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EFFECTS OF MICROHABITAT, FLOCKING, CLIMATE AND MIGRATORY GOAL ON ENERGY EXPENDITURE IN THE ANNUAL CYCLE OF RED KNOTS¹

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Abstract. We quantify seasonal changes in the maintenance energy requirements of Red Knots (*Calidris canutus islandica*). This subspecies breeds on the tundra of northeast Canada and north Greenland, migrates through Iceland and spends the winter in the coastal regions of western Europe. Maintenance Metabolism (M_{maint}) is defined as Basal Metabolic Rate plus extra costs for thermoregulation at environmental temperatures below the thermoneutral zone. M_{maint} of Red Knots resting in different microhabitats was estimated on the basis of measurements with heated taxidermic mounts, which were calibrated with forced convection against postabsorptive live birds resting over a range of air temperatures (i.e., against their Standard Metabolic Rate). Based on a physically realistic regression model for heat loss, we established the relationships between the electric power consumption of the mounts and three critical weather variables affecting dry heat loss: air temperature, wind speed and global solar radiation. Observations of Red Knots' use of different microhabitats (including their occurrence in flocks of different bird density) and orientation into the wind were collected on the wintering and on the breeding grounds. At lower standard operative temperatures on the coastal wintering grounds they foraged in tighter flocks and more often faced into the wind, saving 8% compared to solitary birds standing with their flanks exposed. We then used (1) microhabitat-specific equations, (2) long-term meteorological data sets, and (3) estimates of habitat use and wind orientation of free-living Red Knots at the different locations and times of the year, to reconstruct the seasonal patterns in M_{maint} in the field. Average predicted M_{maint} varied between 2.93 W in January and 1.64 W in August on the Dutch wintering areas. The maximum monthly M_{maint} in winter was higher than that reached on the Canadian breeding grounds (2.28 W, or 0.78 times the Dutch January cost) and on the Icelandic staging grounds (2.27 W, or 0.77 × the Dutch cost in January, in spring, and 1.98 W, or 0.68 ×, in fall). Based on 31 years of weather data from the Dutch Wadden Sea in the period 1960–1991 (assuming that Red Knots have not changed their behavior), the long-term overwinter average of M_{maint} was 2.57 W, with an average monthly minimum of 1.87 W and a maximum of 3.05 W. The west-central coast of France, 900 km more to the south, offers energetically cheaper conditions (0.76 × values for the Dutch coast in January) in the nonbreeding season than the Wadden Sea. If *islandica* knots moved on to West Africa during the nonbreeding season they would incur a saving of 1.13 W on M_{maint} , and pay an extra 0.13–0.22 W to cover the cost of travel.

Key words: Arctic; climate; energetics; flocking; maintenance metabolism; microhabitat; migration; Red Knot; roosting.

INTRODUCTION

With a resting core temperature of 40–41°C, 3–5°C higher than mammals, birds are the highest

temperature endothermic vertebrates (Whittow 1986, review in Prinzinger 1990). The environment is usually cooler than their bodies and the insulation provided by plumage is comparatively small. The smallest birds have the highest relative conductance as well as the narrowest temperature range over which they do not have to

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metabolize extra fuel to remain warm (the thermoneutral zone; Aschoff 1981). Hence, under the same climatic conditions, the smallest bird species incur the highest relative heat loss (Visser 1991). Because wind increases conductance (Bakken 1980, 1990, 1991), relatively small birds living under windy conditions must have particularly high levels of maintenance metabolism (M_{maint}), which is the Basal Metabolic Rate plus extra costs for thermoregulation at environmental temperatures below the thermoneutral zone.

Shorebirds using coastal habitats are relatively small and live exposed to the elements (Piersma, in press). Analysis of latitudinal variation in the energetics of Sanderlings (*Calidris alba*) by Castro et al. (1992), has shown that use of environments which are costly in terms of heat loss are indeed accompanied by high field metabolic rates. Shorebirds migrate enormous distances, encountering a large variety of climates in the course of their annual cycles. Whether this leads to greater or smaller seasonal variation in energy expenditure than a sedentary way of life in a single seasonal environment remains unknown.

