LOW LEVELS OF ENERGY EXPENDITURE IN A NOCTURNAL, FOREST-DWELLING WADER, THE EURASIAN WOODCOCK *SCOLOPAX RUSTICOLA*

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Ecological energetics have been extensively studied in the Scolopacidae, but mostly focused on coastal and wetland species. Living in forests and meadows, the Eurasian Woodcock *Scolopax rusticola* (mean body mass 317 g) is an exceptional species among waders. Standard Metabolic Rate (SMR, including Basal Metabolic Rate (BMR) and thermoregulation costs, measured at rest in a respirometer chamber) and T3 hormone levels were measured on wild woodcocks wintering in France. While the Lower Critical Temperature followed predictions from allometric equations (17.5°C), BMR was low (1.2 W) and plumage insulation high compared with other shorebirds. T3 was positively correlated with SMR in the laboratory. In the field, we used T3 levels to predict Field Metabolic Rate (FMR); in winter the average FMR was around 2.8 times BMR (3.4 W). The energetic requirements of Eurasian woodcocks are lower than those of typical waders living in windy unsheltered habitats, which in turn may lead to their low BMR. Woodcocks could save energy by resting during the day in sheltered habitat and being active at night, when the costs for thermoregulation are higher.

Keywords: *Scolopax rusticola* - BMR - FMR - inland waders - T3 - thermoregulation

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INTRODUCTION

In waders (Scolopacidae, Charadriidae and Haematopodidae), energetic aspects of various life history stages (reproduction, migration, wintering) have been much studied (Piersma *et al.* 1991; Piersma 2002). Kersten & Piersma (1987) found high levels of energy expenditure and high basal metabolic rates (BMR) in waders of temperate area, exceeding values for most other families of birds. They hypothesized that waders have an energetically expensive way of life, mainly because they are time-constrained by their long transcontinental migrations (Piersma *et al.* 1996b)

and because they live in unsheltered habitats (e.g. mudflats and beaches), and face especially wind which is known to markedly increase heat loss (Wiersma & Piersma 1994). In this case, metabolic rates would be reduced in waders that do not face such adverse conditions, for instance in inland waders. However, nearly all studies have been conducted on the waders living on the seashore (Castro *et al.* 1992; Piersma 1994; Kersten 1997; Piersma 2003). In this paper, we test this hypothesis using a species that lives outside the typical marine wader habitat. The Eurasian Woodcock *Scolopax rusticola*, living in forest habitats, is one of the most widely distributed species of the Scolopacidae family (Cramp & Simmons 1983). Only two studies have dealt with energetics in woodcocks; one that indicates a metabolism measurement on a single individual of Eurasian Woodcock (Gavrilov & Dolnik 1985) and one on the American Woodcock *Scolopax minor* (Vander Haegen *et al.* 1994).

The approaches and aims of this study, undertaken on Eurasian woodcocks during winter, are multiple. (1) We measured variations in Basal Metabolic Rate (BMR), defined as the minimum rate of energy expenditure of homeotherms under thermoneutral and post-absorptive conditions in the inactive phase of the circadian cycle (Aschoff & Pohl 1970). We also determined the energetic costs for thermoregulation by measuring the metabolism at various ambient air temperatures. (2) We compared BMR of this nocturnal forest-dwelling wader with literature data on coastal waders and explored the link between energy requirements and habitat. (3) Because recapturing woodcocks is very difficult, usual methods to measure Field Metabolic Rate (FMR) such as doubly labelled water (Speakman 1997) and heart rate recorders (Bevan *et al.* 1995; Weimerskirch *et al.* 2002) cannot be used in wild woodcocks because they require a recapture of the animal at a determined lapse of time. We therefore investigated a new method to estimate FMR. Thyroid hormones, especially triiodothyronine (T3), are important controllers of the regulation of energy metabolism in birds and many specific aspects of thyroid hormone-triggered metabolic effects have been established (McNabb 2000). A recent study has shown that a significant part of inter-individual variations in BMR is accounted for by differences in plasma T3 (Chastel *et al.* 2003). Hence, we measured the T3 levels in the blood and examined relationships between T3 levels and metabolism in order to estimate BMR and FMR of free-living birds using T3 levels.

METHODS

Measures of BMR and calibration of T3 were conducted in November 2000 and November 2001 in a population of free-living woodcocks wintering in the Chizé forest, located around the CNRS-Centre d'Etudes Biologiques de Chizé, near the Atlantic coast of France (46°09'N; 0°24'W). Twenty-eight birds (6 adults and 8 juveniles in 2000 and 9 adults and 5 juveniles in 2001) were captured at the beginning of the night, as they were feeding in fields surrounding the Chizé forest, with a headlight and a 1.5 m wide net fitted on a 2-4 m long stick (Gossmann *et al.* 1988). Estimates of FMR using T3 on free-living woodcocks were made in the Beffou forest (48°30'N, 3°28'W) in Brittany, France. In the fields around the forest, 38 woodcocks (12 adults and 26 juveniles) were caught with the same technique in December 2001 and January 2002.

