V}O_2$ at a particular test temperature. Oxygen consumption was calculated according to steady-state methods (Hill 1972, equation 2).

MAXIMAL THERMOGENIC CAPACITY

Methods for measuring maximal thermogenic capacity were similar to those for BMR and metabolic response to temperature except that a gas mixture of approximately 79% helium/21% oxygen (helox) was used as the respiratory gas instead of air. Helox has a higher thermal conductivity than air and elicits maximal cold-induced $\dot{V}O_2$ at relatively moderate temperatures (Rosenmann and Morrison 1974). Thermogenic capacity tests were conducted between 10:45 and 17:00 in both seasons. Birds were placed in the metabolic chamber which was then flushed with helox for 5 min at 1,590–1,810 ml min^{-1} before immersion into the water/ethylene-glycol bath. These flow rates were used for all thermogenic capacity tests and kept oxygen concentration in excurrent air above 19.7%. Helox cold stress tests involved exposing individual birds to a decreasing series of temperatures until $\dot{V}O_2$ no longer increased with a further decrease in temperature. Cold stress tests were initiated at −12°C in winter and −3 to −12°C in late spring. During cold stress tests, chamber temperature was decreased by 3°C at approximately 35 min, and again every 20–30 min thereafter if $\dot{V}O_2$ had not reached a plateau. For late spring birds, we initially began helox cold stress tests at −3°C, but only two individuals became hypothermic even after prolonged exposure to decreasing helox temperatures even though $\dot{V}O_2$ had reached a plateau. Therefore, we initiated helox cold stress for the final six individuals tested in late spring at −12°C, the same as for winter birds. At both seasons, metabolic tests were conducted for 60–90 min or until birds became hypothermic as indicated by a steady decline in $\dot{V}O_2$ over several minutes. Fractional concentration of oxygen in dry, CO_2-free excurrent gas was measured every 60 sec over the test period. We calculated $\dot{V}O_2$ as instantaneous $\dot{V}O_2$ (Bartholomew et al. 1981). Mean $\dot{V}O_2$ was calculated over successive 10-min intervals over the test period and the highest 10-min mean was designated $\dot{V}O_{2\,sum}$, with the initial 10 min excluded to allow excurrent O_2 concentration to stabilize (Dawson and Smith 1986). All values of $\dot{V}O_2$ were corrected to STP.

Upon removal from the metabolism chamber at the completion of metabolic tests in both air and helox, cloacal temperature (20 gauge thermocouple and thermocouple thermometer) and mass were measured. Bobwhite with a T_b < 36.0°C (a value 3°C below mean diurnal T_b in winter, and 1.7°C below mean diurnal T_b in summer) were considered hypothermic. Mass loss was assumed to be constant throughout the test period. We calculated mass-specific metabolic

rates using mass values corrected for mass loss over the test period.

STATISTICS

Data are reported as means ± SD. Mean values for BMR, maximal thermogenic capacity, body mass, T_b, mass-specific thermal conductance, and time to hypothermia were compared by Student's *t*-test, or by Mann-Whitney *U*-test if sample variances were unequal (determined by *F*-test). For maximal thermogenic capacity, we measured the same 12 individuals in both summer and winter and used paired two-tailed *t*-tests for comparison of $\dot{V}O_{2\ sum}$ and body mass in these birds. Comparison of BMR between sexes and seasons was by Kruskal-Wallis test, because variances were not homogenous among groups (*F*-test). We used Fisher's exact test to compare percentages of birds becoming hypothermic during helox cold stress tests in late spring and winter. Regressions were performed by the method of least squares, and regression lines were compared by ANCOVA. We calculated Pearson's correlation coefficients for mass, $\dot{V}O_{2\ sum}$, and residuals of $\dot{V}O_{2\ sum}$ vs. body mass in individual quail in late spring and winter to determine whether individual $\dot{V}O_{2\ sum}$ was consistent between seasons. Statistical significance was accepted at $P \leq 0.05$.

