# Metabolic and Ventilatory Acclimatization to Cold Stress in House Sparrows (*Passer domesticus*)

Jeremy R. Arens Sheldon J. Cooper\*

Department of Biology and Microbiology, University of Wisconsin, Oshkosh, Wisconsin 54901-8640

Accepted 9/7/2004; Electronically Published 5/18/2005

## ABSTRACT

Passerines that overwinter in temperate climates undergo seasonal acclimatization that is characterized by metabolic adjustments that may include increased basal metabolic rate (BMR) and cold-induced summit metabolism  $(M_{sum})$  in winter relative to summer. Metabolic changes must be supported by equivalent changes in oxygen transport. While much is known about the morphology of the avian respiratory system, little is known about respiratory function under extreme cold stress. We examined seasonal variation in BMR,  $M_{sum}$ , and ventilation in seasonally acclimatized house sparrows from Wisconsin. BMR and  $M_{sum}$  increased significantly in winter compared with summer. In winter, BMR increased 64%, and M<sub>sum</sub> increased 29% over summer values. The 64% increase in winter BMR is the highest recorded for birds. Metabolic expansibility  $(M_{sum})$ BMR) was 9.0 in summer and 6.9 in winter birds. The metabolic expansibility of 9.0 in summer is the highest yet recorded for birds. Ventilatory accommodation under helox cold stress was due to changes in breathing frequency (f), tidal volume, and oxygen extraction efficiency in both seasons. However, the only significant difference between summer and winter ventilation measures in helox cold stress was f. Mean f in helox cold stress for winter birds was 1.23 times summer values.

#### Introduction

Small, nonmigratory passerines that occupy cold temperate regions require prolonged high rates of energy expenditure for thermoregulation in winter. In winter, birds have decreased foraging times because of shorter days and may have lower food availability because of increased snow or ice cover. In addition, winter birds must fast longer during the rest phase compared with summer. The high thermoregulatory costs in small birds are exacerbated by their large surface area to volume ratios (Kleiber 1961). In addition, small birds are limited in plumage insulation since an increase in mass will reduce flight performance and may increase predation risks (Witter and Cuthill 1993; Metcalfe and Ure 1995). Small passerine birds acclimatize to winter conditions primarily through metabolic adjustments (reviews: Dawson and Marsh 1989; Marsh and Dawson 1989a, 1989b; Dawson and O'Connor 1996). These metabolic adjustments facilitate greater cold tolerance (Barnett 1970; Pohl and West 1973) and higher thermogenic endurance (Dawson et al. 1983; Swanson 1990; O'Connor 1995) in winter birds compared with summer. In addition, many winter birds that have enhanced cold tolerance under cold stress also show significant increases in summit metabolism ( $M_{sum}$ ; Dawson and Smith 1986; Swanson 1990; Cooper and Swanson 1994; Liknes and Swanson 1996; Cooper 2002). Increased  $M_{sum}$  is correlated with increased cold tolerance for several avian species. (Swanson 2001).

While the metabolic adjustments that passerines use to support thermogenesis under cold conditions have received a fair amount of attention (Marsh and Dawson 1989a, 1989b; Swanson 1990), relatively little is known about ventilatory adjustments to cold stress. Metabolic adjustments to cold stress require accommodations in oxygen  $(O_2)$  transport. The first step in the O<sub>2</sub> transport pathway is pulmonary ventilation. 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. Changes in breathing frequency (f), breath volume or tidal volume  $(V_{\rm T})$ , and the percentage of oxygen absorbed or oxygen extraction efficiency (Eo<sub>2</sub>) can vary to accommodate changes in metabolism or oxygen consumption  $(Vo_2)$ . Ventilatory accommodation to changing oxygen demands may be met through adjustments in one, all, or any combination of these variables (Chappell and Dawson 1994).

The majority of birds studied to date show significant increases in minute volume ( $\dot{V}_{I}[V_{T} \times f]$ ) in response to increasing  $\dot{V}o_{2}$  at temperatures below thermoneutrality. Birds seem to rely heavily on changing  $V_{T}$  more than f to increase  $\dot{V}_{I}$  (Morgan et al. 1992). Among birds in which the relation of Eo<sub>2</sub> to metabolic rate below thermoneutrality has been studied, parrots (Bucher 1981, 1985; 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 frog-

<sup>\*</sup> Corresponding author; e-mail: cooper@uwosh.edu.

Physiological and Biochemical Zoology 78(4):579–589. 2005. © 2005 by The University of Chicago. All rights reserved. 1522-2152/2005/7804-4065\$15.00

mouths (Bech and Nicol 1999) respond with increasing  $V_1$  while Eo<sub>2</sub> 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  $\dot{V}_{\rm I}$  and substantial increases in Eo2. Two small passerine birds studied by Clemens (1988), rosy finches and house finches, showed significant changes in  $V_{\rm T}$  that involved increases in both f and  $V_{\rm T}$  without changes in Eo<sub>2</sub>. In fact, house finches at low and high altitude and rosy finches at high altitude have decreasing Eo<sub>2</sub> with declining ambient temperature  $(T_a)$ . However, the only passerine bird studied under severe (helox) cold stress, the black-capped chickadee, increased Eo, to support metabolism (Cooper and Same 2000). Johansen and Bech (1983) have suggested that an increase in Eo<sub>2</sub> in response to cold may be an adaptation to reduce respiratory heat loss by reducing  $V_1$ . However, the number of passerine birds studied so far is insufficient to establish any possible patterns of ventilatory accommodation to increased oxygen demands.

In this study, we examined the seasonal metabolic and ventilatory acclimatization to cold stress in house sparrows (*Passer domesticus*). House sparrows are small, mostly nonmigratory passerine birds successfully introduced into North America in the 1850s. They are widely distributed in North America, ranging from Canada (including northern Manitoba) to southern Central America (Lowther and Cink 1992). The objective of this study was to examine the effects of cold stress on metabolism and ventilation in seasonally acclimatized house sparrows from Wisconsin. Specifically, we measured  $M_{sum}$ , BMR, and ventilation parameters (f,  $V_T$ ,  $\dot{V}_1$ , and Eo<sub>2</sub>) in house sparrows under thermoneutral and cold stress conditions.