Biometry and blood samples

At Chizé, biometric measures and blood samples were all done in the laboratory. Tarsus and bill lengths were measured (± 0.1 mm) with callipers and folded wing length was measured to the nearest millimetre with a ruler. In 2001, we also measured skull and ulna lengths with callipers. The age (adult [>1 year old] *vs.* juvenile) was determined by wing feather details and moult status (Clausager 1973, Fadat 1994). Blood samples (100-200 µl) were collected in 200 µl heparinized micro-tubes from the brachial vein following puncture with a 27-gauge needle. Blood samples were taken within 5 minutes after the end of metabolic rate measurement, and immediately centrifuged at 2000 rpm for 8 minutes to separate

plasma from blood cells. Plasma and red cells were stored at –20°C until final analysis. Body mass was measured to the nearest gram with an electronic balance. At Beffou, ringing, biometry and blood sample collection were performed in the field within 5 minutes following the capture. The protocol was the same as described above with the difference that body mass was measured with a Pesola spring balance, and blood samples were temporarily stored in an icebox until return to the station for centrifuging and storage at –20°C.

Body condition and sexing

The lean body mass was calculated as the fresh body mass minus the total mass of lipids. To estimate the total mass of lipids, we used the following predictive equations based on dissections and fat extractions of 22 woodcocks in winter (Boos 2000): Total mass of lipids (in g) = 0.548*(body mass in g) – 1.932*(skull length in mm) – 5.213*(ulna length in mm) + 336.40 (r^2 = 0.703, P < 0.001). The total mass of proteins was estimated following predictive equations (Boos 2000): Total mass of proteins (in g) = 0.084*(body mass in g) + 3.451*(sex [0 for males and 1 for females]) + 23.377 (r^2 = 0.600, P < 0.001). The sex cannot be certainly determined visually or by body measurements (Fadat 1995) thus, birds were sexed using a molecular method (Lessells & Mateman 1996, Baker *et al.* 1999). For the laboratory measurements in Chizé, 21 birds out of 28 have been sexed successfully (13 females and 8 males) but because of unsolved technical problems, only two could be sexed for the field measurements in Beffou.

Metabolic rates

Within the half-hour after the capture, woodcocks were transported to the laboratory and placed in a rubber fleece-lined box in the dark at 25°C for the rest of the night. Most studies on bird metabolism are done at night in the dark, during the resting period of the daily cycle (Aschoff & Pohl 1970). Because the night is believed to be the most active period for woodcocks during migration and winter (Cramp & Simmons 1983, Ferrand & Gossmann 1995), we measured resting metabolic rates during the day while the birds were in the light. A similar procedure was adopted for other nocturnal species such as owls and frogmouths (Wijnandts 1984 and Bech & Nicol 1999). Moreover, as metabolism measurements must be done in a post-absorptive state, the first night (at least ten hours) was used to let the bird calm down and finish digestion. It is likely that digestion in woodcocks is completed in four hours (Granval 1988).

Metabolic rates were determined by open circuit respirometry. The bird was placed in an airtight transparent Plexiglas box (31 x 20.5 x 21 cm, i.e. 13.3 l) and placed inside a climate room in which the temperature could vary between –20°C and 40°C. The atmospheric air was pumped through the metabolic chamber at a constant rate of 1.40 $l.min^{-1}$, similar at every temperature, measured downstream with an infrared Platon Model 2044 flowmeter, and converted to standard values (Standard Temperature and Pressure Dry: 0°C, 1015 hPa, dry gas). After leaving the chamber, the air was dehumidified by channelling it through two successive dryers systems: first, through an aluminium tube submerged in a tank containing alcohol frozen at –20°C by a compressor, and secondly, through two successive water scrubbers (Drierite). O_2 concentration was measured with a paramagnetic gas analyser (Servomex Model 1100, resolution ± 0.01%) and converted for changes in atmospheric pressure during the course of the experiment. O2 consumption (VO_2) was calculated according to appropriate equations given by Hill (1972). VO_2 was measured every 20 seconds. Metabolic rate values used were from the lowest part of the curve, when they reached a plateau and were stable for at least 10 minutes. The Respiratory Quotient was not measured, therefore, to convert VO_2 into metabolic rate (W), we used an energetic equivalent of 20 kJ l^{-1} O_2, which has been used in most studies on waders under various climates (Kersten & Piersma 1987, Wiersma & Piersma 1994, Kersten *et al.* 1998, Kvist & Lindström 2001). Since woodcocks remained quiet unless they detected the presence of a human, the

windows of the climate room were covered and the birds were watched using a video-camera inside the chamber. Measuring the birds in the light allowed monitoring of their behaviour (stress-induced movements and position). Hence we tested whether metabolic rates and the birds' stress were different in the dark and in the light and no differences were detected.

