SEASONAL AND DIURNAL VARIATION IN METABOLISM AND VENTILATION IN HOUSE SPARROWS

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Abstract. Passerines that are year-round residents in temperate climates undergo seasonal acclimatization that facilitates maintenance of thermoregulatory homeostasis. These changes in thermoregulatory metabolism must be supported by equivalent changes in oxygen transport. We measured the effects of ambient temperature and time of day on metabolism and ventilation in House Sparrows (*Passer domesticus*) in summer and winter. House Sparrows were exposed to ambient temperatures (T_a) ranging from $-12°C$ to $15.5°C$ in summer and $17.5°C$ in winter. Open-circuit respirometry was used to measure oxygen consumption ($\dot{V}O_2$) and ventilation was recorded using whole-body plethysmography. In both summer and winter, $\dot{V}O_2$ increased with decreasing T_a. $\dot{V}O_2$ was significantly higher during the active phase compared to the resting phase of the daily cycle in both summer and winter. Thermal conductance was significantly lower in nighttime birds compared to daytime birds. With increased oxygen demands, minute volume ($\dot{V}_I$) increased in both summer and winter. In summer, only respiratory frequency (f) was significantly affected by time of day. In winter, active-phase birds had significantly higher respiratory frequency and minute volume ($\dot{V}_I$) than rest-phase birds. Winter birds in their rest phase had significantly higher oxygen extraction efficiency (EO_2) than active-phase birds. Winter birds at rest phase also had significantly higher EO_2 than summer birds.

Key words: House Sparrow, metabolism, oxygen consumption, Passer domesticus*, seasonal acclimatization, ventilation.*

Variación Estacional y Diaria en el Metabolismo y la Ventilación en *Passer domesticus*

Resumen. Las aves paserinas que residen a lo largo del año en climas de la zona templada pasan por un proceso de aclimatación estacional que facilita el mantenimiento de su homeostasis termorregulatoria. Estos cambios en el metabolismo termorregulatorio deben estar apoyados por cambios equivalentes en el transporte de oxígeno. En este estudio medimos los efectos de la temperatura del ambiente y la hora del día sobre el metabolismo y la ventilación en *Passer domesticus* en verano e invierno. Las aves fueron expuestas a temperaturas ambiente (T_a) en un rango de $-12°C$ a $15.5°C$ en el verano, llegando a $17.5°C$ en el invierno. Empleamos respirometría de circuito abierto para medir el consumo de oxígeno ($\dot{V}O_2$) y registramos la ventilación usando pletismografía de cuerpo entero. Tanto en el verano como en el invierno, $\dot{V}O_2$ aumentó con disminuciones en T_a. $\dot{V}O_2$ fue significativamente mayor durante la fase activa en comparación con la fase de descanso del ciclo diario, tanto en verano como en invierno. La conductancia térmica fue significativamente menor en aves estudiadas en la noche que en aves estudiadas durante el día. Con incrementos en la demanda de oxígeno, el volumen minuto ($\dot{V}_I$) aumentó en verano y en invierno. En verano, sólo la frecuencia respiratoria (f) fue afectada por la hora del día. En invierno, la frecuencia respiratoria y el volumen minuto ($\dot{V}_I$) fueron significativamente mayores en las aves en fase activa que en las aves en fase de descanso. Las aves de invierno en su fase de descanso presentaron una eficiencia de extracción de oxígeno (EO_2) siginificativamente mayor que la de las aves en fase activa. La EO_2 de las aves de invierno en fase de descanso también fue significativamente mayor que la de las aves de verano.

INTRODUCTION

Small passerine birds that reside in cold temperate regions year-round undergo seasonal acclimatization in order to support thermogenesis in winter. Seasonal acclimatization in birds seems to be due primarily to metabolic adjustments (Dawson and Marsh 1989, Marsh and Dawson 1989a, 1989b, Dawson and O'Connor 1996). Generally, these metabolic adjustments include increases in cold tolerance, thermogenic endurance, and maximum thermogenic capacity or summit metabolism in winter-acclimatized birds relative to summer birds. In mammals that face seasonally changing environments, in-

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creased insulation is a major compensatory adjustment to reduce heat loss (Irving et al. 1955, Marsh and Dawson 1989a). Insulatory changes are commonly recorded as changes in thermal conductance or the net rate of heat transfer from the organism to the environment (Schmidt-Nielson 1997). When insulation is increased, the cost of thermoregulation below the lower critical temperature (T_{lc}) is reduced and the T_{lc} may also be reduced (Aschoff 1981, Feist and White 1989). Increased insulation in winter birds relative to summer does not appear to be a major component of seasonal acclimatization (Marsh and Dawson 1989a).

In most birds that live in cold climates, feathers are replaced in an annual basic molt that usually occurs in late summer or early fall after breeding (Palmer 1972). Thus, at any particular time, the degree of plumage insulation is primarily a function of the extent of feather replacement and the time since the last molt (Marsh and Dawson 1989a). Small passerine birds may be especially limited in insulatory adjustments since substantial increases in plumage mass can affect their ability to fly and elude predators (Witter and Cuthill 1993, Metcalfe and Ure 1995). In several small passerine birds, including North American populations of House Sparrows (*Passer domesticus*), plumage mass has been shown to vary seasonally (Barnett 1970, Kendeigh 1976, Middleton 1978, Swanson 1991). However, insulatory changes due to plumage variation have only been shown conclusively in Rufous-collared Sparrows (*Zonotrichia capensis*, Novoa et al. 1994), Mountain Chickadees (*Poecile gambeli*, Cooper 1998), and Willow Ptarmigans (*Lagopus lagopus*, West 1972a). Thus, the importance of insulatory adjustments in seasonally acclimatized passerine birds is still unclear.

The House Sparrow is a small, nonmigratory passerine bird that was first released in New York in 1851 and now occupies most of North America (Lowther and Cink 1992). House Sparrows inhabiting temperate climates, such as Wisconsin, encounter a wide range of ambient temperatures due to seasonal changes. In order to tolerate the harsh conditions of winter, House Sparrows exhibit metabolic adjustments including increased summit metabolism in winter-acclimatized birds (Arens and Cooper 2005). The metabolic adjustments that birds employ to support thermogenesis under cold conditions have

received a fair amount of attention (Marsh and Dawson 1989b, Dawson and O'Connor 1996); however, the diurnal changes in metabolism and thermal conductance in seasonally acclimatized passerine birds have received little attention (Aschoff 1981, Schleucher and Withers 1999).