## Material and Methods

## Birds

House sparrows (Passer domesticus) were captured by mist net before 1000 hours (CST) in Oshkosh, Winnebago County, Wisconsin, in summer and winter in 2002 and 2003. Birds were trapped under state (SCP.NER.131) and federal (MB003340-1) collecting permits. Upon capture, body mass was determined to the nearest 0.1 g using an Ohaus Scout II portable electronic balance. Fat was scored visually using a 0-5 scale (Helms and Drury 1960), and wing chord length, tarsus length, and tail length were recorded. Age was determined by skull ossifications and breeding characteristics (Pyle et al. 1997). Adult birds were then transported to the laboratory and housed in separate cages at room temperature (20°-25°C). Caged birds were allowed free access to food (millet and chick starter mash) and water for at least 2 h before metabolic tests. All BMR and  $M_{sum}$  tests were performed on the day of capture in order to avoid captivity effects on metabolic rate (Warkentin and West 1990). After metabolic tests, birds were banded with a U.S. Fish and Wildlife Service leg band and released at site of capture. Birds were

banded with federal banding permit 22934. Sparrows tested from May 28 to August 6 were designated summer birds, and birds tested from January 13 to March 3 were designated winter birds. The Institutional Animal Care and Use Committees protocol number was 26-000126-10-02-01.

#### Helox Cold Stress

A helox gas mixture of ~79% helium and ~21% oxygen was used to elicit maximum cold-induced thermogenesis or  $M_{sum}$ . The higher thermal conductivity of helox compared with air facilitates heat loss that allows  $M_{sum}$  to be measured at relatively moderate temperatures (Rosenmann and Morrison 1974). Despite the physical differences between helium and nitrogen, helox gas has not been shown to have an effect on respiratory variables in quietly resting animals (Brice and Welch 1983). In addition, the effect of helox gas on sugar gliders has been shown to be limited to an increase in heat loss below the lower critical temperature (Holloway and Geiser 2001). We measured Vo<sub>2</sub> in helox at 30°C in order to determine whether helox has a significant effect on respiratory variables. Sparrows in helox at 30°C were not within the thermoneutral zone; however, at a given  $\dot{V}o_2$ , ventilation was in close agreement in air and helox (appendix). Thus, we believe helox gas itself is not a factor that affects respiratory variables.

A sliding cold exposure technique was used to elicit  $M_{sum}$  in individual sparrows (Swanson et al. 1996). Sliding temperatures of 8°C, 5°C, and 2°C were used in summer and -9°C, -12°C, and -15°C in winter. Variable sliding temperature schemes were needed to trigger all birds to become hypothermic (indicated by a steady decline in Vo<sub>2</sub> over 3 min) at each season and at relatively similar times in the test periods. Cold stress tests were performed between 1100 hours and 1600 hours (CST). Birds were placed in 1-L glass metabolic chambers (equipped with a perch over a layer of mineral oil) located inside a Hotpack incubator (model 352602), in which temperature could be controlled within  $\pm 0.1^{\circ}$ C. Chamber temperature was continually monitored and recorded  $(\pm 0.1^{\circ}C)$  by a Sable Systems TC1000 thermocouple meter. Birds were weighed immediately before and after each test. We allowed 15 min of equilibration in helox at the initial temperature in the metabolic chamber, and then birds were exposed to each sliding temperature for 15 min. Individual trials lasted a total of 60 min or until a bird became hypothermic, in which case the bird was removed from the metabolic chamber and rewarmed. Upon removal from the metabolic chamber, body temperature  $(T_{\rm b})$  was recorded ( $\pm 0.1^{\circ}$ C) with a Cole-Parmer thermocouple thermometer and 30-gauge copper-constantan thermocouple.  $T_{\rm b}$  was taken within 30 s, and the thermocouple was inserted into the cloaca at a depth where further insertion did not alter the reading. All birds became hypothermic during the middle or lower sliding temperatures in summer and winter. A cloacal temperature of <37°C was considered hypothermic.

## Summit Metabolic Rate

Once a bird was placed in the metabolic chamber, Vo<sub>2</sub> (mL O<sub>2</sub> min<sup>-1</sup>) was measured during helox cold stress using opencircuit respirometry. Gas flow rates of dry, CO<sub>2</sub>-free helox between 1,138 and 1,148 mL min<sup>-1</sup>  $\pm$  1% were maintained upstream of the metabolic chamber by a Cole-Parmer precision rotameter calibrated with helox to  $\pm 1\%$  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%. Fractional concentration of oxygen in dry, CO<sub>2</sub>-free efflux gas was determined from a 100 mL min<sup>-1</sup> subsample using a Sable Systems FC-1B oxygen analyzer (Las Vegas, NV). Measurements of dry, CO<sub>2</sub>free efflux gas were recorded every 1 s on a computer using Datacan 5.0 software and a UI2 converter. The first 15 min of each record were omitted in order for efflux oxygen concentrations to stabilize. Oxygen consumption values were calculated as instantaneous rates (Bartholomew et al. 1981). M<sub>sum</sub> data were attained by averaging instantaneous Vo2 measurements over consecutive 10-min periods (Dawson and Smith 1986; Swanson 1990).  $M_{\rm sum}$  at a given test temperature was considered to be the highest 10-min mean Vo2. Vo2 data collected with Datacan 5.0 was imported into and analyzed by Warthog Systems LabAnalyst (Riverside, CA).

## Basal Metabolic Rate

Measurements of BMR were similar to procedures for  $M_{sum}$ measurements. However, air was used instead of helox, and two birds were tested at a time. A Sable Systems multiplexer (model TR-RM4) allowed switching between two metabolic chambers in which each chamber was recorded at 15-min intervals. Before BMR tests, birds were fasted for at least 4 h to assure postabsorptive conditions. Upon placement in the metabolic chamber, birds were allowed 1 full hour of equilibration in the chamber before 30 min of measurements were used. Before all metabolic measurements, the chambers were checked for leaks by momentarily monitoring efflux gas flow rates with a flow rotameter. Leaks would have been evident as a marked decrease in flow rate compared with the upstream mass flow meter. No leaks were detected in our chambers. Flow rates of dry, CO<sub>2</sub>-free air of 488–520 mL min<sup>-1</sup>  $\pm$  1% were maintained upstream of the metabolic chambers for all tests using an Omega mass flow controller (model FMA-A2048). The oxygen analyzer was referenced against incurrent gas before and after each measurement period. Chamber temperatures were maintained at  $30^{\circ} \pm 0.1^{\circ}$ C for BMR measurements, which is within the thermoneutral zone for house sparrows (Hudson and Kimzey 1966). BMR tests were completed from 2200 hours to 0300 hours (CST) in summer and from 2000 hours to 2400 hours (CST) in winter. BMR data are reported as 10-min averages from the last 30 min of a trial. Oxygen consumption was calculated as steady state  $\dot{V}o_2$  and corrected for STP (Hill 1972, eq. [2]).