RESULTS

Bobwhite used for seasonal measurement of BMR and metabolic response to temperature consisted of two separate cohorts, the first was tested in summer 1991 and winter 1992 and the second in summer 1992 and winter 1993. Mean mass did not vary significantly between cohorts so data were pooled. Mean masses for summer birds (210 ± 38 g, $n = 22$) and winter birds (228 ± 36 g, $n = 16$) were not significantly different ($t_{36} = 1.48$). For measurement of maximal thermogenic capacity (winter and late spring of 1996), 12 individuals were measured in both winter and late spring and body mass in winter individuals (234 ± 19 g, $n = 12$) was significantly greater than mass in late spring individuals (220 ± 19 g, $n = 12$; $t_{11} = 3.76$, $P < 0.01$). An additional six individuals were tested for maximal thermogenic capacity in winter, and if these birds are included in calculations of mean mass, winter mass becomes 231 ± 19 g ($n = 18$) which is not significantly different from late spring mass ($t_{28} = 1.61$, $P = 0.12$).

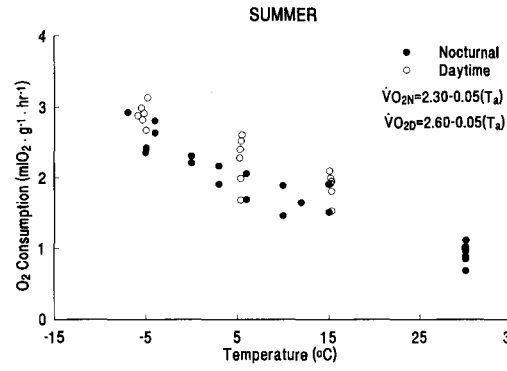

FIGURE 1. Relationship of nocturnal and diurnal mass-specific oxygen consumption to ambient temperature in summer acclimatized bobwhite. The equations provided were derived by least squares regression and describe oxygen consumption as a function of ambient temperature below thermoneutrality for nocturnal ($\dot{V}O_{2N}$) and diurnal ($\dot{V}O_{2D}$) birds. Slopes of nocturnal and diurnal equations were not significantly different, but diurnal intercept was significantly higher ($P < 0.001$) than nocturnal intercept.

BMR was 3.45 ± 0.78 ml O_2 min^{-1} (0.95 ± 0.13 ml O_2 g^{-1} hr^{-1}) in summer ($n = 9$) and 3.76 ± 0.64 ml O_2 min^{-1} (1.01 ± 0.11 ml O_2 g^{-1} hr^{-1}) in winter ($n = 8$). These values were not significantly different ($t_{15} = 0.87$ and 1.15 for total and mass-specific BMR, respectively). The relationship between mass-specific metabolic rate (ml O_2 g^{-1} hr^{-1}) and ambient temperature (°C) below thermoneutrality (Figs. 1 and 2) is best described by the following equations.

summer diurnal: $\dot{V}O_2 = 2.60 - 0.05(T_a)$, $n = 18$ (9 birds), $R^2 = 0.76$
winter diurnal: $\dot{V}O_2 = 2.59 - 0.06(T_a)$, $n = 18$ (8 birds), $R^2 = 0.76$
summer nocturnal: $\dot{V}O_2 = 2.30 - 0.05(T_a)$, $n = 16$ (13 birds), $R^2 = 0.78$
winter nocturnal: $\dot{V}O_2 = 2.12 - 0.05(T_a)$, $n = 18$ (8 birds), $R^2 = 0.72$

ANCOVA indicated no significant seasonal differences in either slope or intercept for either nocturnal or diurnal $\dot{V}O_2$. However, at both seasons intercepts were significantly higher ($P < 0.001$) during the day than at night and in winter diurnal slope was significantly steeper ($P < 0.05$) than nocturnal slope. Lower Critical Temperature (LCT) was calculated by determining the intersection of the line relating nocturnal $\dot{V}O_2$ to T_a below thermoneutrality with a line