In order for small birds to support increased metabolism at low ambient temperatures, oxygen delivery must also increase. While much is known about the morphology of the avian respiratory system (Piiper and Scheid 1975, Smith et al. 1986), very little is known about potential seasonal changes in respiratory function in passerine birds. Birds showing metabolic increases during exposure to cold ambient temperatures require appropriate accommodations in oxygen transport. Changing oxygen consumption rates may be accommodated through changes in breathing frequency (*f*), breath volume or tidal volume (V_T), and the percentage of oxygen used per breath or oxygen extraction efficiency (EO_2). Adjustments in one, all, or any combination of these ventilatory variables can support ventilatory accommodation to changing oxygen demands (Chappell and Dawson 1994).

The majority of birds studied to date show significant increases in minute volume ($\dot{V}_I$) in response to increasing oxygen consumption ($\dot{V}O_2$) at temperatures below thermoneutrality. Birds seem to rely heavily on changing tidal volume more than breathing frequency to increase minute volume (Morgan et al. 1992). Among birds in which the relation of oxygen extraction efficiency to metabolic rate below thermoneutrality has been studied: parrots (Bucher 1981, Bucher and Morgan 1989), Chukars (Chappell and Bucher 1987), Prairie Falcons (Kaiser and Bucher 1985), Storm-Petrels, Kelp Gulls, Skuas (Morgan et al. 1992), and Tawny Frogmouths (Bech and Nicol 1999) respond with increasing minute volume while oxygen extraction efficiency is not significantly altered. Some birds, such as European Coots (Brent et al. 1984) Pekin Ducks (Bech et al. 1984), Kittiwakes (Brent et al. 1983), and Giant Petrels (Morgan et al. 1992) instead show constant or decreasing minute volume and substantial increases in oxygen extraction efficiency. Two small passerine birds studied by Clemens (1988), Rosy Finches and House Finches, showed significant changes in minute volume that involved increases in both breathing frequency and tidal volume without changes in oxygen extraction efficiency. In fact, House

Finches at low and high altitude and Rosy Finches at high altitude have decreasing oxygen extraction efficiency with declining ambient temperature.

Although ventilation in birds is becoming more clearly understood, two factors, time of day and season, that are known to influence metabolism (Aschoff and Pohl 1970; Swanson, in press) and may affect respiratory function have not been studied. If seasonal and diurnal variations in ventilatory parameters are evident in the House Sparrow, time of day and season may be important factors to consider when interpreting respiratory function in birds.

Our goal was to investigate the seasonal and daily differences in metabolism, ventilation, and thermal conductance in seasonally acclimatized House Sparrows exposed to a range of ecologically relevant colder temperatures. Therefore, we measured the change in metabolic rate, ventilation (f, V_T, and EO_2) and thermal conductance of House Sparrows in response to a range of cold temperatures during both daytime and nighttime in summer and winter.

METHODS

BIRDS

House Sparrows were captured in summer (May–August 2002 and 2003) and winter (January–March 2003) with mist nets in Oshkosh, Winnebago County, Wisconsin (44°01′N, 88°32′W). Birds were trapped under state (SCP.NER.131) and federal (MB003340-1) collecting permits. Upon capture, body mass was measured using an Ohaus Scout II (Pine Brook, New Jersey) portable electronic balance to the nearest 0.1 g. Visible fat deposits in abdominal and furcular regions were visually estimated using a 0–5 scale (Helms and Drury 1960). In addition, wing chord, tarsus, and tail length were recorded after capture. Adult birds, based on breeding characteristics and skull pneumatization (Pyle et al. 1997), were transported to the laboratory and separately caged at room temperature (20–25°C). Water, grit, and food (millet and chick starter mash) were supplied to caged birds as needed. All birds maintained mass (±2%) while in captivity. Birds were tested the day of capture or the following day in order to eliminate effects of captivity on metabolic rate (Warkentin and West 1990). Tests were completed between 10:00 and 16:00 during the day

and from 21:00 to 02:00 (CST) during the night, in summer and winter. Sparrows captured from 28 May to 6 August were considered ''summer birds'' and birds tested from 13 January to 3 March were considered ''winter birds.'' After testing, birds were banded with U.S. Fish and Wildlife Service aluminum bands (Master permit # 22934) and released at the site of capture. Thus, no birds were used in more than one trial.

LABORATORY METABOLISM MEASUREMENTS

Birds were allowed to feed prior to active-phase metabolic tests but were not allowed to feed for at least 4 hr prior to rest-phase measurements. Metabolic tests were conducted during the daytime (active phase) and nighttime (rest phase). We measured the metabolic rate of House Sparrows by measuring their oxygen consumption ($\dot{V}O_2$) at stable air temperatures between −12°C and 15.5°C in summer and between −12°C and 17.5°C in winter. Birds were placed in 1-L glass metabolic chambers, which were equipped with a wire platform affixed over a container of mineral oil. Each chamber was located inside a Hotpack incubator (model 352602, Philadelphia, Pennsylvania), in which temperature could be controlled within 0.1°C. Each metabolic test lasted a total of 90 min. Birds were permitted 1 hr to acclimate to chamber conditions before taking measurements. After the 1-hr equilibration at the test temperature, a 10-min period of mean VO_2 during the last 30 min was used as the metabolic rate for the trial. Prior to metabolic measurements, chambers were checked for leaks by momentarily monitoring efflux gas flow rates with a rotameter. Leaks would have been evident as a marked decrease in flow rate from the upstream mass flow meter; no leaks were detected in our chambers.

An open-circuit respirometry system was utilized to measure metabolic rates and $\dot{V}O_2$ was recorded with a Sable Systems (Las Vegas, Nevada) FC-1B oxygen analyzer. A Sable Systems multiplexer (model TR-RM4) allowed switching between two channels and the testing of two birds at a time. Airflow through each chamber was maintained continuously even if the chamber was not selected by the multiplexer. Measurements were recorded every other 15 min for each channel during the 90-min experiments. Measurements were screened for activity by examining the ventilation records for abrupt

changes and by a motion activity detection system (MAD-1, Sable Systems) in about half of the trials. Chamber temperature was monitored using a Sable Systems thermocouple thermometer (TC-1000). An Omega mass flow controller (model FMA-A2048, Stamford, Connecticut) was employed to sustain flow rates of dry, CO_2-free air at 488–520 mL min^{-1} and calibrated to $\pm1\%$ accuracy by a soap bubble meter. These rates provided changes in oxygen content between influx and efflux gas of ~0.4%–0.8%, and maintained oxygen content of efflux gas above 20.1%. The oxygen analyzer was referenced against incurrent gas before and after each measurement period. Oxygen consumption was calculated as steady state $\dot{V}O_2$ and corrected for standard temperature and pressure (Depocas and Hart 1957, Hill 1972, Eq. 2). At the end of each run, body temperature (T_b) was taken within 30 sec by inserting a 30-gauge copper-constantan thermocouple into the birds' cloaca at a depth where further insertion did not alter the reading.