## Ventilatory Measurements

Ventilation was measured using whole-body plethysmography in the open-circuit respiratory system (Malan 1973; Bucher 1981). A uniform flow of air was maintained to the chambers at all times. A differential pressure transducer PT-100B (Sable Systems) was used to record the pressure differences in the chamber due to warming and wetting of inspired air. Data were recorded every 0.05 s with a Sable Systems Datacan 5.0. For  $M_{\rm sum}$  tests, ventilation was recorded in 10-min increments at each of the sliding temperatures following a 15-min equilibration period. For BMR tests, birds were allowed 1 h in the chamber before respiratory parameters were recorded for 10 min. Continuous measurements of the dew point  $(\pm 0.1^{\circ}C)$  in the metabolic chamber were recorded by a Sable Systems Rh-100 humidity meter. A known volume of air (1 mL) was injected into the chamber (10-15 times) at the end of each run for calibration. Deflection kinetics during calibration injections were similar to those during ventilation. We compared calibration deflections with ventilation deflections to compute  $V_{\rm T}$ according to Malan (1973, eq. [6]).  $V_{\rm T}$  (mL min<sup>-1</sup>) and f  $(\min^{-1})$  were measured simultaneously with  $\dot{V}o_2$  measurements. The periodicity of ventilation deflections was used to calculate f. Eo<sub>2</sub> was calculated as Eo<sub>2</sub>% =  $\dot{V}o_2/(FEo_2 \times \dot{V}_1) \times$ 100, where  $FEo_2$  is the fractional oxygen concentration of excurrent air from the metabolic chamber. All ventilatory values were recorded in both BTPS and STPD.

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 that used in this study, one important potential source of error is time decay of the pressure signal. Typically, this is accounted for by matching the deflection kinetics during calibration injections with those during ventilation (Malan 1973; Bucher 1981). However, this does 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 decaycompensated signal by characterizing the time rate of pressure decay in an open-flow system. Before applying equation (6) of Malan (1973) to our data to compute  $V_{\rm T}$ , we followed Szewczak and Powell's (2003) suggestions and characterized the pressure decay of our plethysmography system. We did not find a significant pressure versus frequency response in our system and thus did not employ this type of correction factor (fig. A1).

Evaporative water loss (EWL) was calculated using dew point as EWL =  $FR(F_eH_2O - F_iH_2O)$  from Warthog Systems Lab Analyst (Riverside, CA). FR is the flow rate (mL min<sup>-1</sup>),  $F_eH_2O$  is the fractional excurrent water vapor density, and  $F_iH_2O$  is the fractional incurrent water vapor density. At  $T_a$ 's of 0°C and below, a small amount of frost formed on the chamber walls; thus, EWL may have been underestimated. In order to determine how much error this may have caused, we used equation (56) of Calder and King (1974) to compute evaporative heat loss from  $\dot{V}o_2$  and  $T_a$  (see Chappell and Souza 1988). We then calculated evaporative water loss by converting the evaporative heat loss to water loss assuming 2.43 J mg<sup>-1</sup> of water evaporated. In all cases, equation (56) of Calder and King (1974) yielded lower estimates of EWL than we determined using dew point. Thus, we report EWL values based on our dew point calculations.

#### Statistics

Values are presented as mean  $\pm$  SD. Before analysis, the data were analyzed for normality (Shapiro-Wilks test) and homogeneity (Levene's test). Morphometric, metabolic rate, body temperature ( $T_b$ ), ventilation, and EWL data were compared by two-way ANOVA using season and gender as independent variables. Student's *t*-tests were used for pairwise comparisons if significant effects were detected. All data are presented on a whole-organism basis because this may be more instructive when doing seasonal comparisons (Dawson and Smith 1986; Swanson 1991*a*), and it avoids confounding effects of ratios (Packard and Boardman 1999). All statistics were computed using SPSS 8.0 (SPSS, Chicago). Statistical significance was accepted at *P* < 0.05.

### Results

## **Morphometrics**

Analysis of at capture morphometric data by two-way ANOVA revealed significant seasonal and gender differences in wing chord. Visible furcular fat deposits were significantly higher in winter birds compared with summer birds (Table 1). There were no significant seasonal ( $F_{1,98} = 0.01$ , P = 0.91) or gender ( $F_{1,98} = 0.70$ , P = 0.41) differences in body mass.

## Cold Tolerance and Thermal Conductance

Birds were able to tolerate colder helox temperatures during winter tests compared with summer tests. All summer birds became hypothermic at temperatures ranging from 5°C to 2°C. For winter birds, hypothermia was not induced until temperatures were between  $-12^{\circ}$ C and  $-15^{\circ}$ C. Mean  $T_{\rm b}$  of birds after summer and winter  $M_{\rm sum}$  tests was significantly lower than after BMR tests in summer (n = 38, t = 8.77, P < 0.001) and winter (n = 34, t = 8.56, P < 0.001). In summer,  $T_{\rm b}$  averaged  $35.3^{\circ} \pm 1.1^{\circ}$ C after  $M_{\rm sum}$  and  $38.8^{\circ} \pm 1.4^{\circ}$ C after BMR tests. In winter, mean  $T_{\rm b}$  was  $35.1^{\circ} \pm 2.2^{\circ}$ C after winter  $M_{\rm sum}$  and  $40.0^{\circ} \pm 1.0^{\circ}$ C after winter BMR (Fig. 1).

The helox temperature in which  $M_{sum}$  was attained, termed

Table 1: Mean $(\pm SD)$ seasonal differences in morphological
characteristics of house sparrows at the time of capture

		Body Mass	Fat Score	Wing Chord				
Season	n	(g)	Furcula <sup>a</sup>	Abdomen	$(mm)^{b}$			
Summer:								
Male	21	$27.6~\pm~1.4$	$.43 \pm .6$	$.19 \pm .4$	76.9 ± 2.1			
Female	25	$28.2~\pm~2.3$	$.44 \pm .9$	$.16 \pm .4$	$76.2 \pm 2.0$			
Pooled	46	$27.9~\pm~1.9$	$.43 \pm .8$	$.17 \pm .4$	$76.5 \pm 2.0$			
Winter:	Winter:							
Male	27	$28.5~\pm~2.2$	$.89 \pm .8$	$.37 \pm .6$	79.0 ± 2.0			
Female	29	$27.3~\pm~1.6$	.93 ± .8	$.24 \pm .4$	$75.8 \pm 1.8$			
Pooled	56	$27.9~\pm~2.0$	$.91~\pm~.8$	$.30 \pm .5$	77.3 ± 2.5			

Note. n = sample size.

