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# METABOLIC RATE OF AMERICAN WOODCOCK

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ABSTRACT.—We measured metabolic rate of captive-reared American Woodcock (*Scolopax minor*) by indirect calorimetry. Basal metabolic rate (BMR) averaged 1.22 ± 0.18 ml $O_2$ $g^{-1}h^{-1}$ (N = 5). Lower critical temperature was 22°C. Below thermoneutrality, the relationship between metabolic rate ($VO_2$) and ambient temperature ($T_a$) was best described by the equation: $VO_2 = 2.047 - 0.0375(T_a)$, ($r^2 = 0.62$, N = 29). Although BMR for American Woodcock was greater than that predicted by some generalized equations for non-passerines, it did not follow the elevated pattern for shorebirds predicted by the equation of Kersten and Piersma (1987). Lower BMR in American Woodcock may result from lower annual peaks of energy use compared to other shorebirds. *Received 29 Jan. 1993, accepted 15 Sept. 1993.*

Laboratory measurements of metabolic rate have been reported for few shorebirds. In those shorebirds that have been studied, metabolic rates were consistently above those predicted by published allometric equations for non-passerines (Castro 1987, Kersten and Piersma 1987, Mathiu et al. 1989), prompting Kersten and Piersma (1987) to develop a separate equation specific to shorebirds. Their equation is based on data from six species but it is unclear how broadly it may be applied to other shorebirds. The American Woodcock (*Scolopax minor*) is an upland shorebird with life history characteristics different from most other shorebirds (Sheldon 1967). As part of a study on reproductive energetics of American Woodcock, we raised Woodcock in captivity and determined values for metabolic parameters; here we report measured values for basal metabolic rate (BMR), lower critical temperature (LCT), and standard metabolism below the thermoneutral zone (TNZ).

## METHODS

American Woodcock (2 M, 3 F) were reared from eggs collected on the Moosehorn National Wildlife Refuge, Calais, Maine. From July through mid-September 1988, birds were housed in outside pens at ambient temperature and photoperiod at Orono, Maine. From mid-September 1988 until the beginning of experiments in November, birds were housed in individual cages in an environmental chamber which was maintained at constant 19°C air temperature. Photoperiod in the chamber was maintained at September levels (13:11, L:D) through December 1989, and then advanced gradually to normal levels following

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termination of the experiments. All birds used in the analysis had completed their postjuvenile molts. Birds were fed earthworms (*Lumbricus terrestris*) ad libitum and were handled daily and habituated to captivity (Vander Haegen et al. 1993a).

Metabolic rates were measured in a 4.6 l plexiglass metabolism chamber, during the resting phase of the birds' daily cycle and in complete darkness. Birds were fasted for 6 h prior to being placed in the chamber and were in a post-absorptive state. Oxygen consumption ($VO_2$) and carbon dioxide production ($VCO_2$) were measured in an open circuit system using a Beckman 755 $O_2$ analyzer and a Beckman 864 infrared $CO_2$ analyzer. Water vapor was removed from the air stream immediately downstream from the metabolic chamber. Flow rates were measured downstream from the metabolic chamber and ranged from 2.5 to 3.0 l/min. The system was calibrated to standard gas mixtures and zeroed to ambient air at the beginning of each run. Temperature in the metabolism chamber ($T_a$) and in the air stream at the entrance to the flow meter was measured with 28-ga thermocouples. Gas concentrations and temperatures were sampled every second by a CR21X micrologger (Campbell Scientific, Logan, Utah), averaged every 60 sec, and recorded by a microcomputer. $T_a$ was controlled by placing the metabolic chamber in a walk-in environmental chamber.

Metabolism was measured at 2–3 temperatures per night, always proceeding from higher to lower temperature (Pohl 1969). Following a 1-h adjustment period at each temperature, gas concentrations were monitored for 30 min. $VO_2$ and $VCO_2$ were derived in two ways: first, by averaging the final 15 min of each trial; and second, by averaging $\geq 4$ min of the lowest period of constant values obtained during each trial (both methods appear in the literature and could conceivably yield different results). $VO_2$ obtained by these two methods differed by only 2.3% at air temperatures >20°C. Therefore, we used the final 15 min to calculate metabolic rate. All gas volumes were corrected to standard temperature and pressure. Metabolism was calculated using equation 3b in Withers (1977). BMR for each bird was determined by averaging all values obtained from 23 to 30°C and assuming a conversion factor of 20.08 kJ per liter of $O_2$ consumed. LCT was determined as the point where the line representing BMR intersected the regression line for all points $\leq 20$°C. Least-squares regression was used to evaluate the effect of temperature on metabolic rate below the TNZ. Means are reported ± 1 SE.

## RESULTS

The mean BMR for 5 woodcock was $1.22 \pm 0.18$ ml $O_2$ $g^{-1}h^{-1}$. Table 1 compares BMR measured in this study to values predicted from published allometric equations. LCT was estimated as 22°C (Fig. 1). Below this temperature, the relationship between metabolic rate and ambient temperature was best described by the equation: $VO_2 = 2.047 - 0.0375(T_a)$, ($r^2 = 0.62$, $N = 29$). Mean mass of captive woodcock over all metabolic experiments was $156.7 \pm 16.0$ g.

When $VO_2$ for American Woodcock was set to zero, the regression of $VO_2$ on $T_a$ (below LCT) extrapolated to a value of 55°C which is 15° above the average body temperature for birds (Calder and King 1974). This discrepancy indicates that, like many birds, American Woodcock vary their thermal conductance at ambient temperatures below the TNZ (Schmidt-Nielsen 1983:268).