In the morning, birds were weighed and placed in the respirometer chamber. Birds could be submitted to two treatments. For the first treatment, seven birds (one in 2000 and six in 2001) were measured at constant temperature of 23°C, to investigate whether the metabolic rate varied in relation to the time of the day (morning vs. noon vs. afternoon). For the second treatment, birds were measured at several air temperatures. In this case, the metabolic rate was first measured for 2 hours at high temperature (25-30°C). Birds were then weighed again and the temperature of the room was lowered to 10-15°C, with the bird inside the room. When the temperature was stable, the metabolic rate was measured for 2 hours. One or two more series of measures at lower temperatures (0 to –10°C) were performed depending on the behaviour of each bird (level of stress) and time left before nightfall. We started the measurements at high temperatures and finished at low ones because birds were acclimatised to the thermoneutral temperature at which they spent their first night, which was chosen to minimise the possible loss of mass linked to heat loss. Secondly, this order of decreasing temperatures minimised the condensation in the box, probably not comfortable for the bird. At the beginning of the night, the bird was released and another individual was captured for the following day. No bird was kept more than one day. In 2001, after estimating LCT to be about 17°C in 2000, four experimental temperatures were used: two temperatures above LCT (25° and 20°C) and two temperatures below LCT (10° and –5°C). The metabolic rates measured were called BMR at temperatures above LCT and Standard Metabolic Rate (SMR = BMR + thermoregulatory costs) below LCT.

T3 measures and radioimmunoassays

In 2001, two blood samples were taken at different temperatures to measure the association between T3 hormone levels and metabolic rate. The first blood sample was taken after VO_2 had been measured at thermoneutrality (23 or 25°C) and the second one was taken after the last VO_2 measure in the cold at –5°C. For the six birds in 2001 in which VO_2 was measured at constant thermoneutral temperatures, T3 levels were measured in the morning and evening. Total plasma T3 was determined at the CEBC (Chastel *et al.* 2003) in one assay without extraction in the presence of 8-anilino-1-naphtalen sulfonic acid (ANS) on duplicate samples of 20 µl plasma. ^{125}I-T3 was obtained from CIS Biointernational (OCPE89 T3, 150KBq). Standard T3 (T2877) and T3-binding Antiserum developed from rabbits (T2777) were obtained from Sigma Chem. Comp. Reagents were diluted in 0.075 M barbital buffer (pH 8.6) which contained 0.1% Azide and 26% normal rabbit serum. ^{125}I-T3 bound to antibody was precipitated with appropriate diluted sheep antirabbit delta-globulin serum. The lowest concentration detectable was 0.038 ng ml^{-1}. The intra-assay coefficient of variation was 2.3% (n = 6 duplicates).

Influence of wind and air temperature on FMR

In the field, wind and solar radiation can have large effect on thermoregulation and FMR (Dawson & O'Connor 1996). Weather data (standard air temperatures, direction and wind speed) were collected hourly at Louargat (14 km from Beffou) by Météo France. For a better estimate of the effect of wind on FMR, we used the Standard operative temperature (T_{es}) which combines solar radiation, wind speed and air temperature to give the temperature of a thermally equivalent laboratory enclosure (Bakken *et al.* 1981, Bakken 1990). T_{es} is calculated using the following equation:

$$(1) \qquad T_{es} = T_b - (K_e / K_{es}) \cdot (T_b - T_a)$$

where T_b is body temperature (assumed to be 41°C in woodcock), K_e is the convection-free

conductance, K_{es} is the overall conductance at a wind speed of 1 m s^{-1} and T_a is the air temperature (in °C). The conductance values (in W/°C) are given by the slopes of the regression lines of SMR with T_a.T_{es} can also be calculated as $T_{es} = T_b - H_{sm} / K_{es}$, where H_{sm} is the heat loss for a taxidermic heated mount. Wiersma & Piersma (1994) measured T_{es} in Red Knot *Calidris canutus* using taxidermic heated mounts in various arctic and temperate environments. They calculated H_{sm} according to the formula:

$$(2) \qquad H_{sm} = (K_e + K_u \cdot u^{0.75}).(T_b - T_a) - K_r \cdot R_g$$

where K_u is the conductance of various microhabitats (in W/°C), u is the wind speed (in m s^{-1}), K_r is the radiative conductance in various microhabitats (in W/°C) and R_g is the global solar radiation (in W m^{-}?). Our estimate of T_{es} is done at night and thus $K_r \cdot R_g$ equalled zero. Because the wind effect increases when the body is higher from the surface, Wiersma & Piersma (1994) gave formulas to estimate T_{es} in other species of shorebirds, taking leg length into account. Considering that the Woodcock has an average height of 0.10 m (instead of 0.09 in the knot), we multiplied the wind speed by a corrective factor of 1.036. The value for K_e in the Woodcock is 0.029 W/°C (see results), which is 64.4% below the value in knots (0.045). As a consequence, in woodcocks, $H_{sm} = (0.029 + 0.644 \cdot K_u [u(1.036)]^{0.75}) \cdot (41 - T_a)$. We captured woodcocks in three types of habitats: meadows, wheat seedbeds and corn stubbles. For meadows, we applied the value of 0.00478 W/°C for K_u, measured in vegetated salt marsh by Wiersma & Piersma (1994). For seedbeds and stubbles, we used their value of 0.00809 W/°C for K_u, measured in mudflat and bare marsh. In knots, the ratio K_{es} / K_e is 0.055 / 0.045 = 1.2. Assuming the same ratio in woodcock, $K_{es} = 1.2 \cdot K_e = 0.035$. Therefore, T_{es} in woodcock can be estimated as $T_{es} = 41 - H_{sm} / 0.035$.

Statistical analyses

The LCT was determined using least-squares regressions. Below LCT, we fitted a regression line according to SMR = a1 + b1*Temperature. Above LCT, the slope of the line was set equal to 0. The determination of the best curve fits above and below LCT, based on minimising the combined r^2, was performed with Sigma-plot v.7.0 2001. Means are reported ± 1 SD, unless specified. We used SPSS v.10.0 (SPSS 1999) for comparing means with Student *t*-tests and linear models. To avoid pseudo-replication (Hurlbert 1984), we used stepwise General Linear Mixed Models (GLMM), performed with SAS v.8 (SAS Institute 2000), with individual as random variable to give the same weight to every individual, whatever the number of recordings (Littel *et al.* 1991). To assess the relationships between SMR or T3 with environmental factors and individual characteristics, we performed a set of stepwise GLM. Individual characteristics that were correlated were included separately in the analysis.

RESULTS

Body mass

The mean body mass of woodcocks at the time of capture at Chizé was 317.3 ± 19.2 g (n = 28) for both years. There was no difference between years (318.4 ± 21.5 g in 2000 (n = 14) and 316.1 ± 17.4 g in 2001 (n = 14); $t_{26} = 0.310$, $P = 0.759$). For both years, body mass did not differ between adults and juveniles (322.6 ± 20.5 g (n = 15) and 311.2 ± 16.2 g (n = 13) respectively, $t_{26} = 1.619$, $P = 0.117$) but females were heavier than males (322.5 ± 16.4 g (n = 13) and 304.8 ± 15.1 g (n = 8) respectively, $t_{19} = -2.48$, $P = 0.023$). Woodcocks caught near the Beffou forest had similar masses (mean 311.4 ± 20.2 g, n = 38) to those caught near Chizé at the time of capture ($t_{64} = -1.197$, $P = 0.236$). At the time of BMR measurement (i.e. after a night of fast), the mean body mass was 286.0 ± 19.3 g for the 28 birds and the lean body mass was 258.2 ± 15.6 g (n = 14 birds because measures of skull and ulna, necessary to estimate lean mass, were only available in 2001).

Metabolic rates

For the seven birds measured at 23°C, there was a significant difference in SMR and body

mass during different times of the day and a strong individual effect (GLMM : $F_{1,11} = 6.58$, $P = 0.026$ for period of the day; $F_{1,11} = 7.60$, $P = 0.019$ for body mass; $F_{1,11} = 5.78$, $P = 0.035$ for interaction period * body mass), with values for SMR being 1.27 ± 0.30 W in the morning, 1.16 ± 0.38 W at noon and 1.10 ± 0.28 W in the evening. However, as the birds lost mass during the day, when SMR was weighed by body mass, the effect "period of the day" was no longer significant (GLMM : $F_{1,13} = 3.21$, $P = 0.097$ for period of the day). BMR was 1.211 ± 0.317 W (n = 49 measurements on 28 individuals) i.e. 104.6 ± 27.5 kJ d^{-1} (Fig. 1). There was no significant relationship between mean BMR and mean mass at the time of measurement (r? = 0.032, $F_{1,25} = 0.816$, $P = 0.375$, $n = 27$). LCT was 17.5 ± 3.7 (SE)°C. The regression equation between SMR and air temperature (T_a) was SMR (in W) = –0.029 T_a(°C) + 1.725 (r? = 0.413). Extrapolating T_a to SMR = 0 resulted in an estimated T_b of 59.5°C.