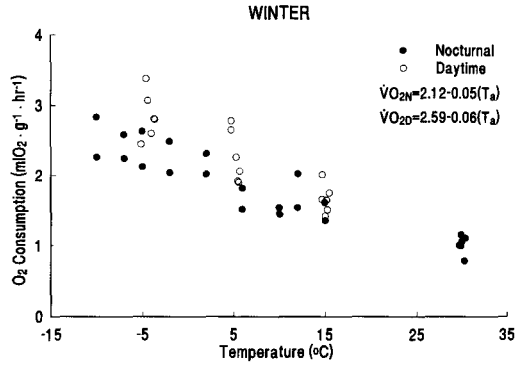

FIGURE 2. Relationship of nocturnal and diurnal mass-specific oxygen consumption to ambient temperature in winter acclimatized bobwhite. The equations provided were derived by least squares regression and describe oxygen consumption as a function of ambient temperature below thermoneutrality for nocturnal ($\dot{V}O_{2N}$) and diurnal ($\dot{V}O_{2D}$) birds. Diurnal intercept was significantly higher ($P < 0.001$) than nocturnal intercept. In addition, diurnal slope was significantly steeper ($P = 0.05$) than nocturnal slope, suggesting improved insulation at night. Neither slopes nor intercepts differed on a seasonal basis in either nocturnal or diurnal birds.

through BMR. Winter LCT was 22.4°C and summer LCT was 25.5°C.

Regressions of T_a against T_b following metabolic tests below LCT were not significantly different from zero slope in any of the four treatment groups. This indicates that T_b is independent of T_a below LCT over the range of temperatures studied, so T_b values were pooled. Mean T_bs of the four treatment groups were: summer diurnal, 38.9 ± 1.1°C ($n = 18$); winter diurnal, 37.7 ± 1.1°C ($n = 18$); summer nocturnal, 37.0 ± 1.0°C ($n = 16$); and winter nocturnal, 37.4 ± 1.1°C ($n = 18$). Diurnal T_b was significantly higher than nocturnal T_b in summer ($t_{32} = 5.52$, $P < 0.001$), but not in winter ($t_{34} = 0.93$). Summer diurnal T_b also was significantly higher than winter diurnal T_b ($t_{34} = 3.23$, $P < 0.01$), although nocturnal T_b did not differ between seasons ($t_{32} = 1.39$). After BMR measurement, summer T_b was 39.2 ± 0.5°C ($n = 9$), which was significantly greater than winter T_b (37.6 ± 0.8°C, $n = 8$; $t_{15} = 5.21$, $P < 0.001$).

Mass-specific thermal conductance (C) was calculated as $C = \dot{V}O_2/(T_b - T_a)$ for metabolic tests below thermoneutrality (Table 1). Conductance was significantly greater during the day than at night in both summer ($t_{32} = 2.01$, $P = 0.05$) and winter ($t_{34} = 4.53$, $P < 0.001$). Diurnal conductance did not differ significantly between seasons ($t_{34} = 0.20$), but nocturnal conductance was significantly higher in summer than in winter ($t_{32} = 2.28$, $P < 0.05$).

For those birds where helox cold stress tests were initiated at −12°C ($n = 18$ in winter, $n = 6$ in late spring), 27.8% (5/18) were normothermic ($T_b > 36$°C) on removal from the metabolic chamber (after $\dot{V}O_2$ had attained maximum levels) in winter (removed after 60–70 min), whereas 16.7% (1/6) were normothermic in late spring (removed after 90 min). These percentages were not significantly different. However, mean time to hypothermia in those birds becoming hypothermic was 62.4 ± 10.3 min in winter and 48.6 ± 10.5 min in late spring. The winter duration is significantly ($t_{16} = 2.53$, $P = 0.02$) longer than the late spring duration, which suggests that winter birds are marginally more cold tolerant than late spring birds.

Maximal thermogenic capacity in late spring was 20.19 ± 3.94 ml O_2 min^{-1} (5.50 ± 0.92 ml O_2 g^{-1} hr^{-1}, $n = 12$). Winter maximal thermogenic capacity was 22.02 ± 2.14 ml O_2 min^{-1} (5.74 ± 0.62 ml O_2 g^{-1} hr^{-1}, $n = 18$). These values did not differ significantly on either whole-animal (Mann-Whitney $U_{12,18} = 139$) or mass-specific ($t_{28} = 0.87$) bases. Furthermore, maximal thermogenic capacity of the 12 individuals tested in both winter and late-spring (see above) did not differ significantly ($t_{11} = 1.42$ and 0.31 for whole-animal and mass-specific comparisons, respectively) between seasons (winter thermogenic capacity = 21.65 ± 1.82 ml O_2 min^{-1}, 5.59 ± 0.63 ml O_2 g^{-1} hr^{-1}, $n = 12$). Metabolic expansibility ($\dot{V}O_{2\,sum}$/BMR, Dawson and Carey 1976) on a per-bird basis was 5.9 in both late spring and winter.