The few published studies measuring the contribution of M_{maint} to annual energy budgets all dealt with sedentary groups of birds (Kendeigh 1972, Kendeigh et al. 1977, Mugaas and King 1981, Walsberg 1983b, Wijnandts 1984, Masman et al. 1988, Warkentin and West 1990). In his pioneering work, Pearson (1954) predicted the energy requirements of free-living hummingbirds on the basis of metabolic measurements under free convection and in the absence of short-wave radiation (Standard Metabolic Rate). Later studies (Mugaas and King 1981, Warkentin and West 1990, Weathers and Sullivan 1989) were more sophisticated in estimating the modifying effects of wind and radiation on M_{maint} in different habitats, using either the theoretical tools of environmental physics (Birkebak 1966, Porter and Gates 1969, Campbell 1977, Gates 1980, Monteith and Unsworth 1990), or the slightly more "empirical" approach employing heated taxidermic mounts advocated by Bakken and coworkers (Bakken et al. 1981, 1983, 1985; Bakken 1992; see Buttemer 1985 and Masman et al. 1988 for applications).

The current study describes seasonal changes in M_{maint} of a long-distance migrant shorebird that breeds in the High Arctic. We take as our example one of the five subspecies of Red Knot (*Calidris canutus islandica*) (Piersma and Davidson 1992), which breeds in north Greenland

and northeast Canada and spends the nonbreeding season along the seashores of northwestern Europe (Davidson and Wilson 1992), being the only subspecies that winters north of the tropics. Red Knots are well suited for the purpose of analyzing maintenance and thermoregulatory requirements, as they live in rather simple, two-dimensional habitats with little variation in the climate-microclimate relationships, wherever they occur. This study is part of a larger research program aimed at unraveling the energetic costs, benefits and constraints of long-distance migration between the High Arctic and a variety of nonbreeding latitudes (e.g., Piersma et al. 1991, 1993a).

By integrating laboratory and field approaches to describe the thermal environments of a migrant species throughout the annual cycle while also examining the behavioral responses by which the birds modify these, we address some of the major research challenges identified by Walsberg (1983a) in his review of ecological energetics. We have done so by exploiting as fully as possible the "heated taxidermic mount" approach of predicting standard operative temperatures (or, inversely, maintenance metabolism), leading to microhabitat-specific equations based on a few commonly measured standard weather variables. This makes it possible to use the great potential of the existing meteorological databases to shed light on the seasonal energetics of a worldwide traveler.

METHODS

THE APPROACH

Empirical functions to predict maintenance metabolism of free-living Red Knots in different microhabitats on the basis of the three standard weather variables (air temperature, wind speed and global solar radiation), were derived from series of measurements with heated taxidermic mounts, combined with the function to convert heat loss of the mounts into heat loss of live birds (Fig. 1). The latter function was derived from the two linear functions of heat loss (of mounts and of live birds) on temperature measured under similar wind- and radiation-conditions in the laboratory (Fig. 1). The development of a physically realistic regression model (see below) made the microhabitat-specific functions linear, except for the fact that the heat loss (or maintenance metabolism) of live birds is never lower than