 $^{\rm a}$  Visible furcular fat deposits were significantly greater in winter compared with summer ( $F=9.32,\ P=0.003).$ 

 $^{\rm b}$  There were significant seasonal (F=4.68,~P=0.03) and gender (F=23.82,~P<0.001) differences in wing chord length.

the temperature at cold limit ( $T_{cl}$ ; Saarela et al. 1989), was also used as an indicator of cold tolerance. House sparrows showed significant seasonal variation in  $T_{cl}$  ( $F_{1,32} = 357.79$ , P < 0.001) but showed no significant gender differences ( $F_{1,32} = 2.79$ , P = 0.11; Fig. 2). Seasonal changes in thermal conductance might influence cold tolerance in birds. Thus, thermal conductance ( $C = M_{sum}/[T_b - T_a]$ ; Scholander et al. 1950) was calculated for individual birds. We used  $M_{sum}$  and  $T_b$  for each individual measured at each test temperature. C was significantly different between summer ( $0.29 \pm 0.04$  mL O<sub>2</sub> min<sup>-1</sup> °C<sup>-1</sup>, n = 16) house sparrows ( $F_{1,27} = 14.59$ , P = 0.001). However, there were no significant gender differences in C ( $F_{1,27} = 0.20$ , P = 0.66)

#### Summit and Basal Metabolic Rates

In winter birds,  $M_{sum}$  was significantly greater than in summer  $(F_{1,30} = 0.37, P < 0.001)$ , but there were no significant gender differences  $(F_{1,30} = 31.01, P = 0.55;$  Fig. 2). BMR was also significantly higher in winter house sparrows compared with summer  $(F_{1,35} = 35.40, P < 0.001)$ , with no significant gender variations in BMR  $(F_{1,35} = 0.86, P = 0.36)$ . Metabolic expansibilities  $(M_{sum}/BMR)$  were 9.02 times in summer sparrows and 6.94 in winter (Table 2).

### Ventilation

Ventilatory parameters for house sparrows under helox cold stress and thermoneutral zone (TNZ) conditions are presented in Table 3. Respiratory frequency increased significantly under helox cold stress compared with TNZ in summer (t = -10.19, P < 0.001) and winter (t = -9.63, P < 0.001). In addition, mean f was significantly higher in winter compared with summer for both TNZ



Figure 1. Seasonal variation in body temperature for house sparrows after exposure to thermoneutral zone (*TNZ*) and helox cold stress (*COLD*) temperatures. The horizontal line indicates the median, the rectangle represents the twenty-fifth and seventy-fifth percentiles, and the vertical lines indicate the 95% confidence interval. Asterisk indicates significant body temperature differences within season (P < 0.05).

 $(F_{1,30} = 21.11, P < 0.001)$  and helox cold stress  $(F_{1,29} = 9.53, P = 0.005)$ . There were no significant gender variations in *f* for TNZ  $(F_{1,30} = 0.21, P = 0.65)$  or helox cold stress  $(F_{1,29} = 0.34, P = 0.57;$  Fig. 3).

Tidal volume increased significantly under maximal cold stress compared with thermoneutral conditions in summer (t = -3.94, P = 0.001) and winter (t = -8.42, P < 0.001). There were no significant seasonal or gender differences in  $V_{\rm T}$  within TNZ ( $F_{\rm I,30} = 2.51, P = 0.13; F_{\rm I,30} = 0.37, P = 0.55$ ) or under helox cold stress ( $F_{\rm I,29} = 2.30, P = 0.14; F_{\rm I,29} = 0.28, P = 0.60$ ; Fig. 3).

Minute volume also increased significantly under helox cold stress compared with TNZ in summer (t = -5.88, P < 0.001) and winter (t = -8.92, P < 0.001). Mean  $\dot{V}_1$  during helox cold stress increased 5.49 times over TNZ values in summer and 4.65 times over TNZ values in winter. In addition,  $\dot{V}_1$  increased significantly in winter birds compared with summer for both the TNZ ( $F_{1,30} = 13.55$ , P = 0.001) and helox cold stress ( $F_{1,29} = 7.27$ , P = 0.01) test conditions. We found no significant gender differences in  $\dot{V}_1$  under TNZ ( $F_{1,30} = 0.04$ , P = 0.85) or helox cold stress ( $F_{1,29} = 0.09$ , P = 0.77; Fig. 3).

Mean oxygen extraction was significantly higher under helox cold stress compared with TNZ in summer (t = -3.18, P = 0.007) and winter (t = -2.98, P = 0.01). There were no significant seasonal or gender differences in Eo<sub>2</sub> under TNZ ( $F_{1,30} = 2.28$ , P = 0.14;  $F_{1,30} = 0.03$ , P = 0.87) and helox cold stress ( $F_{1,29} = 2.24$ , P = 0.15;  $F_{1,29} = 0.05$ , P = 0.83; Fig. 3).

Mean evaporative water loss in helox for summer house sparrows was  $11.27 \pm 3.23$  mg min<sup>-1</sup> and  $8.13 \pm 3.41$  mg min<sup>-1</sup> for winter birds. Differences in EWL were significant between the seasons ( $F_{1,32} = 7.76$ , P = 0.009) but not between gender ( $F_{1,32} = 0.60$ , P = 0.45). In addition, EWL significantly varied seasonally ( $F_{1,32} = 33.1$ , P < 0.0001) within the TNZ but did not significantly differ between gender ( $F_{1,32} = 0.36$ , P = 0.554). In summer birds, mean EWL at TNZ was  $3.05 \pm 1.11$  mg min<sup>-1</sup>, and in winter birds, mean EWL was  $5.00 \pm 1.40$  mg min<sup>-1</sup>.

#### Discussion

## Morphometrics

House sparrows from this study did not exhibit seasonal differences in body mass. Although visible furcular fat deposits were higher in winter birds compared with summer, visible abdominal fat deposits did not vary. A common trend in coldtemperate wintering passerine birds is to increase fat mass relative to summer. This general pattern enables winter birds to meet thermoregulatory demands and provides a temporary buffer against foraging restrictions during severe weather conditions (Dawson and Marsh 1986; O'Connor 1995). This is especially true of ground-foraging birds such as house sparrows, since food availability in winter is less predictable when compared with tree-foraging birds (Rogers 1987). In spite of this, house sparrows, with the exception of furcular fat, do not increase fat deposits and body mass to the extent that is expected from a small, ground-foraging bird. This finding agrees with Barnett (1970), in which he reported that house sparrows were not exceptionally fat in winter compared with summer. This result has been attributed to their relatively close association with humans and their ability to exploit highly predictable food sources, such as bird feeders (Barnett 1970; Lowther and Cink 1992). Seasonal increases in body mass and fat stores do not appear to be a primary component of winter acclimatization in the house sparrow.

#### Cold Tolerance and Thermal Conductance

The cold tolerance of house sparrows improved in winter, since winter birds were able to endure colder temperatures compared



Figure 2. Seasonal variation in  $M_{\rm sum}$  and cold tolerance for summerand winter-acclimatized house sparrows from Wisconsin. Bars represent the mean  $\pm$  SD.