TABLE 1. Diurnal and nocturnal mass-specific thermal conductance (C) in captive bobwhite acclimatized to summer and winter. The number of birds used to derive the sample size (n) is listed in the "Individual birds" column.

Treatment	n	Individual birds	C (ml O_2 g^{-1} hr^{-1} $°C^{-1}$)
Summer diurnal	18	9	0.070 ± 0.009[a]
Winter diurnal	18	8	0.069 ± 0.008[b]
Summer nocturnal	16	13	0.064 ± 0.008[c]
Winter nocturnal	18	8	0.058 ± 0.007

[a] Significantly greater than same-season nocturnal C at $P = 0.05$.
[b] Significantly greater than same-season nocturnal C at $P < 0.001$.
[c] Significantly greater than opposite-season nocturnal C at $P < 0.05$.

TABLE 2. Seasonal means (± SD) for BMR and maximal thermogenic capacity for sex classes. Seasonal comparisons within sex classes were by paired *t*-test, whereas within-season sexual comparisons were by independent Student's *t*-test.

	n	Mass (g)	BMR (ml O_2 min^{-1})	*n*	Mass (g)	$\dot{V}O_{2sum}$ (ml O_2 min^{-1})
Winter						
Male	5	231.2 ± 41.5	3.89 ± 0.78	6	240.3 ± 9.6	21.65 ± 1.86
Female	3	210.1 ± 3.53	3.53 ± 0.29	6	227.1 ± 24.3	21.65 ± 1.95
Late spring/summer						
Male	6	234.3 ± 44.7	3.64 ± 0.90	6	228.0 ± 17.9	23.08 ± 2.10
Female	3	189.7 ± 7.4	3.08 ± 0.33	6	211.9 ± 17.2[a]	17.30 ± 3.13[b]

[a] Significantly less ($P < 0.05$) than mass of winter females.
[b] Significantly less ($P < 0.01$) than values for both spring males and winter females.

Although sample sizes for within and between sex comparisons were relatively small, for individuals measured at both seasons, late spring males, but not winter males, exhibited significantly greater thermogenic capacity than same-season females on both whole-animal ($t_{10} = 3.76$, $P = 0.004$) and mass-specific ($t_{10} = 2.98$, $P = 0.014$) bases (Table 2). Furthermore, $\dot{V}O_{2\,sum}$ in winter females was significantly greater than that for late spring females ($t_{10} = 3.57$, $P < 0.02$). There were no sexual or seasonal differences in BMR, although again sample sizes were relatively small (Table 2).

Because maximal thermogenic capacity was measured in 12 individuals in both late spring and winter, we tested whether metabolic rates of individual bobwhite were correlated between seasons. Whole-animal maximal thermogenic capacity in individual bobwhite was not significantly correlated between seasons ($r = 0.43$, $P = 0.16$), although the trend was in the expected direction (Fig. 3a). However, individual body mass was significantly correlated between seasons ($r = 0.77$, $P = 0.003$, Fig. 3b). We corrected for possible confounding effects of body mass on thermogenic capacity in late spring birds by plotting log mass against log $\dot{V}O_{2\,sum}$, and calculating residuals from the regression equation to remove effects of body mass. Winter birds showed no significant relationship between log mass and log $\dot{V}O_{2\,sum}$, so winter residuals were calculated by subtracting mean $\dot{V}O_{2\,sum}$ (rather than allometrically predicted $\dot{V}O_{2\,sum}$) from measured $\dot{V}O_{2\,sum}$. Residuals of $\dot{V}O_{2\,sum}$ were not significantly correlated between seasons ($r = 0.15$, $P = 0.65$), indicating that maximal thermogenic capacity in individual bobwhite between seasons (Fig. 3c) was not consistent, relative to mass-adjusted mean $\dot{V}O_{2\,sum}$.