VENTILATORY MEASUREMENTS

Ventilation was also measured during metabolic tests by whole-body plethysmography (Malan 1973, Bucher 1981). We allowed each bird a 1-hr equilibration period in the chamber before ventilation was recorded. Pressure differences in the chamber due to the warming and wetting of the inspired air were recorded every 0.05 sec on a differential pressure transducer PT-100B (Sable Systems). Continuous measurements of the dew point ($\pm0.1°C$) in the metabolic chamber were recorded by a Sable Systems Rh-100 humidity meter in order to calculate tidal volume. A uniform flow of air was maintained to the chambers at all times. At the end of each run a known volume of air (1 mL) was injected into the chamber (10 to 15 times) for calibration purposes. We compared calibration deflections to ventilation deflections to compute tidal volume (V_T) according to Malan (1973, Eq. 6).

Whole-body plethysmography has been widely used because it allows noninvasive measurement of ventilation in unrestrained animals. Mortola and Frappell (1998) provided a good overview of whole-body plethysmography including several potential sources of error. For open-flow systems such as was used in this study, one important potential source of error is time-decay of the pressure signal. This is usually accounted for by matching the deflection kinet-

ics during calibration injections with those during ventilation (Malan 1973, Bucher 1981). However, this may not completely compensate for pressure decay because ventilatory effort can vary from breath to breath (Szewczak and Powell 2003). Szewczak and Powell (2003) suggested a technique to generate a pressure-decay compensated signal by characterizing the time rate of pressure-decay in an open-flow system. Before applying Equation 6 (Malan 1973) to our data to compute tidal volume, we followed Szewczak and Powell's (2003) suggestions and characterized the pressure-decay of our plethysmography system. We did not find a significant pressure vs. frequency response in our system and thus, did not employ this type of correction factor (Arens and Cooper 2005).

Tidal volume (V_T) and respiratory frequency (f) were measured simultaneously with oxygen consumption measurements. The periodicity of ventilation deflections was used to calculate f. Minute volume ($\dot{V}_I$) was calculated as:

$$\dot{V}_I = f \times V_T. \qquad (1)$$

Oxygen extraction efficiency (EO_2) was calculated using the following equation:

$$EO_2 = \dot{V}O_2 \, (FEO_2 \times \dot{V}_I)^{-1}, \qquad (2)$$

where FEO_2 is the fractional oxygen concentration of effluent air from the metabolic chamber.

STATISTICAL ANALYSES

Values are presented as mean $\pm$ SD. All ventilatory volumes are given in mL body temperature pressure saturated (BTPS). Standard temperature and pressure dry volumes were used to calculate oxygen extraction efficiency. Since body mass did not significantly differ between season and sex, all data are reported on a whole-organism basis. This may be more informative when comparing seasonal data (Dawson and Smith 1986, Swanson 1991) and it also avoids potential confounding effects of using mass-specific values, which are ratios (Packard and Boardman 1999). Regression lines were fit by the method of least squares and the slopes and intercepts were compared by ANCOVA. The effect of ambient temperature on body temperature (T_b), metabolic rate, and thermal conductance (C), was analyzed by two-way analysis of variance (ANOVA). The effect of $\dot{V}O_2$ on breathing frequency, tidal volume, minute volume, and oxygen extraction efficiency was also analyzed by

two-way ANOVA. Tukey's tests or *t*-tests were used for pairwise comparisons if significant effects were detected. Oxygen extraction efficiency data were arcsine transformed for ANOVAs. All statistics were computed using SPSS 8.0 (SPSS, 2000). Significance was reported when *P* < 0.05.

RESULTS

BODY MASS

Analysis of body mass revealed no significant differences due to season and time of day ($F_{3,70}$ = 0.5, *P* = 0.66) or gender ($F_{1,70}$ = 0.6, *P* = 0.43). Mean body masses of sparrows for each season and time of day were: summer daytime, 26.8 ± 1.2 g (*n* = 16); summer nighttime, 26.7 ± 2.2 g (*n* = 17); winter daytime, 27.0 ± 2.1 g (*n* = 18); and winter nighttime, 27.4 ± 1.9 g (*n* = 20).

METABOLIC RATE, THERMAL CONDUCTANCE, AND BODY TEMPERATURE

The relationship between $\dot{V}O_2$ (mL min^{-1}) and ambient temperature (Fig. 1) below the thermoneutral zone was best described by the following equations:

summer nighttime:

$$\dot{V}O_2 = 2.22 - 0.079T_a \tag{3}$$

(*n* = 17, r^2 = 0.65, *P* < 0.001);

summer daytime:

$$\dot{V}O_2 = 2.86 - 0.095T_a \tag{4}$$

(*n* = 16, r^2 = 0.51, *P* < 0.01);

winter nighttime:

$$\dot{V}O_2 = 2.11 - 0.026T_a \tag{5}$$

(*n* = 20, r^2 = 0.41, *P* < 0.01);

and winter daytime:

$$\dot{V}O_2 = 2.78 - 0.035T_a \tag{6}$$

(*n* = 18, r^2 = 0.31, *P* < 0.02).

The regression equations relating $\dot{V}O_2$ to T_a for summer night compared to winter night were significantly different in slopes ($F_{1,36}$ = 11.8, *P* < 0.01) but not in intercepts ($F_{1,37}$ = 3.4, *P* = 0.08). The regression equations for summer day and winter day were significantly different in slopes ($F_{1,30}$ = 4.6, *P* = 0.04) but not in intercepts ($F_{1,31}$ = 2.5, *P* = 0.13). The lower critical
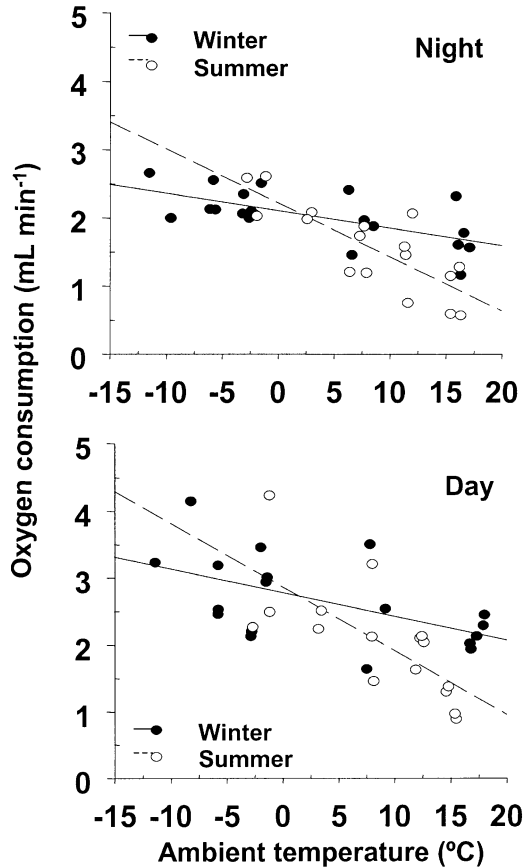