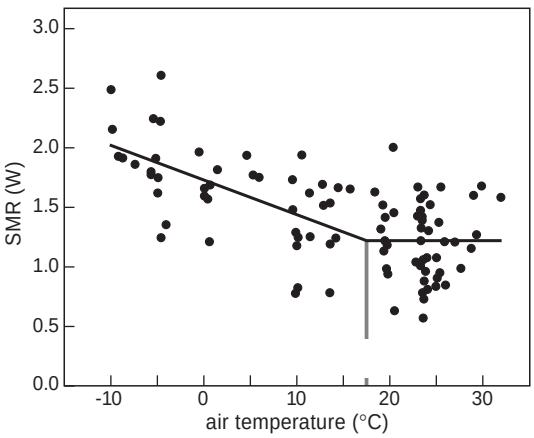

Fig. 1. Standard Metabolic Rate (SMR) in relation to ambient air temperature (Ta, °C). LCT indicates the Lower Critical Temperature (dashed line). The data are from 28 individuals, from two years.

SMR was only influenced by temperature and an individual effect, but not by individual characteristics (age, sex, total body mass, lean body mass, mass of proteins), date (year, date in the month) and behaviour (position = standing *vs.* resting on tarsi *vs.* laying) (GLMM: for temperature : $F_{1,37} = 56.99$, $P < 0.0001$; all $P > 0.05$ for the other parameters). Likewise, there was no relationship between BMR and estimated lean body mass (r? = 0.009, $F_{1,12} = 0.110$, $P = 0.746$, $n = 14$) and between BMR and estimated protein mass (r? = 0.016, $F_{1,18} = 0.294$, $P = 0.595$, $n = 20$).

Calibration between T3 and metabolic rates

At constant temperature, levels of T3 were similar in the morning and in the afternoon (paired t-tests $t_3 = -0.731$, $P = 0.517$, $n = 4$ because there was no blood sample in the afternoon for two individuals out of the six measured in 2001). The relationship between T3 levels and SMR was not significant at thermoneutrality (r? = 0.145, $F_{1,12} = 2.039$, $P = 0.179$, $n = 14$ individuals, including 8 individuals measured at variable temperature and 6 measured at constant temperature) although there was a positive trend at –5°C, ($r^2 = 0.433$, $F_{1,6} = 4.578$, $P = 0.076$, $n = 8$). However, T3 levels were significantly increasing when SMR was increasing in response to decreasing temperature from 25°C to –5°C ($r^2 = 0.525$, $F_{1,20} = 22.08$, $P < 0.0001$; SMR = 0.815 + 0.338*T3; Fig. 2). Levels of T3 at low ambient

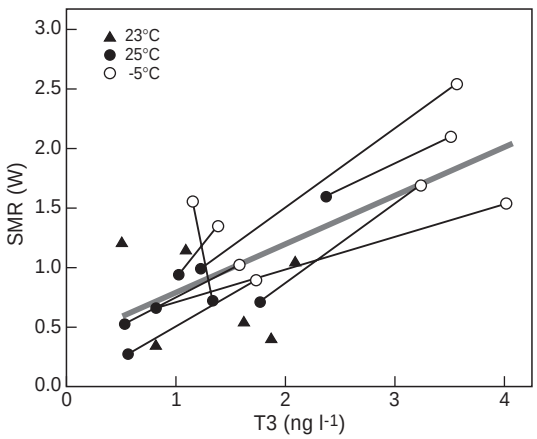

Fig. 2. Relationships between T3 and SMR for 8 individuals measured at two temperatures [at 25°C (black dots) and at –5°C (white dots), lines connecting measurements of the same individuals] and for 6 individuals measured twice at 23°C (black triangles representing the mean of the two measures).

temperature (–5°C) were twice as high as at thermoneutrality (+ 209%) (2.53 ± 1.12 ng l^{-1} at –5°C *vs.* 1.21 ± 0.63 ng l^{-1} at 25°C, n = 8; paired t-test t_7 = -3.511, P = 0.010). For the same individuals, the elevation of metabolic rate between 25°C and –5°C was significant (+ 160%; paired t-test t_7 = –5.268, $P < 0.001$).