Season	п	Body Mass (g)	BMR	Body Mass (g)	$M_{ m sum}$	M <sub>sum</sub> /BMR
Summer	15	$25.4 \pm 1.3$	.98 ± .24	$26.4 \pm 1.3$	$8.35 \pm 1.09$	9.02
Winter	16	$26.0 \pm 2.1$	$1.61 \pm .32^{a}$	$27.6~\pm~1.6$	$10.91 \pm 1.41^{a}$	6.94

Table 2: Mean  $(\pm SD)$  metabolic rates and body mass on a whole-organism basis for house sparrows in summer and winter

Note. n = sample size. Body masses are means for the treatment group.

<sup>a</sup> Indicates significant difference in seasonal comparisons (P < 0.05).

with summer. Temperature at cold limit in summer birds was about 5°C compared with -11°C in winter birds (Fig. 2). Cold tolerance is likely associated with the elevated thermogenic capacity  $(M_{sum})$  and an increased shivering endurance (Marsh and Dawson 1989a; Swanson 2001, forthcoming). We estimated air temperature equivalents to helox test temperature by extrapolation.  $M_{sum}$  values were inserted into equations for summer and winter sparrows that relate  $\dot{V}o_2$  to  $T_a$  below thermoneutrality (Arens 2004) and were solved for  $T_a$ . The estimated air temperature at  $M_{\rm sum}$  was -57.8°C for summer birds and -232.3°C for winter birds. The actual air temperatures were probably not this low since thermal conductance may change with  $T_a$  below thermoneutrality, especially at very low temperatures. However, it is clear that house sparrows are capable of tolerating acute cold stress well below temperatures faced under natural conditions. Daily mean minimum temperatures are 16°C in July and -13°C in January in Oshkosh, Wisconsin (National Climatic Data Center, National Oceanic and Atmospheric Association). Factors such as wind, humidity, and radiation might reduce the effective minimum air temperatures. However, it seems that house sparrows have a considerable safety margin when exposed to natural cold environmental cold stress.

Thermal conductance in helox exceeded allometrically predicted *C* values in air below the  $T_{cl}$  by 3.3 times in summer and by 2.7 times in winter. These values are similar to factorial increments reported for other temperate wintering passerine birds that range from 1.72 to 3.10 (Cooper 2002). The *C* value for summer birds is markedly higher than that reported for house sparrows (1.72) from Poland in Koteja (1986). The decrease in C during helox exposure in winter birds compared with summer is not typical of most songbird species but is similar to that reported for mountain chickadees (Cooper 2002). C in winter exceeded summer values by 1.21 times. However, C is not unusually lower in winter helox cold stress compared with summer, which suggests that plumage insulation is not an important component in winter acclimatization in house sparrows. This result coincides with other studies of passerine birds that emphasize the importance of metabolic adjustments to seasonal acclimatization (Hart 1962; Dawson and Carey 1976; Swanson 1991*a*; Liknes et al. 2002).

## Summit and Basal Metabolic Rates

The increase in BMR in winter-acclimatized house sparrows compared with summer is similar to the trends reported for other passerine birds (Dawson and O'Connor 1996; Cooper and Same 2000; Cooper 2002; Liknes et al. 2002). However, the 64% increase in BMR from summer to winter is the highest yet recorded for birds. Mean BMR for house sparrows was relatively consistent with allometrically predicted values. BMR in summer birds was 79.4% of allometrically predicted values, while winter BMR was 130.5% of predicted values (Aschoff and Pohl 1970). The role of elevated BMR in most winter passerine birds is still unclear since some passerines do not exhibit seasonal variations in BMR (Dawson et al. 1985; O'Connor 1995; Sharbaugh 2001). However, it has been suggested that this re-

Table 3: Mean  $(\pm SD)$  ventilatory parameters of house sparrows under thermoneutral and helox cold stress conditions in summer and winter

		f	$V_{\mathrm{T}}$		$\dot{V}_{\mathrm{I}}$		
Season	п	(breaths min <sup>-1</sup> )	btps (mL)	stpd (mL)	BTPS (mL min <sup><math>-1</math></sup> )	stpd (mL min <sup>-1</sup> )	$Eo_2$ (%) stpd
Summer	15						
BMR		$48.0 \pm 6.71$	$.67 \pm .40$	$.58 \pm .34$	$31.5 \pm 18.1$	$27.2 \pm 15.4$	$20.59 \pm 7.44$
$M_{ m sum}$		$107.8 \pm 22.9^{a}$	$1.61 \pm .71^{a}$	$1.41 \pm .60^{a}$	$173.0 \pm 87.5^{a}$	$151.9 \pm 74.6^{a}$	$30.93 \pm 9.48^{\circ}$
Winter	16						
BMR		$65.2 \pm 13.4^{\rm b}$	.84 ± .21	$.74 \pm .18$	$55.9 \pm 19.8^{\circ}$	$47.9 \pm 20.1^{b}$	$17.11 \pm 6.30$
$M_{ m sum}$		$132.4 \pm 19.0^{a,b}$	$1.94 \pm .51^{a}$	$1.75 \pm .46^{a}$	$260.1 \pm 88.2^{a,b}$	$240.1 \pm 74.8^{a,b}$	$25.38 \pm 9.82^{\circ}$

Note. n = sample size.

 $^{\rm a}$  Indicates significant ventilatory difference within season (P < 0.05).

<sup>b</sup> Indicates significant ventilatory difference between seasons (P < 0.05).



Figure 3. Mean ventilatory frequency (f), tidal volume ( $V_T$ ), minute volume ( $\dot{V}_1$ ), and oxygen extraction efficiency (Eo<sub>2</sub>) in house sparrows during testing in the thermoneutral zone (*TNZ*) and helox cold stress (*COLD*) in summer and winter. Asterisk indicates significant ventilatory difference within each season (P < 0.05). Two asterisks indicate significant ventilatory difference between seasons (P < 0.05).

sponse may be attributed to the higher metabolic costs associated with thermogenesis in winter (Swanson 1991*b*). These metabolic costs may be due to the maintenance of increased pectoralis muscle mass, which is required for enhanced shivering thermogenesis in winter. Increases in winter pectoralis muscle mass have been reported in passerine birds such as darkeyed juncos, house finches, mountain chickadees, and juniper titmice (Swanson 1991*b*; O'Connor 1995; Cooper 2002).