FIGURE 1. Relationship between oxygen consumption ($\dot{V}O_2$) and ambient temperature (T_a) below the lower critical temperature for summer and winter-acclimatized House Sparrows during nighttime and daytime.

temperature (T_{lc}) was determined as the intersection of the regression line below thermoneutrality with a horizontal line through the mean $\dot{V}O_2$ at 30°C (Arens 2004). The T_{lc} was 15.7°C for birds tested during summer nighttime and 19.2°C for birds tested during winter nighttime.

The slope of the line relating metabolic rate to ambient temperature is equivalent to the thermal conductance only if the curve extrapolates to body temperature at zero metabolism. Our equations for summer and winter birds do not conform to this Newtonian cooling model, where the regression lines should intersect zero metabolism at a point in the normal body temperature range for birds of ~38°C to 41°C. The data for summer and winter sparrows below the thermoneutral zone, in which the regression line
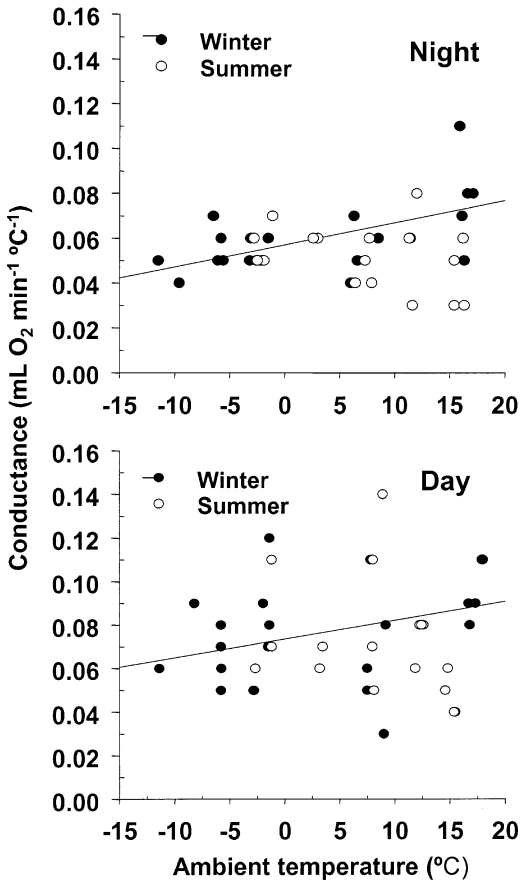
FIGURE 2. Relationship between thermal conductance (C) and ambient temperature (T_a) below the lower critical temperature for summer and winter-acclimatized House Sparrows during nighttime and daytime.

passes through a point at zero metabolism associated with body temperature (T_b) yield a T_b of 28.1°C in summer and 81.2°C in winter. This body temperature value is considerably lower in summer and higher in winter relative to the normal body temperature range. Thus, thermal conductance was calculated as $C = \dot{V}O_2 (T_b - T_a)^{-1}$ (Scholander et al. 1950). Mean thermal conductance in sparrows was 0.07 ± 0.02 mL O_2 min^{-1} °C^{-1} ($n = 16$) during summer daytime and 0.05 ± 0.02 mL O_2 min^{-1} °C^{-1} ($n = 17$) during nighttime. In winter, thermal conductance was 0.08 ± 0.02 mL O_2 min^{-1} °C^{-1} ($n = 18$) during daytime and 0.06 ± 0.02 mL O_2 min^{-1} °C^{-1} ($n = 20$) during nighttime (Fig. 2). Thermal conductance was significantly different among groups ($F_{3,63} = 7.4$, $P < 0.001$). Thermal conductance

was significantly lower at nighttime compared to daytime for both summer (Tukey's test, $P = 0.04$) and winter (Tukey's test, $P < 0.01$). Conductance was significantly different between genders ($F_{1,63} = 5.9$, $P = 0.02$). In winter, conductance was significantly higher in male sparrows compared to females during the daytime ($t_{1,18} = 5.1$, $P < 0.001$). The winter analyses below the lower critical temperature (T_{lc}) yielded the following relationships between thermal conductance (C) and ambient temperature (T_a).

Winter nighttime sparrows:

$$C = 0.0575 + 0.0011T_a \qquad (7)$$

($n = 20$, $r^2 = 0.50$, $P < 0.01$);

Winter daytime sparrows:

$$C = 0.0734 + 0.0013T_a \qquad (8)$$

($n = 18$, $r^2 = 0.43$, $P < 0.01$).

In summer, mean body temperature was 38.5 ± 0.8°C during daytime ($n = 16$) and 37.9 ± 0.6°C ($n = 17$) during nighttime tests. Winter T_b was 39.2 ± 1.1°C ($n = 18$) for daytime birds and 38.0 ± 1.0°C ($n = 20$) for nighttime birds. Body temperature was significantly different among groups ($F_{3,63} = 7.8$, $P < 0.001$). The difference between daytime and nighttime birds in winter was the only significant pairwise comparison (Tukey's test, $P < 0.001$). There were no significant gender differences in T_b ($F_{1,63} = 1.6$, $P = 0.21$).