T3 measures in the field

The mean T3 value in the field was 3.43 ± 1.10 ng l^{-1} (range 1.81 to 6.41 ng l^{-1}, Fig. 3). Temperatures at the time of capture averaged 4.2 ± 2.8 °C but ranged from -2.5°C to 10.4°C, providing a good representation of the average winter temperatures in Brittany. This average field value of T3 was 2.8 times the value at BMR in the laboratory. In the field, T3 levels were only influenced by the standard operative temperatures T_{es} (Stepwise GLM: r^2 = 0.18; $F_{1,36}$ = 7.905, P = 0.008), not by age, total body mass, lipid mass, lean body mass, air temperature, date, cold spell (before, during, after), hour (all $P > 0.05$) (Fig. 3). The regression line between T3 and T_{es} in the field was almost parallel but c. 10% higher than the regression line representing SMR in the laboratory (Fig. 3). When extrapolating the residuals of the data in the field following this field regression to the T_{es} corresponding to LCT (LCT_{es} = 22°C), T3 was estimated at 1.327 ± 0.996 ng l^{-1}. Following the regression from Fig. 2, this gave an extrapolated value of FMR of 1.263 ± 0.337 W i.e. 4.3% higher than the BMR measured in the laboratory but with a similar standard deviation.

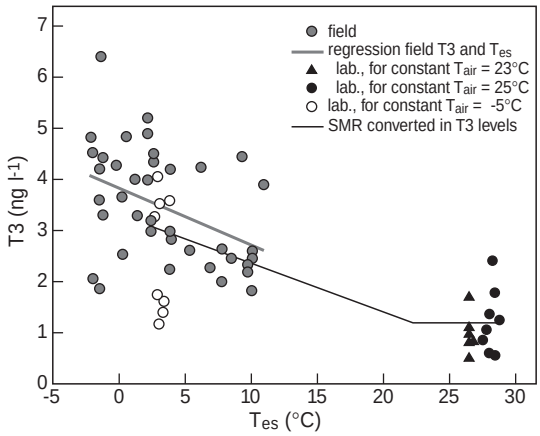

Fig. 3. T3 levels in relation to standard operative temperature Tes. Laboratory measures included 8 individuals measured at 25°C (black dots) and –5°C (white dots) and 6 individuals measured at constant 23°C (black triangles representing the mean of the two measures). The dashed line represents SMR converted to T3 values (following the relationship in Fig. 2) and with a LCT of 17.5°C. Grey dots represent field measures, at wind speed varying between 0 and 6 m s^{-1} (n = 38 individuals). The solid line is the regression between T3 in the field and Tes (T3 = 3.829 – 0.113*Tes, r? = 0.18; F1,36 = 7.905, P= 0.008).

DISCUSSION

Gavrilov & Dolnik (1985) measured a single Eurasian Woodcock and reported a BMR of 186.7 kJ d^{-1} (= 2.15 W) for this bird (430g), that was 1.5 times heavier than the woodcocks used in our study. This difference in body mass may explain why their value of BMR exceeded our average BMR by 178%. Our BMR value was 40% lower than predicted for shorebirds (Haematopodidae, Scolopacidae and Charadriidae) during winter in temperate zone (Kersten & Piersma 1987) (Fig. 4). It was also 15% to 39% below the values for non-passerine birds estimated by Lasiewski & Dawson (1967), Aschoff & Pohl (1970), Kendeigh *et al.* (1977) and Daan *et al.* (1990). Our results are consistent with the low levels of BMR found in the American Woodcock (Vander Haegen *et al.* 1994). BMR in American woodcocks was 18% below the values predicted by Kersten & Piersma (1987) and Daan *et al.* (1990), but 8%, 17% and 3% above the values predicted by Lasiewski & Dawson (1967), Aschoff & Pohl (1970) and Kendeigh *et al.* (1977) respectively.

Vander Haegen *et al.* (1994) suggested two hypotheses to explain the low values of BMR in woodcocks. First, birds used for their experiments were raised in captivity for several months which may have affected their metabolic rates. Our results from wild birds confirm the low BMR and thus make this hypothesis less likely. Second, woodcocks have different natural history than "typical shorebirds". If BMR is associated with