The 31.0% increase in  $M_{\rm sum}$  for winter sparrows compared with summer is consistent with that recorded for other passerine birds that ranged from 0% to 52% (Cooper and Swanson 1994; Liknes and Swanson 1996; Cooper 2002). The mean value of 8.35 mL O<sub>2</sub> min<sup>-1</sup> in summer birds was approximately 14.4% higher than that reported by Koteja (1986). The marked increase in  $M_{\rm sum}$  and cold tolerance ( $T_{\rm d}$ ) in winter compared with summer suggest that these two responses are correlated. This correlation has been documented for several small passerine species (Swanson 2001). This pattern of metabolic acclimatization, where thermogenic capacity and thermogenic endurance vary in tandem, is consistent with the variable maximum model of winter acclimatization described by Liknes et al. (2002). This pattern coincides with the general positive correlation between endurance and aerobic capacity in vertebrates (Bennett 1991).

 $M_{\rm sum}$  values for house sparrows were within 2% of allo-

metrically predicted values in summer and were 28.2% higher than predicted values in winter (Dutenhoffer and Swanson 1996). The allometric  $M_{sum}$  comparison for winter birds illustrates that house sparrows have the ability to markedly increase their  $M_{sum}$  over other temperate wintering passerine birds.

Metabolic expansibility ( $M_{sum}$ /BMR) was 9.0 in summer birds and 6.9 in winter. The metabolic expansibility of 9.0 in summer is the highest yet recorded for birds, with a range from 3.3 to 8.4 reported (Marsh and Dawson 1986; Saarela et al. 1989; Liknes and Swanson 1996; Cooper 2002). These high metabolic expansibilities demonstrate that both summer and winter birds have the ability to tolerate extremely cold temperatures through increases in metabolism to support thermogenesis relative to thermoneutral metabolic rates.

### Ventilation

At low  $T_a$  in summer and winter, increases in oxygen consumption were supported by significant increases in breath frequency, tidal volume, and oxygen extraction efficiency. House finches and rosy finches showed similar trends in f and  $V_T$  but showed a reduction in Eo<sub>2</sub>% below 0°C (Clemens 1988). The data for house sparrows contrast with all other data for passerine birds in that house sparrows show increases in all three ventilatory variables. Other passerine birds show increases in one or two of the ventilatory variables at low  $T_a$  but not all three (Clemens 1988; Cooper and Same 2000).

A higher Eo<sub>2</sub>% at low  $T_a$  may be an adaptation to reduce respiratory heat loss (Johansen and Bech 1983), which would be beneficial in extreme cold conditions. We calculated the rates of respiratory heat for house sparrows under helox cold stress according to Chappell and Bucher (1987). Expired air temperature was not measured but was assumed to be 5°C in summer and 0°C in winter (Brent et al. 1984). The metabolic heat production  $(M_{sum})$  was 167.7 J min<sup>-1</sup> in summer birds and 218.9 J min<sup>-1</sup> in winter birds under helox cold stress. House sparrows at helox cold stress conditions lost about 24.8 J min<sup>-1</sup> in summer and 30.7 J min<sup>-1</sup> in winter as respiratory water loss (using our EWL data and according to the assumption that expired air is saturated) and 3.3 J min<sup>-1</sup> in summer and 5.0 J min<sup>-1</sup> in winter as heat transferred to tidal air. Therefore, respiratory heat loss was 11.3% of total heat loss in summer and 18.3% of total heat loss in winter. Using measured Eo<sub>2</sub>% from thermoneutral tests (BMR) in place of cold stress Eo<sub>2</sub>%, we found that the computed respiratory heat loss would be 11.7% of the total heat loss in summer and 18.6% in winter. The difference in heat loss between helox and thermoneutral Eo<sub>2</sub>% values for both seasons is minimal; thus, it appears that the respiratory heat loss savings as a result of increased Eo<sub>2</sub>% in house sparrows under helox cold stress compared with thermoneutral conditions are negligible. This agrees with an article by Morgan et al. (1992) in which they stated that reducing respiratory heat by increasing Eo<sub>2</sub>% at low ambient temperature is not likely a common phenomenon in birds.

The increases in  $\dot{Vo}_2$  in winter birds under helox cold stress compared with summer were supported by increases in  $\dot{V}_1$ . The elevated  $\dot{V}_1$  for winter birds was supported primarily by significant increases in breath frequency, which was approximately 1.23 times the summer value. Winter  $V_T$  in helox was higher than summer helox values but not significantly. In addition, Eo<sub>2</sub>% remained seasonally stable under extreme cold stress. This contrasts with data from another passerine, the black-capped chickadee, which responded to helox cold stress with decreasing f and increasing Eo<sub>2</sub>% (Cooper and Same 2000) in winter relative to summer. This suggests that winter-acclimatized house sparrows primarily use changes in f to accommodate higher  $\dot{Vo}_2$  at low  $T_a$ .

Mean frequency under thermoneutral conditions was relatively consistent with allometrically predicted values. f at TNZ was 80.1% of allometrically predicted values in summer birds and 108.9% of predicted values in winter birds (Frappell et al. 2001). Minute volume was 14% higher in summer birds at TNZ compared with allometrically predicted values, which is in relatively close agreement given the small number of passerine birds used in calculating allometric predictions (Frappell et al. 2001). However, in winter birds,  $V_1$  increased 2.0 times over allometrically predicted values according to Frappell et al. (2001). Tidal volume was also considerably elevated compared with allometric predictions.  $V_{\rm T}$  for birds at TNZ increased 1.5 times over allometrically predicted values in summer birds and 1.8 times over predicted values in winter birds (Frappell et al. 2001). These substantial increases over predicted values in  $V_{I}$ and  $V_{\rm T}$  show that the elevated BMR in winter house sparrows is mainly supported by these two respiratory variables.

Summer- and winter-acclimatized house sparrows from Wisconsin appear to primarily use metabolic adjustments in response to extreme cold stress. These metabolic adjustments are supported through increases in f,  $V_{\rm T}$ , and Eo<sub>2</sub>% under helox cold stress relative to thermoneutral conditions. In addition, winter-acclimatized birds have an enhanced capacity to tolerate colder temperatures because of an increased  $M_{\rm sum}$  compared with summer, with this rate being primarily supported by increases in *f*.

## Acknowledgments

We thank Dr. Todd Sandrin and Dr. Susie Sandrin for allowing us to use their property for trapping birds. This study was supported in part by a graduate student–faculty collaborative research program grant from the University of Wisconsin, Oshkosh, to J.R.A. and from a faculty development research grant to S.J.C.