VENTILATORY RESPONSE TO METABOLISM

Ventilatory responses to varying $\dot{V}O_2$ are shown in Figure 3. The regression equations showing significant relationships between ventilatory parameters and $\dot{V}O_2$ are shown in Table 1. Since tidal volume and frequency were not linearly related to $\dot{V}O_2$ under all conditions, ANCOVA could not be performed for all seasonal or diurnal comparisons. Regression equations for summer and winter nighttime minute volume were not significantly different in slopes ($F_{1,33} = 0.1$, $P = 0.78$) but intercepts were significantly different ($F_{1,34} = 7.5$, $P = 0.01$). For seasonal comparisons of daytime tidal volume below thermoneutrality, the slopes were not significantly different ($F_{1,30} = 0.1$, $P = 0.71$) and the intercepts were not significantly different ($F_{1,31} = 0.2$, $P = 0.70$). For seasonal comparisons of daytime minute volume below thermoneutrality,
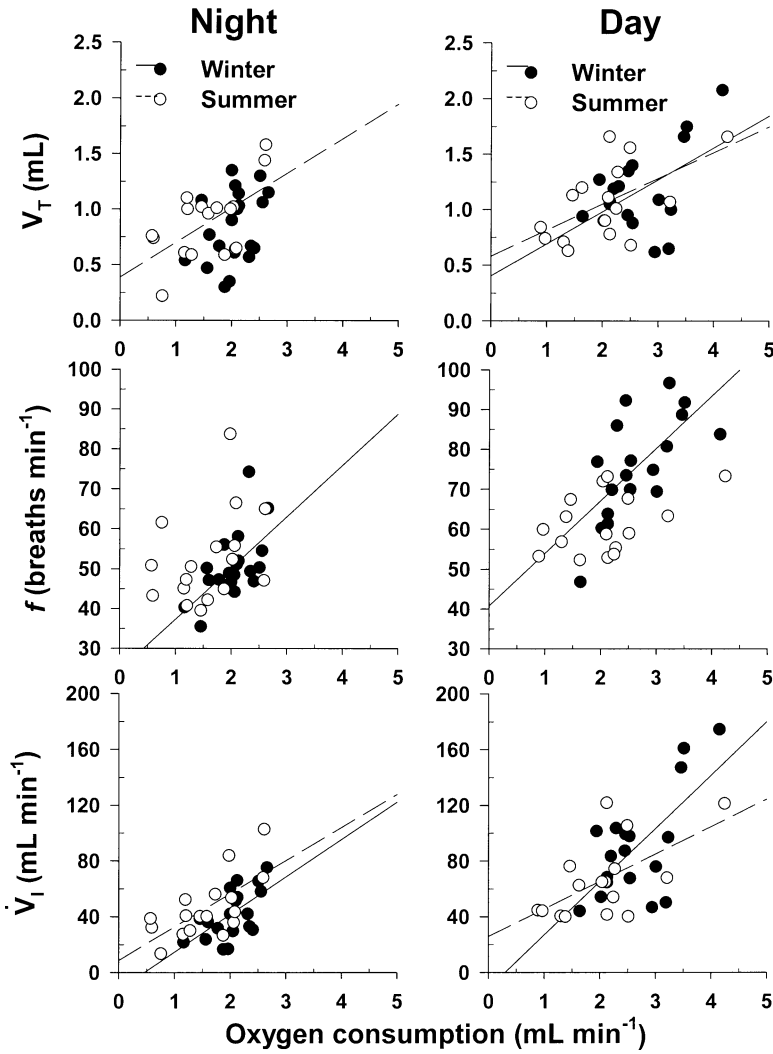
FIGURE 3. Relationships between tidal volume (V_T), respiratory frequency (f), and minute volume ($\dot{V}_I$) and oxygen consumption ($\dot{V}O_2$) for summer and winter-acclimatized House Sparrows during nighttime and daytime. Only lines for significant regression equations are shown.

TABLE 1. Relationship of breathing frequency (f, breaths min^{-1}), tidal volume (V_T, mL $breath^{-1}$), and minute volume ($\dot{V}_I$ mL min^{-1}) to oxygen consumption ($\dot{V}O_2$, mL min^{-1}) below the lower critical temperature for House Sparrows from Wisconsin. Only significant regression relationships are shown.

Season and time	n	Regression equation	r^2	P
Summer daytime	16	$V_T = 0.58 + 0.23\ \dot{V}O_2$	0.33	0.02
		$\dot{V}_I = 25.91 + 19.72\ \dot{V}O_2$	0.36	0.01
Summer nighttime	17	$V_T = 0.39 + 0.31\ \dot{V}O_2$	0.35	0.01
		$\dot{V}_I = 8.68 + 23.82\ \dot{V}O_2$	0.46	<0.01
Winter daytime	18	$f = 40.79 + 13.17\ \dot{V}O_2$	0.45	<0.01
		$V_T = 0.40 + 0.29\ \dot{V}O_2$	0.26	0.03
		$\dot{V}_I = -11.77 + 38.40\ \dot{V}O_2$	0.44	<0.01
Winter nighttime	20	$f = 24.45 + 8.58\ \dot{V}O_2$	0.35	<0.01
		$\dot{V}_I = -12.43 + 26.92\ \dot{V}O_2$	0.36	<0.01

TABLE 2.   Time of day comparisons of breathing frequency (f, breaths min^{-1}), tidal volume (V_T, mL breath^{-1}), and minute volume ($\dot{V}_I$ mL min^{-1}) to oxygen consumption ($\dot{V}O_2$, mL min^{-1}) below the lower critical temperature using analysis of covariance (ANCOVA) for House Sparrows from Wisconsin.

Variable	Slope			Intercept		
	F	df	P	F	df	P
Summer day compared to summer night						
V_T	0.5	1, 28	0.49	0.1	1, 29	0.77
$\dot{V}_I$	0.3	1, 28	0.59	1.2	1, 29	0.27
Winter day compared to winter night						
f	0.003	1, 34	0.10	28.6	1, 35	<0.01
$\dot{V}_I$	0.5	1, 34	0.05	9.2	1, 35	<0.01

the slopes were not significantly different ($F_{1,30} = 2.1$, $P = 0.15$) and the intercepts were not significantly different ($F_{1,31} = 0.5$, $P = 0.47$).

For within season daily comparisons, breathing frequency in response to increasing $\dot{V}O_2$ was significantly greater in the winter daytime compared to winter nighttime (Table 2). Mean breathing frequency in summer nighttime was 52.5 ± 11.5 breaths min^{-1} which was significantly lower than mean breathing frequency in summer daytime sparrows (61.4 ± 7.4 breaths min^{-1}, $t_{31} = -2.6$, $P = 0.01$). There were no significant differences in tidal volume in summer daytime and nighttime birds. The change in minute volume with changing $\dot{V}O_2$ was significantly different between daytime and nighttime in winter but not summer (Table 2).