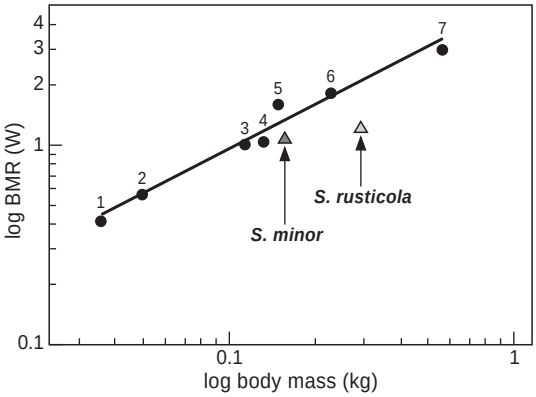

Fig. 4. Basal Metabolic Rate (BMR) in relation to body mass for 2 species of woodcocks [triangles : *Scolopax minor* (Vander Haegen et al. 1994) and *S. rusticola* (this study)] and for 7 species of shorebirds wintering in temperate areas [dots: (1) Little Ringed Plover *Charadrius dubius* (Kendeigh *et al.* 1977); (2) Sanderling *Calidris alba* (Castro 1987); (3) Turnstone *Arenaria interpres* (Kersten & Piersma 1987); (4) Knot *Calidris canutus* (Piersma *et al.* 1996a); (5) Redshank *Tringa totanus* (Speakman 1984); (6) Grey Plover *Pluvialis squatarola* (Kersten & Piersma 1987); and (7) Oystercatcher *Haematopus ostralegus* (Kersten & Piersma 1987)]. The line represents BMR predicted for shorebirds in temperate winter (Kersten & Piersma 1987).

Daily Energy Expenditure (DEE) (Kersten & Piersma 1987; Daan *et al.* 1990; Nilsson 2002), differences in ecology and behaviour causing differences in DEE, would result in differences in BMR. The largest difference between woodcocks and other shorebirds is the type of habitat used. Woodcocks, which live all year-round in a sheltered forested habitat, are probably more protected from wind than shorebirds living in coastal or grassland habitats (Vander Haegen *et al.* 1994). For a single Red Knot at 0°C, energetic expenditure increases by 30% when wind speed increases from 0 to 1 $m.s^{-1}$ (Wiersma & Piersma 1994). Using heated taxidermic mounts, Wiersma & Piersma (1994) showed that heat loss was lowest in dense vegetation, compared to mudflats, tundra or birds in flocks. Metabolic rate of the Ruffed Grouse *Bonasa umbellus*, exposed to a wind speed of 4.4 $m.s^{-1}$ and a temperature of –20°C, was 2.3 x BMR (Thompson & Fritzell 1988b). Ruffed Grouse can save 4 times more energy by resting in coniferous instead of deciduous trees (Thompson & Fritzell 1988a). Wind speeds in coniferous roosts were approximately 25% of those in the open and in deciduous roosts about 50% of those that in the open (Thompson & Fritzell 1988a). Shielding from wind is the major energetic benefit of roost use (Walsberg 1986). A high level of BMR as a protection from heat loss would not be useful in a temperate sheltered habitat. Comparing families of birds, Bennett & Harvey (1987) showed that families living in forest or woodlands had lower BMR than families living in marshes, tundra or at sea. This hypothesis is also supported by the fact that migratory waders have a lower BMR in tropical wintering grounds than in temperate areas and increase their BMR when breeding in the Arctic (Castro *et al.* 1992; Lindström 1997; Kersten *et al.* 1998; Kvist & Lindström 2001; Lindstrom & Klaassen 2003). Another difference in natural history between woodcocks and shorebirds relates to nocturnal habits. Low levels of BMR are also found in nocturnal birds such as owls (Strigiformes; Wijnandts 1984; Weathers *et al.* 2001), nightjars (Caprimulgiformes; McNab & Bonaccorso 1995; Bech & Nicol 1999), kiwis (Apterygidae; Calder & Dawson 1978) and in another nocturnal wader, the Stone Curlew *Burhinus oedicnemus* (Duriez, unpubl. data). It was suggested that a lower BMR may be an adaptation to the nocturnal life (Wijnandts 1984; Bennett & Harvey 1987; Bech & Nicol 1999). A nocturnal bird could choose a favourable microclimate (warmer due to the sun rays and shelter in the case of the Woodcock) for the diurnal resting phase and thus may have low thermoregulatory costs at this time. During the night, when heat loss is maximal in diurnal birds, thermoregulation costs should also be lowered in nocturnal birds because the heat generated by locomotion and foraging could partly substitute to thermoregulation process (Paladino & King 1984; Webster & Weathers 1990; Zerba & Walsberg 1992; Bruinzeel & Piersma 1998). It is not currently possible to separate these two hypotheses (sheltered habitat or nocturnal life) to explain the

low levels of BMR in woodcocks, and more studies are needed on the energetics of inland waders (lapwings, plovers, snipes, pratincoles), in summer as well as in winter.