DISCUSSION

Many large birds, including several Galliformes, possess very effective winter insulation so that with selection of favorable microclimates (e.g., snow burrows) thermoregulatory costs are minimal (Marjakangas et al. 1984, Stokkan 1992). Some of these species show winter improvement of insulation relative to summer, but in others insulation remains seasonally constant (West 1972, Sherfy and Pekins 1994). For Mute Swans (*Cygnus olor,* Bech 1980) and Black Grouse (*Tetrao tetrix,* Rintimaki et al. 1983), winter conductance exceeds summer conductance at moderate temperatures. However, winter birds in both species reduce conductance as T_a decreases, whereas conductance in summer birds remains essentially constant with T_a. This results in seasonally similar conductance, or lower conductance in winter, at low temperatures. Basal metabolic rate (BMR) does not vary consistently on a seasonal basis in large birds, and winter increases (Bech 1980, Rintimaki et al. 1983, Sherfy and Pekins 1994), seasonal stability (Schwann and Williams 1978) and winter decreases (Hart 1962, West 1972, Mortensen and Blix 1986) in BMR relative to summer have all been reported. Maximal capacity for heat production is greater in winter than in summer (13–22%) for pigeons, *Columba livia* (Hart 1962), but is unstudied in other large birds. Thus, it appears that metabolic adjustment occurs to some degree in large birds, but effective cold resistance in these birds is primarily conferred by effective insulation. This pattern of heavy reliance on insulation for winter acclimatization contrasts markedly with that of small birds that show only minor seasonal variation in insulation and must elevate heat production for thermoreg-

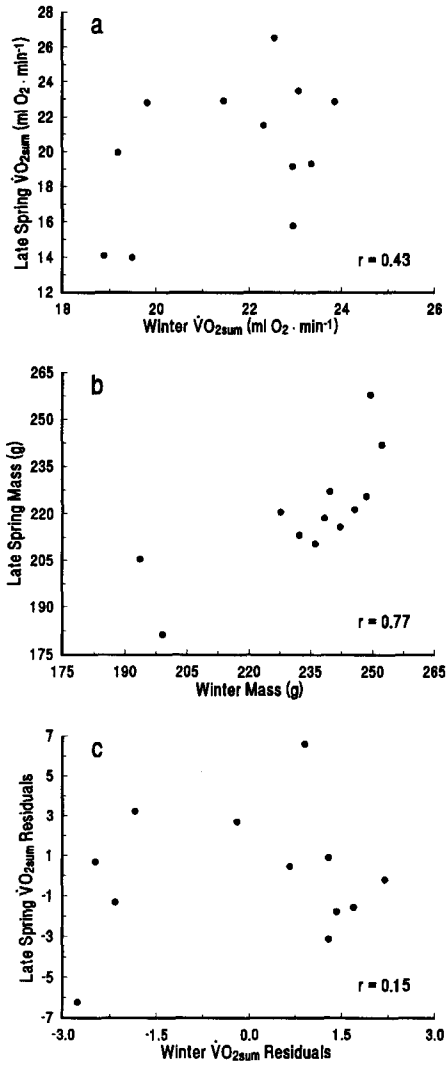

FIGURE 3. Correlations between seasons for (a) $\dot{V}O_{2\,sum}$, (b) mass, and (c) mass-independent residuals of $\dot{V}O_{2\,sum}$ in individual bobwhite. Only the mass correlation was significant ($P = 0.003$), which indicates that $\dot{V}O_{2\,sum}$ in individual bobwhite was not repeatable between seasons.

ulation even at moderate temperatures. This indicates that winter acclimatization is primarily a metabolic process in small birds (see Marsh and Dawson 1989 for review).

Because the Northern Bobwhite is a relatively large bird, it might be expected that effective insulation could obviate the need for marked seasonal metabolic adjustment. However, this study indicates that insulation in bobwhite is poorer at both seasons than predicted allometrically. Lower critical temperatures in bobwhite were relatively high and varied little with season (22.4°C in winter, 25.5°C in summer). These high LCTs are similar to those reported for many small birds (Weathers and van Riper 1982). Allometric equations for LCT for nonpasserine birds, similar to those calculated for passerine birds by Weathers and van Riper (1982), can be generated from allometric equations for BMR (Aschoff and Pohl 1970) and conductance (Aschoff 1981) in nonpasserines. The allometric equation thus calculated for nonpasserines is:

$$LCT = T_b - 4.24(Mass)^{0.317}$$

where LCT and T_b are in °C and Mass is in grams. LCT in winter bobwhite is 8.7°C higher than predicted by this equation, and summer bobwhite LCT is 11.6°C higher than predicted. Furthermore, although diurnal conductance values for bobwhite are similar to allometric predictions (Aschoff 1981), nocturnal conductance is 45.0% and 52.4% higher than predicted allometrically in winter and summer, respectively. Summer nocturnal conductance is significantly (10.3%) higher than winter nocturnal conductance, suggesting some improvement in insulation in winter, possibly resulting from the gradual season-long molt that summer birds underwent from mid-June through August (pers. observ.), but metabolism must be elevated above basal levels for thermoregulation even at moderate temperatures in both seasons. In addition, regressions of metabolism on T_a below thermoneutrality do not differ between seasons, which suggests little winter improvement of insulation. These data indicate that bobwhite are relatively poorly insulated at both seasons and must expend substantial amounts of energy on thermoregulation at cold temperatures. This is a situation at odds with most other larger Galliformes. An alternative explanation for the relatively poor insulation of bobwhite in this study is that captivity resulted in poor plumage condition and consequent poor insulation. However, our values for LCT are similar to those for other relatively small Galliformes (Brush 1965, Roberts and Baudinette 1986), although these studies also involved captive birds. Furthermore, captivity does not preclude seasonal changes in LCT or thermal conductance in other captive Galliformes (West 1972, Mortensen and Blix 1986, Sherfy and Pekins 1994). Thus, although con-

ductance may be artificially high due to poor plumage, the minor seasonal differences in LCT and thermal conductance in this study suggest that plumage changes are relatively unimportant to seasonal acclimatization in bobwhite.

Thermoregulatory costs may be reduced by decreasing body temperature, thereby reducing the gradient for heat loss to the environment. Winter, relative to summer, bobwhites exhibited significantly lower diurnal, but not nocturnal, T_b after metabolic tests below thermoneutrality. This may provide some energetic benefit for winter birds, but it is of only minor importance in reducing thermoregulatory costs. For example, the 1.2°C difference in mean diurnal T_b between winter and summer bobwhite, given seasonally stable thermal conductance (Table 1), results in an energetic savings at 0°C of only 3% in winter birds, and this percentage becomes even smaller at lower ambient temperatures.

Body mass did not vary significantly between seasons within cohorts of bobwhite tested for BMR and metabolic response to temperature. Body mass also did not differ significantly on a seasonal basis among cohorts tested for maximal thermogenic capacity. However, in individuals tested for maximal thermogenic capacity in both late spring and winter, body mass was significantly greater in winter, but only by 6.2%. Although stored fat was not measured directly in this study, the seasonal stability of body mass suggests little difference in stored fat between seasons. Seasonal stability of fat reserves is a condition common to a number of large Galliformes (Thomas 1982, Mortensen et al. 1985).

Winter enhancement of stored energy reserves and insulation apparently are not important components of winter acclimatization in Northern Bobwhite. This suggests that metabolic adjustments may contribute to winter acclimatization to a greater extent than insulative adjustments, a situation similar to small birds. However, basal metabolic rate did not vary seasonally in this study. At both seasons, BMR was close to allometrically predicted values (Aschoff and Pohl 1970), exceeding predicted BMR by only 1.8 and 4.4% in summer and winter, respectively. From the equations describing $\dot{V}O_2$ as a function of T_a below thermoneutrality, crude estimates of thermoregulatory costs can be derived (disregarding radiative and convective effects and heat produced as a by-product of activity). Mean daily temperatures for January and July for Vermillion, Clay County, South Dakota are −8 and 24°C, respectively (United States National Oceanic and Atmospheric Association records). Metabolic rates at these temperatures represent factorial increments of BMR of 3.0 in winter and 1.5 in summer for diurnal metabolism, and 2.5 in winter and 1.2 in summer for nocturnal metabolism. These temperatures elicit thermoregulatory costs of 165.9 kJ day^{-1} in January and 15.2 kJ day^{-1} in July. This represents a 10.9-fold increase in thermoregulatory costs in winter relative to summer and indicates that winter acclimatization in bobwhite must be directed primarily toward maintenance of elevated metabolic rates for prolonged periods.