There were no significant gender differences in oxygen extraction efficiency ($F_{1,70} = 1.2$, $P = 0.28$). There were significant differences in oxygen extraction efficiency due to the different test conditions ($F_{3,70} = 7.3$, $P < 0.001$, Fig. 4). Oxygen extraction efficiency was significantly higher in winter birds at night (0.30 ± 0.12, $n = 20$) compared to winter daytime birds (0.18 ± 0.07, $n = 18$, Tukey's test, $P < 0.01$), summer daytime birds (0.18 ± 0.07, $n = 16$, Tukey's test, $P < 0.01$), and summer nighttime birds (0.21 ± 0.08, $n = 17$, Tukey's test, $P = 0.01$).

DISCUSSION

METABOLIC RATE, THERMAL CONDUCTANCE, AND BODY TEMPERATURE

The metabolic response to low ambient temperature for House Sparrows varied significantly with the time of day and the season. Winter birds
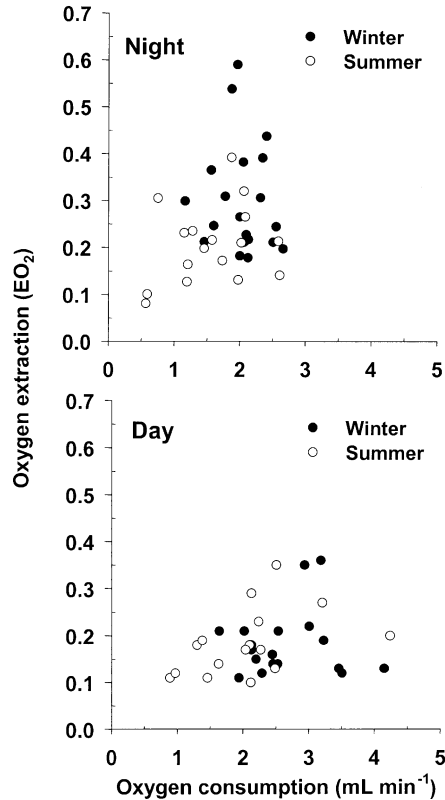

FIGURE 4.   Relationship between oxygen extraction (EO$_2$) and oxygen consumption ($\dot{V}O_2$) for summer and winter-acclimatized House Sparrows during nighttime and daytime.

have higher metabolic rates at warmer temperatures than summer birds, but have lower metabolic rates at colder temperatures compared to summer birds. Since the slopes for the regression equations for day and night relating $\dot{V}O_2$ to ambient temperature are significantly different, comparisons of elevations may not be statistically appropriate. White (2003) recommended the Johnson-Neyman technique to identify regions of nonsignificance. We applied this technique to daytime and nighttime regressions in summer and winter. No regions of nonsignificance were found for elevations of the daytime regression equations. At nighttime, we found that for ambient temperatures between $-11.3°C$ and $7.3°C$ the elevations of the regression equations were not significantly different. Thus, for ambient temperatures below $-11.3°C$, summer birds at night had higher metabolic rates than winter birds at night, and for ambient tempera-

tures above 7.3°C, winter birds at night had higher metabolic rates than summer birds at night. This data suggests that House Sparrows may have metabolic responses to ambient temperature that differ from predicted by the Scholander-Irving model. It also implies that winter birds may be modifying thermal conductance at low ambient temperature to save on metabolic costs of thermoregulation compared to summer. Regression of conductance versus ambient temperature does show a significant relationship only in winter birds.

In diurnal comparisons, the metabolic response to low ambient temperature appears to be higher in daytime birds compared to nighttime. This is probably due to the elevated state of alertness and activity in daytime birds relative to nighttime. In addition, specific dynamic action may also contribute to the elevated metabolism in birds at daytime compared to nighttime. Daytime birds that have food in their gut experience an increase in metabolic activity associated with digestion and assimilation of a meal (Dawson and O'Connor 1996). However, specific dynamic action may instead substitute for thermostatic heat produced by shivering (Chappell et al. 1997).

Lower critical temperature was 15.7°C for House Sparrows tested during summer nighttime and 19.2°C for sparrows tested during winter nighttime. The summer lower critical temperature value for sparrows was 5% lower than allometrically predicted values and the winter lower critical temperature value was 16% higher than predicted values (Weathers and van Riper 1982). The decreased lower critical temperature in summer compared to winter sparrows and the lack of seasonal variation in thermal conductance suggests that insulatory changes are not a prominent part of seasonal acclimatization in House Sparrows. However, the slopes for the data from summer and winter birds do not conform to the Newtonian cooling principle. Thus, the lower critical temperature may be artificially high especially in winter. The slope for the summer data conforms more closely to Newtonian cooling and suggests that thermal conductance is not markedly modified at lower ambient temperatures. The slope for the winter data does not conform closely, which implies that winter birds have the ability to modify thermal conductance at lower ambient temperatures. This type of pattern has been seen in other passerines such as Dark-eyed Juncos, cardueline finches, and Common Redpolls (West 1972b, Dawson and Carey 1976, Swanson 1991). This suggests that winter House Sparrows are more capable of modifying thermal conductance below the lower critical temperature than their summer counterparts (Prinzinger et al. 1992) and that this may be a component of winter acclimatization in House Sparrows.

In summer and winter birds at nighttime, thermal conductance was significantly lower at low ambient temperature compared to daytime birds. This indicates that House Sparrows are better insulated at nighttime compared to daytime. The variation in thermal conductance may be due to increased vasoconstriction and postural changes, including feather ptiloerection, at nighttime compared to daytime. The higher metabolism and activity in daytime birds compared to nighttime birds, may promote blood flow to peripheral tissues, which increases the dissipation of heat. Conversely, when metabolism and activity are lower at night compared to the day, heat can be conserved by minimizing blood flow to peripheral tissues through vasoconstriction (Aschoff and Pohl 1970). The increased insulation at nighttime also agrees with behavioral observation of birds altering their posture in order to maximize feather ptiloerection at nighttime and that nighttime measurements are a better indication of the maximum degree of plumage insulation (Hohtola et al. 1980, Aschoff 1981). For winter birds at night, increased oxygen extraction efficiency may also contribute to a reduction in thermal conductance. With oxygen extraction efficiency increased, minute volume can remain more constant and thus, birds don't have to heat up as much air while breathing, thus reducing their thermal conductance. For example, at 0°C minute volume would be 17 mL min^{-1} lower at nighttime in winter compared to summer.

There was no apparent seasonal variation in body temperature of House Sparrows at nighttime or daytime. The only significant variation indicated a higher body temperature in winter birds during the daytime compared to winter birds during nighttime. Summer birds showed a similar increase in body temperature during daytime tests compared to nighttime, but the change was not significant. The elevated body temperature in daytime birds may be due to their elevated state of vigilance and activity compared to

nighttime. Some birds used hypothermia at nighttime tests in winter and summer but the lowest body temperature recorded was 36.5°C, which indicates only a mild hypothermia.