TABLE 1

COMPARISON OF MEASURED AND PREDICTED BASAL METABOLIC RATE (BMR) IN THE AMERICAN WOODCOCK (VALUES FOR A 157 G BIRD)

| | BMR (kJ day$^{-1}$) | Measured relative to predicted (%) |
|---|---|---|
| Measured value (this study) | 92.5 | |
| Predictive equations | | |
| Aschoff and Pohl (1970)[a] | 79.0 | +17 |
| Lasiewski and Dawson (1967)[b] | 85.9 | +8 |
| Kendeigh et al. (1977)[a] | 94.3 | −2 |
| Kersten and Piersma (1987)[c] | 113.4 | −18 |

[a] Equations for non-passerines at night.
[b] Equation for non-passerines, day and night.
[c] Equation for shorebirds.

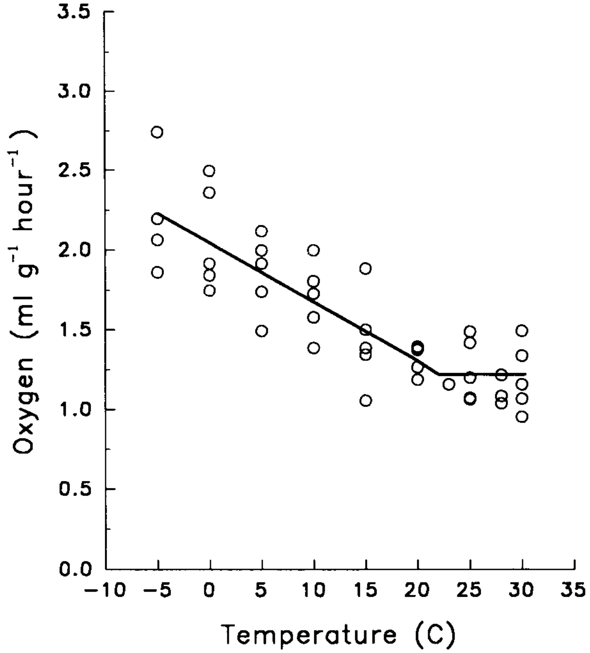

FIG. 1. Effect of ambient temperature on oxygen consumption by American Woodcock during the resting phase of their daily cycle (N = 2 males, 3 females).

## DISCUSSION

Although BMR for American Woodcock was greater than that predicted by some generalized equations for non-passerines, it did not follow the elevated pattern for shorebirds predicted by the equation of Kersten and Piersma (1987) (Table 1). Other shorebirds, however, have been shown to follow this pattern of elevated metabolism. BMRs of Sanderlings (*Calidris alba*) (Castro 1987) and Pacific Golden-Plovers (*Pluvialis fulva*) (Mathiu et al. 1989) measured during the day were greater than those predicted by equations for the active phase or by more generalized equations for day and night (Castro 1987, Mathiu et al. 1989).

Two factors may have contributed to the differences between observed and predicted BMR in American Woodcock. First, the birds in our study were raised in captivity which may have affected their metabolic rates (Warkentin and West 1990). For example, our birds were conditioned to the laboratory environment, which likely reduced their apprehension during the experiments and increased the probability that they achieved a true resting state (Robbins 1983:107). Second, if BMR is associated with daily energy expenditure (DEE) as suggested by Kersten and Piersma (1987) and Daan et al. (1990), the differences in BMR between American Woodcock and other shorebirds may be related to differences in their natural history that influence DEE.

Kersten and Piersma (1987) argued that high BMR in shorebirds may be caused by increased use of skeletal muscles and their supporting abdominal organs at some point of high DEE in their yearly cycle (e.g., pre-migratory hyperphagia, migration, or winter cold periods). If this hypothesis is correct, American Woodcock should not encounter periods of energetic stress of the same magnitude as do other shorebirds. We know that conditions experienced by American Woodcock during early spring on the northern breeding grounds can be severe, with prolonged cold temperatures and periods of reduced food availability (Sheldon 1967, Vander Haegen et al. 1993b). Furthermore, female American Woodcock preparing to nest are active both day and night as they increase stored energy reserves prior to laying a clutch (Vander Haegen 1992). Although these conditions imply a high DEE during the breeding season for American woodcock, it is unlikely that Woodcock attain levels equal to those required of Arctic-nesting shorebirds.

Greater differences in DEE between American Woodcock and other shorebirds may occur during migration and in winter. American Woodcock migrate considerably shorter distances than do many shorebirds, and probably do not incur as high an energetic cost during the pre-migratory and migration periods. American Woodcock also differ from most shorebirds by inhabiting forests, rather than coastal or grassland habitats where convection, and hence the potential for convective heat loss, is typically high. Therefore, the periods proffered by Kersten and Piersma (1987) as candidates for high DEE in shorebirds (i.e., ''long-distance migration'' and ''wintering in unsheltered habitats'') are probably less demanding energetically for American Woodcock than for other shorebirds. Although comparable measurements from other species of upland shorebirds are generally lacking, BMR of one European Woodcock (*S. rusticola*) measured by Gavrilov and Dol'nik (Kendeigh et al. 1977) was 21% below the rate predicted by the equation of Kersten and Piersma (1987), a value similar to the 18% differential reported here for American Woodcock. Like its North American congener, the European Woodcock inhabits forested habitats and migrates relatively short distances (Sheldon 1967).

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