Case and Robel (1974) provided measurements of daily existence energy (EE) for captive bobwhite held under 10L:14D photoperiod at 0–40°C. In these experiments, bobwhite were confined individually in small (48 × 25 × 13 cm) cages over several months. Thus, Case and Robel's (1974) values for EE undoubtedly underestimate actual daily energy expenditure for free-living bobwhite. Nevertheless, these values should provide a basis for examining the contribution of thermoregulatory costs to daily energy expenditure in winter bobwhite. Case and Robel (1974) report a linear relationship between EE and T_a, with an EE at 0°C of 205.5 kJ day^{-1}. Because the relationship between EE and T_a was linear, EE at the average daily January temperature for Vermillion (−8°C) can be calculated from their equations as 233 kJ day^{-1}. Our estimates of winter thermoregulatory costs for bobwhite comprise 59.4% of EE at 0°C, and 70.8% of EE at −8°C. This indicates that a substantial fraction of winter EE must be devoted to thermogenesis in these birds. In fact, if BMR is added to thermoregulatory costs estimated in our studies, metabolic costs exceed EE measurements. Of course, selection of favorable microclimates and huddling in coveys (Case 1973) may reduce thermoregulatory costs, but thermogenesis still comprises a large fraction of winter energy expenditures. This situation differs from that in a number of larger Galliformes, where winter thermoregulatory costs represent only minor fractions of daily energy expenditures (Marjakangas et al. 1984, Stokkan 1992).

Nevertheless, like BMR and metabolic response to temperature, maximal capacity for thermogenesis did not vary seasonally in bobwhite. Winter $\dot{V}O_{2\ sum}$ was 4.6% below allometric pre-

dictions (Hinds et al. 1993), whereas $\dot{V}O_{2\ sum}$ in summer was 9.8% below predicted values. The allometric equation of Hinds et al. (1993) was derived from eight species during spring and summer. Thus, there appears to be little seasonal metabolic adjustment to cold in Northern Bobwhite, and thermogenic capacity is not elevated above that for other species acclimated to warmer periods of the year. Furthermore, winter birds were only marginally more cold tolerant in helox cold stress tests that late spring birds. This suggests that the lack of seasonal adjustment in metabolism and the relatively poor insulation at both seasons preclude marked seasonal variation in cold tolerance in bobwhite.

Metabolic expansibility ($\dot{V}O_{2\ sum}$/BMR) in birds tested to date ranges from 3.3 (Saarela et al. 1989) to 8.1 (Dutenhoffer and Swanson 1996). Our values for metabolic expansibility in bobwhite (5.9 at both seasons) fall well within this range. Rough estimates of equivalent air temperatures at helox temperatures eliciting $\dot{V}O_{2\ sum}$ can be generated by entering values for $\dot{V}O_{2\ sum}$ into equations describing diurnal metabolism as a function of T_a below thermoneutrality and solving for T_a. This yields estimated air temperatures at $\dot{V}O_{2\ sum}$ of −58°C in late spring/summer and −53°C in winter. These temperatures are below actual ambient air temperatures encountered in the natural environment at both seasons, which suggests a metabolic reserve available for acute energy expenditures at both seasons, although convective heat loss coupled with extreme cold temperatures may approach conditions eliciting $\dot{V}O_{2\ sum}$ in winter bobwhite.