VENTILATORY RESPONSE TO METABOLISM

House Sparrows showed a wide range of ventilatory responses to increasing oxygen consumption below the lower critical temperature depending upon the time of day and the season. In diurnal comparisons for winter birds, there were significant differences in breathing frequency, minute volume, and oxygen extraction efficiency. Winter daytime birds on average had a 67% higher breathing frequency, a 64% higher minute volume, and a 60% lower oxygen extraction efficiency compared to nighttime winter birds. The two ventilatory parameters that varied significantly during nighttime between winter and summer birds were minute volume and oxygen extraction efficiency. Winter birds showed a decrease in minute volume and a 43% increase in oxygen extraction efficiency compared to summer birds at nighttime. Thus, metabolism below the lower critical temperature in winter compared to summer, appears to be supported by increased in oxygen extraction efficiency at nighttime. The increase in oxygen extraction efficiency at night in winter appears to be a component of winter-acclimatization in House Sparrows tested at ecologically relevant colder ambient temperatures. Winter sparrows use a greater percentage of oxygen per breath to support higher oxygen demands due to elevated shivering thermogenesis at low ambient temperature compared to summer.

In summer, House Sparrows rely more on changing tidal volume than breathing frequency to increase minute volume needed to accommodate increasing oxygen consumption demands. This is similar to most birds studied thus far (Morgan et al. 1992). However, winter sparrows rely on changing breathing frequency at night and both changing breathing frequency and tidal volume in the daytime to increase minute volume to support increasing metabolic rates. In addition, oxygen extraction efficiency appears to be important for ventilatory accommodation in winter sparrows at night.

These data from House Sparrows demonstrate that time of day and season may be important considerations when interpreting ventilation responses to ambient temperature below the lower critical temperature in birds. For birds that undergo seasonal acclimatization, the potential differences in respiration must be accounted for with testing at both seasons. In addition, the measurement and comparison of daytime and nighttime ventilation should provide a more complete interpretation of the respiratory function in birds.

LITERATURE CITED

ARENS, J. R. 2004. Metabolic and ventilatory adjustments to cold stress in seasonally acclimatized House Sparrows (*Passer domesticus*). M.S. thesis, University of Wisconsin Oshkosh, Oshkosh, WI.

ARENS, J. R., AND S. J. COOPER. 2005. Metabolic and ventilatory acclimatization to cold stress in House Sparrows (*Passer domesticus*). Physiological and Biochemical Zoology 78, in press.

ASCHOFF, J., AND H. POHL. 1970. Rhythmic variations in energy metabolism. Federation Proceedings 29: 1541–1552.

ASCHOFF, J. 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. Comparative Biochemistry and Physiology A 69:611–619.

BARNETT, L. B. 1970. Seasonal changes in temperature acclimatization of the House Sparrow, *Passer domesticus*. Comparative Biochemistry and Physiology 33:559–578.

BECH, C., AND S. C. NICOL. 1999. Thermoregulation and ventilation in the Tawny Frogmouth, *Podargus strigoides*: a low-metabolic avian species. Australian Journal of Zoology 47:143–153.

BECH, C., K. JOHANSEN, R. BRENT, AND S. NICOL. 1984. Ventilatory and circulatory changes during cold exposure in the Pekin Duck *Anas platyrhynchos*. Respiration Physiology 57:103–112.

BRENT, R., J. G. RASMUSSEN, C. BECH, AND S. MARTINI. 1983. Temperature dependence of ventilation and O_2-extraction in the kittiwake, *Rissa tridactyla*. Experientia 39:1092–1093.

BRENT, R., P. F. PEDERSEN, C. BECH, AND K. JOHANSEN. 1984. Lung ventilation and temperature regulation in the European Coot (*Fulica atra*). Physiological Zoology 57:19–25.

BUCHER, T. L. 1981. Oxygen consumption, ventilation and respiratory heat loss in a parrot (*Bolborhynchus lineola*) in relation to ambient temperature. Journal of Comparative Physiology B 142:479–488.

BUCHER, T. L., AND K. R. MORGAN. 1989. The effect of ambient temperature on the relationship between ventilation and metabolism in a small parrot (*Agapornis roseicollis*). Journal of Comparative Physiology B 159:561–567.

CHAPPELL, M. A., AND T. L. BUCHER. 1987. Effects of temperature and altitude on ventilation and gas exchange in Chukars (*Alectoris chukar*). Journal of Comparative Physiology B 157:129–136.

CHAPPELL, M. A., AND T. J. DAWSON. 1994. Ventilatory accommodation of changing oxygen consumption in dasyurid marsupials. Physiological Zoology 67: 418–437.

CHAPPELL, M. A., G. C. BACHMAN, AND K. A. HAMMOND. 1997. The heat increment of feeding in House Wren chicks: magnitude, duration, and substitution for thermostatic costs. Journal of Comparative Physiology B 167:313–318.

CLEMENS, D. T. 1988. Ventilation and oxygen consumption in Rosy Finches and House Finches at sea level and high altitude. Journal of Comparative Physiology B 158:57–66.

COOPER, S. J. 1998. The role of cold acclimatization on the biogeography of the Mountain Chickadee (*Parus gambeli*) and the Juniper Titmouse (*Parus ridgwayi*). Ph.D. dissertation, Utah State University, Logan, UT.

DAWSON, W. R., AND C. CAREY. 1976. Seasonal acclimatization to temperature in cardueline finches: I. Insulative and metabolic adjustments. Journal of Comparative Physiology 112:317–333.

DAWSON, W. R., AND R. L. MARSH. 1989. Seasonal acclimatization to cold and season in birds, p. 83–94. *In* C. Bech and R. E. Reinertsen [EDS.], Physiology of cold adaptation in birds. Plenum Press, New York.

DAWSON, W. R., AND T. P. O'CONNOR. 1996. Energetic features of avian thermoregulatory response, p. 85–124. *In* C. Carey [ED.], Avian energetics and nutritional ecology. Chapman & Hall, New York.

DAWSON, W. R., AND B. K. SMITH. 1986. Metabolic acclimatization in the American Goldfinch (*Carduelis tristis*), p. 427–434. *In* H. C. Heller, X. J. Musacchia, and L. C. H. Wang [EDS.], Living in the cold: physiological and biochemical adaptations. Elsevier, New York.