## Appendix

In order to insure that the helox gas itself does not affect respiration, we measured  $\dot{V}o_2$  during the day in house sparrows

Table A1: Mean ( $\pm$  SD) ventilatory values for summer and winter house sparrows in response to helox gas at 30°C compared with expected calculated values in air at the same  $\dot{V}o_2$ 

Condition	Ϋo	f (breaths min <sup>-1</sup> )	$V_{\rm c}$ (mI)	$\dot{V}$ (mI min <sup>-1</sup> )	Fo (%)	
Condition	V 0 <sub>2</sub>	j (breaths him )	$v_{\rm T}$ (IIIL)	(IIII IIIII )	LO <sub>2</sub> (70)	
Summer:						
30°C/helox	$2.74 \pm .43$	$68.0 \pm 8.4$	$1.02 \pm .11$	$69.47 \pm 12.04$	$22.16 \pm .04$	
Calculated	2.74	64.0	1.22	78.27	20.80	
Winter:						
30°C/helox	$2.69 \pm .42$	$66.8 \pm 10.4$	$1.25 \pm .23$	$83.70 \pm 23.87$	$18.6 \pm .04$	
Calculated	2.69	76.2	1.17	89.34	21.00	

in the summer (n = 8) and winter (n = 10) at 30°C in helox gas. Vo<sub>2</sub> was significantly higher in house sparrows in helox at 30°C compared with air at 30°C (Arens 2004). The mean f,  $V_{\rm T}$ ,  $\dot{V}_{\rm I}$ , and Eo<sub>2</sub>% in helox at 30°C were compared with predicted values based on regression equations of respiratory variables versus Vo<sub>2</sub> for daytime house sparrows in summer and winter (Arens 2004). Table A1 shows the observed values in helox and the calculated values based on the level of Vo<sub>2</sub>.



Figure A1. The following settings were used to record pressure (Pa) from our PT-100B pressure meters A and B (Sable Systems International, Las Vegas, NV): gain 10 × , filter 100 Hz, offset 10 s, calibration injections of 1 mL. We altered the injection frequency to match the range of frequencies recorded from birds in our experiments. Neither pressure meter A nor B showed any significant relationship of pressure versus frequency of calibration injections in air or helox. Linear and polynomial relationships are commonly used to calibrate instrument response, so we have shown those statistics here: meter A in air (linear:  $r^2 = 0.077$ , P = 0.32; cubic:  $r^2 = 0.21$ , P = 0.43), meter B in air (linear:  $r^2 = 0.002$ , P = 0.88; cubic:  $r^2 = 0.20$ , P = 0.46), meter A in helox (linear:  $r^2 = 0.06$ , P = 0.49; cubic:  $r^2 = 0.49$ , P = 0.23).

## Literature Cited

- Arens J.R. 2004. Metabolic and Ventilatory Adjustments to Cold Stress in Seasonally Acclimatized House Sparrows (*Passer domesticus*). MS thesis. University of Wisconsin, Oshkosh.
- Aschoff J. and H. Pohl. 1970. Rhythmic variations in energy metabolism. Fed Proc 29:1541–1552.
- Barnett L.B. 1970. Seasonal changes in temperature acclimatization of the house sparrow, *Passer domesticus*. Comp Biochem Physiol 33:559–578.
- Bartholomew G.A., D. Vleck, and C.M. Vleck. 1981. Instantaneous measurements of oxygen consumption during preflight warm-up and post-flight cooling in sphingid and saturniid moths. J Exp Biol 90:17–32.
- Bech C., K. Johansen, R. Brent, and S. Nicol. 1984. Ventilatory and circulatory changes during cold exposure in the pekin duck *Anas platyrhynchos*. Respir Physiol 57:103–112.

- Bech C. and S.C. Nicol. 1999. Thermoregulation and ventilation in the tawny frogmouth, *Podargus strigoides*: a low-metabolic avian species. Aust J Zool 47:143–153.
- Bennett A.F. 1991. The evolution of activity capacity. J Exp Biol 160:1–23.
- Brent R., P.F. Pedersen, C. Bech, and K. Johansen. 1984. Lung ventilation and temperature regulation in the European coot (*Fulica atra*). Physiol Zool 57:19–25.
- Brent R., J.G. Rasmussen, C. Bech, and S. Martini. 1983. Temperature dependence of ventilation and O<sub>2</sub>-extraction in the kittiwake, *Rissa tridactyla*. Experientia 39:1092–1093.
- Brice A.G. and H.G. Welch. 1983. Metabolic and cardiorespiratory responses to He-O<sub>2</sub> breathing during exercise. J Appl Physiol 54:387–392.
- Bucher T.L. 1981. Oxygen consumption, ventilation and respiratory heat loss in a parrot, (*Bolborhynchus lineola*), in relation to ambient temperature. J Comp Physiol B 142:479– 488.
- ——. 1985. Ventilation and oxygen consumption in *Amazona riridigenalis*: a reappraisal of "resting" respiratory parameters in birds. J Comp Physiol B 155:269–276.
- 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*). J Comp Physiol 159B:561–567.
- Calder W.A. and J.R. King. 1974. Thermal and caloric relations in birds. Pp. 259–413 in D.S. Farner and J.R. King, eds. Avian Biology. Vol. 4. Academic Press, New York.
- Chappell M.A. and T.L. Bucher. 1987. Effects of temperature and altitude on ventilation and gas exchange in chukars (*Alectoris chukar*). J Comp Physiol B 157:129–136.
- Chappell M.A. and T.J. Dawson. 1994. Ventilatory accommodation of changing oxygen consumption in dasyurid marsupials. Physiol Zool 67:418–437.
- Chappell M.A. and S.L. Souza. 1988. Thermoregulation, gas exchange, and ventilation in Adelie penguins (*Pygoscelis adeliae*). J Comp Physiol 157B:783–790.
- Clemens D.T. 1988. Ventilation and oxygen consumption in rosy finches and house finches at sea level and high altitude. J Comp Physiol B 158:57–66.
- Cooper S.J. 2002. Seasonal metabolic acclimatization in mountain chickadees and juniper titmice. Physiol Biochem Zool 75:386–395.
- Cooper S.J. and D.R. Same. 2000. Ventilatory accommodation under cold stress in seasonally acclimatized black-capped chickadees. Am Zool 40:980A.
- Cooper S.J. and D.L. Swanson. 1994. Seasonal acclimatization of thermoregulation in the black-capped chickadee. Condor 87:424–427.
- Dawson W.R. and C. Carey. 1976. Seasonal acclimatization to temperature in cardeuline finches. I. Insulative and metabolic adjustments. J Comp Physiol 112:317–333.
- Dawson W.R. and R.L. Marsh. 1986. Winter fattening in the

American goldfinch and the possible role of temperature in its regulation. Physiol Zool 59:357–368.