Over longer periods (e.g., the entire winter), however, metabolic rates generally cannot be sustained at levels approaching $\dot{V}O_{2\ sum}$. Sustained metabolic scope in vertebrates (in factorial increments of BMR) usually ranges from 1.5 to 5 (Peterson et al. 1990). The highest sustained metabolic scope recorded to date is 7.2 for lactating mice (Hammond and Diamond 1992), although sustained metabolic scope for cold-stressed mice was only 4.7 (Konarzewski and Diamond 1994). Furthermore, Root (1988b) found that the northern range boundaries for a number of passerine species were correlated with average minimum January temperatures producing metabolic rates of about 2.5 times BMR. Because southeastern South Dakota represents the northern extent of the Northern Bobwhite's range, metabolic rates associated with thermoregulation at average minimum January temperatures for this region should exceed BMR by about 2.5 times if Root's (1988b) findings also extend to nonpasserines. Given that mean minimum January temperature for Vermillion, South Dakota is −10°C, our winter nocturnal equation describing $\dot{V}O_2$ as a function of T_a indicates a metabolic rate for winter bobwhite of 2.59 times BMR. Thus, our data are consistent with the broad-scale relationship between climate and distribution described by Root (1988b), which suggests that temperature does influence the northern distribution of the Northern Bobwhite. These data suggest that winter climatic conditions in southeastern South Dakota may be metabolically challenging for bobwhite, and underscore the importance of food availability and behavioral thermoregulation to winter survival of Northern Bobwhite in northern sections of their range.

Thermogenic capacity of males and females did not differ in winter, but females showed reduced thermogenic capacity in late spring. Spring thermogenic capacity was measured in late May, which corresponds to the egg-laying period for females. Perhaps the energetic costs of egg production interfere with thermogenic performance in female bobwhite. Loss of total body and pectoralis muscle mass associated with egg production in female birds have been reported (Houston et al. 1995), and could influence thermogenic performance (Swanson 1991b, O'Connor 1995). Indeed, late spring females in this study were significantly smaller (7.1%) than winter females (Table 2). For late spring females with cold exposure tests initiated at −12°C in helox (n = 4), mean time to hypothermia was 44.5 ± 5.8 min. Two males were subjected to cold exposure tests initiated at −12°C in helox in late spring; one became hypothermic after 65 min and one remained normothermic for the entire 90 min test period. This suggests that differences in thermogenic capacity are related to variation in cold tolerance in bobwhite.

Finally, neither $\dot{V}O_{2\ sum}$ nor mass-independent residuals of $\dot{V}O_{2\ sum}$ were correlated between winter and late spring, suggesting that maximal thermogenic capacity in individual quail is not consistent between seasons. This contrasts with short-term studies (days to weeks) indicating relatively high repeatability of maximal oxygen consumption in individual skinks (*Chalcides*

ocellatus, Pough and Andrews 1984), garter snakes (*Thamnophis sirtalis,* Garland and Bennett 1990), deer mice (*Peromyscus maniculatus,* Hayes and Chappell 1990), and Belding's ground squirrels (*Spermophilus beldingi,* Chappell et al. 1995). Furthermore, individual maximal $\dot{V}O_2$ (both exercise- and cold-induced) in deer mice was repeatable over 3-month acclimation periods, including acclimation to cold (Hayes and Chappell 1990). However, individual exercise-induced maximal $\dot{V}O_2$ was only marginally consistent, and maximal cold-induced $\dot{V}O_2$ was not consistent over 1–2 years in free-living ground squirrels (Chappell et al. 1995).

Studies of the ecology and evolution of aerobic performance assume repeatability of aerobic performance over time. Our data suggest that such an assumption may not be justified over long periods or changing seasons, at least for $\dot{V}O_{2\,sum}$ in bobwhite. The absence of a correlation between seasons in individual $\dot{V}O_{2\,sum}$ in this study might be explained, in part, by plasticity of winter $\dot{V}O_{2\,sum}$ in response to short-term variation in winter temperature. Such plasticity has been suggested for winter-acclimatized passerines (Dutenhoffer and Swanson 1996, Swanson, unpubl. data). In addition, late spring bobwhite exhibited a greater range of variance in $\dot{V}O_{2\,sum}$ (−30.7 to +33.1%, measured as percent deviation from mass-adjusted mean $\dot{V}O_{2\,sum}$) than winter birds (−12.8 to +10.2%), and this could influence seasonal correlations of individual $\dot{V}O_{2\,sum}$. Thus, metabolic plasticity related to variation in winter temperature or to exigencies of breeding and nesting may mask season-to-season correlations of individual $\dot{V}O_{2\,sum}$. Alternatively, maximal thermogenic capacity in individual bobwhite may not be repeatable over long periods. This latter possibility merits further investigation, and a better test of long-term metabolic repeatability without the confounding effects of season and breeding status would be to measure thermogenic capacity from one winter to the next.

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