DEPOCAS, F., AND J. S. HART. 1957. Use of the Pauling oxygen analyzer for measurements of oxygen consumption of animals in open-circuit respirometry and in a shortlag, closed-circuit apparatus. Journal of Applied Physiology 10:388–392.

FEIST, D. D., AND R. G. WHITE. 1989. Terrestrial mammals in cold, p. 327–360. *In* L. C. H. Wang [ED.], Advances in comparative and environmental physiology. Springer-Verlag, Berlin, Germany.

HELMS, C. W., AND W. H. DRURY JR. 1960. Winter and migratory weight and fat field studies on some North American buntings. Bird-Banding 31:1–40.

HILL, R. W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. Journal of Applied Physiology 33:261–263.

HOHTOLA, E., H. RINTÄMKI, AND R. HISSA. 1980. Shivering and ptiloerection as complementary cold defense responses in the pigeon during sleep and wakefulness. Journal of Comparative Physiology B 136:77–81.

IRVING, L., J. KROG, AND M. MONSON. 1955. The metabolism of some Alaskan animals in winter and summer. Physiological Zoology 6:667–680.

KAISER, T. J., AND T. L. BUCHER. 1985. The consequences of reverse sexual size dimorphism for oxygen consumption, ventilation, and water loss in relation to ambient temperature in the Prairie Falcon, *Falco mexicanus*. Physiological Zoology 58: 748–758.

KENDEIGH, S. C. 1976. Latitudinal trends in the metabolic adjustments of the House Sparrow. Ecology 57:509–519.

LOWTHER, P. E., AND C. L. CINK. 1992. House Sparrow (*Passer domesticus*). *In* A. Poole, P. Stettenheim, and F. Gill [EDS.], The birds of North America, No. 12. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

MALAN, A. 1973. Ventilation measured by body plethysmography in hibernating mammals and in poikilotherms. Respiratory Physiology 11:152–166.

MARSH, R. L., AND W. R. DAWSON. 1989a. Avian adjustments to cold, p. 205–253. *In* L. C. H. Wang [ED.], Advances in comparative and environmental physiology. Springer, Berlin, Germany.

MARSH, R. L., AND W. R. DAWSON. 1989b. Energy substrates and metabolic acclimatization in small birds, p. 105–114. *In* C. Bech and R. E. Reinertsen [EDS.], Physiology of cold adaptation in birds. Plenum Press, New York.

METCALFE, N. B., AND S. C. URE. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. Proceedings of the Royal Society of London Series B 261:395.

MIDDLETON, A. L. 1978. Seasonal changes in plumage structure and body composition of the American Goldfinch, *Carduelis tristis*. Canadian Field-Naturalist 100:545–549.

MORGAN, K. R., M. A. CHAPPELL, AND T. L. BUCHER. 1992. Ventilatory oxygen extraction in relation to ambient temperature in four Antarctic seabirds. Physiological Zoology 65:1092–1113.

MORTOLA, J. P., AND P. B. FRAPPELL. 1998. On the barometric method for measurements of ventilation, and its use in small animals. Canadian Journal of Physiology and Pharmacology 76:937–944.

NOVOA, F. F., F. BOZINOVIC, AND M. ROSENMANN. 1994. Seasonal changes of thermal conductance in *Zonotrichia capensis* (Emberizidae), from central Chile: the role of plumage. Comparative Biochemistry and Physiology A 107:297–300.

PACKARD, G. C., AND T. J. BOARDMAN. 1999. The use of percentages and size-specific indices to normalize data for variation in body size: wasted time, wasted effort? Comparative Biochemistry and Physiology A 122:37–44.

PALMER, R. S. 1972. Patterns of molting, p. 65–102. *In* D. S. Farner and J. R. King [EDS.], Avian biology. Academic Press, London, UK.

PIIPER, J., AND P. SCHEID. 1975. Gas transport efficacy of gills, lungs and skin: theory and experimental data. Respiratory Physiology 23:209–221.

PRINZINGER, R., T. SCHÄFER, AND K. L. SCHUCHMANN. 1992. Energy metabolism, respiratory quotient, and breathing parameters in two convergent small bird species: the Fork-tailed Sunbird *Aethopyga christinae* (Nectariniidae) and the Chilean Hummingbird *Sephanoides sephanoides* (Trochilidae). Journal of Thermal Biology 17:71–79.

PYLE, P., S. N. G. HOWELL, D. F. DESANTE, P. YUNICK, AND M. GUSTAFSON. 1997. Identification guide to North American birds. Part 1. Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.

SCHLEUCHER, E., AND P. C. WITHERS. 1999. Re-evaluation of the allometry of wet thermal conductance for birds. Comparative Biochemistry and Physiology A 129:821–827.

SCHOLANDER, P. R., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950. Heat regulation in some arctic and tropical mammals and birds. Biology Bulletin 99:237–258.

SCHMIDT-NIELSON, K. 1997. Animal physiology. Cambridge University Press, Cambridge, UK.

SMITH, J. H., J. L. MEIER, C. LAMKE, P. J. G. NEILL, AND E. D. BOX. 1986. Microscopic and submicroscopic anatomy of the parabronchi, air sacs, and respiratory space of the Budgerigar (*Melopsittacus undulatus*). American Journal of Anatomy 177:221–242.

SWANSON, D. L. 1991 Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. Condor 93:538–545.

SWANSON, D. L. In press. Seasonal metabolic variation in birds: functional and mechanistic correlates. Current Ornithology.

SZEWCZAK, J. M., AND F. L. POWELL. 2003. Open-flow plethysmography with pressure-decay compensation. Respiratory Physiology and Neurobiology 134:57–67.

WARKENTIN, I. G., AND N. H. WEST. 1990. Impact of long-term captivity on basal metabolism in birds. Comparative Biochemistry and Physiology A 96: 379–381.

WEATHERS, W. W., AND C. VAN RIPER III. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: the Palila (*Psittirostra bailleui*) and the Laysan Finch (*Psittirostra cantans*). Auk 99:667–674.

WEST, G. C. 1972a. Seasonal differences in resting metabolic rate of Alaskan ptarmigan. Comparative Biochemistry and Physiology A 42:867–876.

WEST, G. C. 1972b. The effect of acclimation and acclimatization on the resting metabolic rate of the Common Redpoll. Comparative Biochemistry and Physiology A 43:293–310.

WHITE, C. R. 2003. Allometric analysis beyond heterogeneous regression slopes: use of the Johnson-Neyman technique in comparative biology. Physiological and Biochemical Zoology 76:135–140.

WITTER, M. S., AND I. C. CUTHILL. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society of London Series B 340:73–92.