Insulative properties

The LCT of 17.5°C is close to the measured value of 18°C found in Eurasian Woodcock by Gavrilov & Dolnik (1985) and the predicted value of 17°C calculated from Kendeigh *et al.* (1977). The conductance values in Eurasian woodcocks were low compared to waders (Kersten & Piersma 1987) and other birds (48% below the value predicted by Aschoff (1981). As in most studies, if SMR was set equal to zero at an air temperature equal to body temperature (41°C), the LCT would have been 16°C and the conductance would have been 0.044 W/°C (similar to Red Knot and most shorebirds). Our LCT value was close but our approach, without fixing any preconceived value for y0, allowed for independent determination of conductance. Vander Haegen *et al.* (1994) also found an extrapolated body temperature of 55°C, which was 14° above the average body temperature for birds (41°C). Hence, Eurasian and American woodcocks must be well insulated by their plumage (Calder & King 1974; Schmidt-Nielsen 1994), a finding known also from other nocturnal birds such as Long-eared Owls *Asio otus* (Wijnandts 1984). Total plumage mass in woodcocks is about 24.5 g for a mean body mass of 316 g, which represents 7.7% of total body mass (Boos 2000). In Red Knot, the contour feather dry mass varies between 2.5 to 5.5% of total body mass (Piersma *et al.* 1995). Among 16 species of waders (body mass range 27 - 827 g), the mean feather mass represents 5.4 ± 1.0% of the total body mass (T. Piersma and P. Battley, pers. comm.). This supports the idea of a higher insulation of plumage (i.e. low thermal conductance) in woodcocks compared to other shorebirds.

T3 as a predictor of FMR

Metabolic rate responds rapidly to changes in T3 levels because their relationship is causal. Metabolic rates increase shortly after experimental administration of T3, while thiouracil (which blocks T3 action) causes metabolic rate to decrease (McNabb 2000). The turnover rate of T3 in birds is relatively high because birds lack a specific T3-transporting protein in their blood (McNabb 2000). Since metabolism closely tracks variation in T3, T3 measurements will not integrate different behavioural costs and only reflect thermoregulatory requirements of birds under the circumstances of capture. The use of T3 to estimate FMR from a single blood sample, without need to recapture the animal later, will be helpful for difficult and shy species. However, this method still needs improvements because today, it still requires for each species a calibration between metabolic rates measurements (with standard methods) and hormone levels. Further studies should investigate the inter-specific relationship between T3 and metabolic rates, to permit a direct measurement of FMR via T3 levels without calibration experiments, which are time-consuming and difficult for some species.

We assumed that T3-levels provided a good estimate of FMR, rather than BMR, because the woodcocks that we captured in the fields were actively foraging and not resting. From our T3 measurements, we estimated that the woodcock's FMR at night in winter was 2.8 times BMR. These values are lower those commonly found in shorebirds: 4 x BMR (Castro *et al.* 1992; Piersma 2002). They were also low for a 286-g non-passerine bird when compared with existing allometric equations [3.9 to 5.3 x BMR with Nagy (1987); Daan *et al.* (1990); Williams *et al.* (1993) and Hammond & Diamond (1997)].

Elevated T3 levels at low temperatures and significant correlations between T3 and metabolic rate were also found in domestic chickens (Bobek *et al.* 1977), Northern Cardinals *Cardinalis cardinalis* (Burger & Denver 2002), Red knots (Jenni-Eiermann *et al.* 2002), House Sparrows *Passer domesticus* (Chastel *et al.* 2003) and Black-legged Kittiwakes *Rissa tridactyla* (O. Chastel, unpubl. results). In the last two studies, individual variations in T3 explained a significant part of individual variation in BMR. Hence, T3 is an indicator of thermoregulation and of metabolic rate.

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SAMENVATTING

De energetica van steltlopers is uitgebreid bestudeerd, maar deze studies hebben zich met name gericht op steltlopersoorten van kust en moeras. De Houtsnip *Scolopax rusticola*, een soort van bossen en graslanden, neemt dan ook een uitzonderlijke plaats in binnen de steltlopergroep. De auteurs hebben gedurende de winter in Frankrijk de stofwisseling van Houtsnippen bepaald met behulp van metingen aan het zuurstofverbruik in het laboratorium en aan T3-hormoonniveaus in het veld. Houtsnippen hadden een lage kritieke temperatuur (17,5°C), rond de verwachte waarde, een laag basaalmetabolisme (1,2 W) en een hoge isolatie van het verenkleed, vergeleken met andere steltlopersoorten. In het laboratorium was het T3-niveau positief gecorreleerd met de stofwisseling. Met behulp van deze correlatie hebben de auteurs de T3-niveaus van vrij levende Houtsnippen gebruikt om het energieverbruik in de winter in het veld te schatten. Dit energieverbruik was ongeveer 2,8 keer het basaalmetabolisme (3,4 W). Daarmee zijn de energetische bestaanskosten, zowel in het laboratorium als in het veld, voor Houtsnippen lager dan voor steltlopers van winderige, onbeschutte biotopen. Houtsnippen zijn wellicht energiezuinig, doordat ze overdag op een beschutte plek rusten en 's nachts actief zijn. Tijdens de koudere nacht kunnen ze wellicht de warmte die geproduceerd wordt als gevolg van hun activiteit, direct aanwenden voor hun thermoregulatie. (IT)

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