- . 1989. Metabolic acclimatization to cold and season in birds. Pp. 83–94 in C. Bech and R.E. Reinertsen, eds. Physiology of Cold Adaptation in Birds. Plenum, New York.
- Dawson W.R., R.L. Marsh, W.A. Buttemer, and C. Carey. 1983. Seasonal and geographical variation of cold resistance in house finches (*Carpodacus mexicanus*). Physiol Zool 56:353– 369.
- ———. 1985. A reexamination of the metabolic response of house finches to temperature. Condor 87:424–427.
- Dawson W.R. and T.P. O'Connor. 1996. Energetic features of avian thermoregulatory response. Pp. 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*). Pp. 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.
- Dutenhoffer M. and D.L. Swanson. 1996. Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. Physiol Zool 69:1232–1254.
- Frappell P.B., D.S. Hinds, and D.F. Boggs. 2001. Scaling of respiratory variables and the breathing pattern in birds: an allometric and phylogenetic approach. Physiol Biochem Zool 74:75–89.
- Hart J.S. 1962. Seasonal acclimatization in four species of small wild birds. Physiol Zool 35:224–236.
- 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. J Appl Physiol 33:261– 263.
- Holloway J.C. and F. Geiser. 2001. Effects of helium/oxygen and temperature on aerobic metabolism in the marsupial sugar glider, *Petaurus breviceps*. Physiol Biochem Zool 74: 219–225.
- Hudson J.W. and S.L. Kimzey. 1966. Temperature regulation and metabolic rhythms in populations of the house sparrow, *Passer domesticus*. Comp Biochem Physiol A 17:203–217.
- Johansen K. and C. Bech. 1983. Heat conservation during cold exposure in birds (vasomotor and respiratory implications). Polar Res, NS, 1:259–268.
- 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*. Physiol Zool 58:748–758.

Kleiber M. 1961. The Fire of Life. Wiley, New York.

Koteja P. 1986. Maximum cold-induced oxygen consumption

in the house sparrow *Passer domesticus* L. Physiol Zool 59: 43–48.

- Liknes E.T., S.M. Scott, and D.L. Swanson. 2002. Seasonal acclimatization in the American goldfinch revisited: to what extent do metabolic rates vary seasonally? Condor 104:548– 557.
- Liknes E.T. and D.L. Swanson. 1996. Seasonal variation in cold tolerance, basal metabolic rate, and maximum capacity for thermogenesis in white-breasted nuthatches *Sitta carolinensis* and downy woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. J Avian Biol 27:279–288.
- Lowther P.E. and C.L. Cink. 1992. House sparrow. Pp. 1–20 in A. Poole, P. Stettenheim, and F. Gill, eds. The Birds of North America. No. 12. Academy of Natural Sciences, Philadelphia.
- Malan A. 1973. Ventilation measured by body plethysmography in hibernating mammals and in poikilotherms. Respir Physiol 11:152–166.
- Marsh R.L. and W.R. Dawson. 1986. Role of metabolic adjustments in avian survival of cold winters. Proc Int Ornithol Congr 29:2690–2701.
  - . 1989*a*. Avian adjustments to cold. Pp. 205–253 in L.C.H. Wang, ed. Advances in Comparative and Environmental Physiology. Springer, Berlin.
- ——\_\_\_\_. 1989b. Energy substrates and metabolic acclimatization in small birds. Pp. 105–114 in C. Bech and R.E. Reinertsen, eds. Physiology of Cold Adaptation in Birds. Plenum, New York.
- Metcalfe N.B. and S.C. Ure. 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. Proc R Soc Lond B 261:395.
- Morgan K.R., M.A. Chappell, and T.L. Bucher. 1992. Ventilatory oxygen extraction in relation to ambient temperature in four Antarctic seabirds. Physiol Zool 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. Can J Physiol Pharmacol 76:937–944.
- O'Connor T.P. 1995. Metabolic characteristics and body composition in house finches: effects of seasonal acclimatization. J Comp Physiol B 165:298–305.
- Packard G.C. and T.J. Boardman. 1999. The use of percentages and size-specific inidices to normalize physiological data for variation in body size: wasted time, wasted effort? Comp Biochem Physiol 122A:37–44.
- Piiper J. and P. Scheid. 1975. Gas transport efficacy of gills, lungs and skin: theory and experimental data. Respir Physiol 23:209–221.
- Pohl W. and G.C. West. 1973. Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the common redpoll. Comp Biochem Physiol A 45:851–867.
- Pyle P., S.N.G. Howell, D.F. DeSante, P. Yunick, and M. Gustafson. 1997. Identification Guide to North American Birds.1. Columbidae to Ploceidae. Slate Creek, Bolinas, CA.

- Rogers C.M. 1987. Predation risk and fasting capacity: do winter birds maintain optimal body mass? Ecology 68:1051– 1061.
- Rosenmann M. and P. Morrison. 1974. Maximum oxygen consumption and heat loss facilitation in small homeotherms by HeO<sub>2</sub>. Am J Physiol 226:490–495.
- Saarela S., B. Klapper, and G. Heldmaier. 1989. Thermogenic capacity of greenfinches and siskins in winter and summer. Pp. 112–115 in C. Bech and R.E. Reinertsen, eds. Physiology of Cold Adaptation in Birds. Plenum, New York.
- Scholander P.R., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950. Heat regulation in some arctic and tropical mammals and birds. Biol Bull 99:237–258.
- Sharbaugh D.L. 2001. Seasonal acclimatization to extreme climatic conditions by black-capped chickadees (*Poecile atricapilla*) in interior Alaska (64°N). Physiol Biochem Zool 74: 568–575.
- 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*). Am J Anat 177:221–242.

Swanson D.L. 1990. Seasonal variation in cold hardiness and

peak rates of cold-induced thermogenesis in the dark-eyed junco (*Junco hyemalis*). Auk 107:561–566.

- ------. 1991*a*. Seasonal adjustments in metabolism and insulation in the dark-eyed junco. Condor 93:538–545.
- . 1991b. Substrate metabolism under cold stress in seasonally acclimatized dark-eyed juncos. Physiol Zool 64:1578– 1592.
- ———. 2001. Are summit metabolism and thermogenic endurance correlated in winter-acclimatized passerine birds? J Comp Physiol B 171:475–481.
- 2003. Seasonal metabolic variation in birds: functional and mechanistic correlates. Curr Ornithol 17 (forthcoming).
- Swanson D.L., M.W. Drymalski, and J.R. Brown. 1996. Sliding vs. static cold exposure and the measurement of summit metabolism in birds. J Therm Biol 21:221–226.
- Szewczak J.M. and F.L. Powell. 2003. Open-flow plethysmography with pressure-decay compensation. Respir Physiol Neurobiol 134:57–67.
- Warkentin I.G. and N.H. West. 1990. Impact of long-term captivity on basal metabolism in birds. Comp Biochem Physiol A 96:379–381.
- Witter M.S. and I.C. Cuthill. 1993. The ecological costs of avian fat storage. Philos Trans R Soc Lond B 340:73–92.