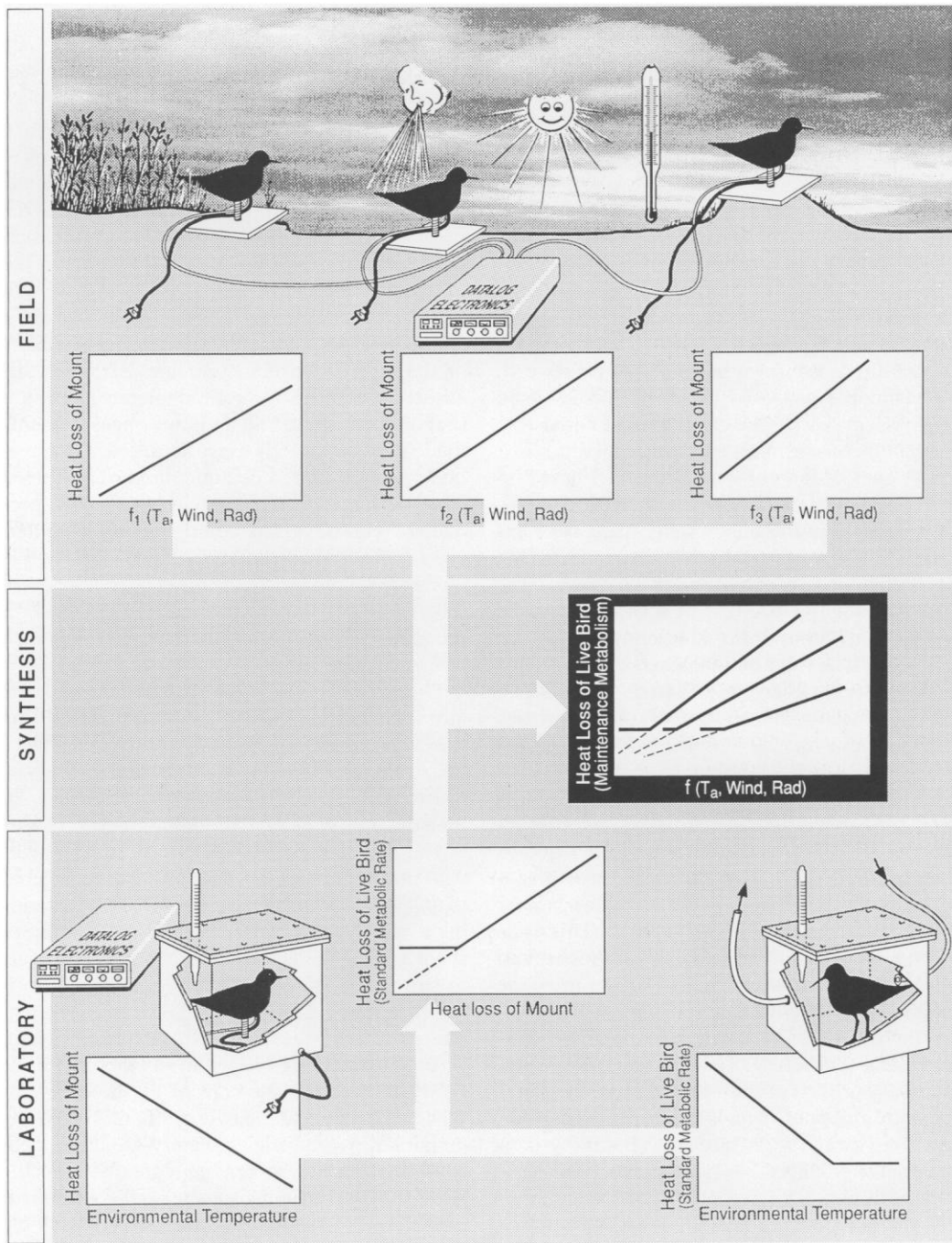


FIGURE 1. Outline of a way to derive a series of microhabitat-specific functions to predict the heat loss of Red Knots based on air temperature (T_a), wind speed (Wind) and global solar radiation (Rad). Heated taxidermic mounts employed in different microhabitats in the field (top row), yield the microhabitat-specific functions of heat loss of the mounts based on a physically realistic regression model (first row of graphs). These functions are converted in functions predicting heat loss of live birds (maintenance metabolism, second “row”) on the basis of the empirical relationships between heat loss of mounts and live birds (third “row”). The latter function is derived from measurements of heat loss of mounts and of live birds under identical environmental conditions (bottom row). For graphical simplicity, standard respirometry boxes instead of the windtunnel, are illustrated here.

basal metabolic rate. This exception explains the breakpoints in the linear relationships between heat loss of live birds and other variables (Fig. 1).

HEATED TAXIDERMIC MOUNTS

The heated taxidermic mounts, or "copper knots," are devices closely resembling live Red Knots but electrically heated to a constant core temperature (T_m) similar to the body temperature (T_b) of the living bird. (Our terminology and abbreviations conform as much as possible to the standards proposed by Bligh and Johnson 1973.) Heat loss to the environment equals the measured consumption of electric energy.

The construction of the mounts was based on the instructions of Bakken et al. (1983, 1985). Since several modifications were made, we summarize our procedure. A carefully skinned Red Knot corpse was used as a mold. To preserve the feathered skin for later use, it was cleaned of fat and dabbed with a Borax solution that also kept it flexible. The remaining feather- and skin-free body was deep-frozen and coated with artificial rubber. When the rubber was dry, the rubber was cut open and carefully peeled off, producing a good quality mold which was then filled with melted beeswax. After the beeswax had hardened, the rubber mold was again peeled off, leaving a wax replica of the skinned Red Knot. A narrow tunnel was drilled from the rear diagonally towards the back, in which a hollow copper tube (diameter 5 mm) was placed. This tube functioned as a bridge strengthening the cast and was used to place thermistors in the centre of the mount. A spiral groove (total length about 1 m) was carved in the wax covering most of the mount (including the head) to accommodate a heater wire. After covering the wax mount with graphite, a thin copper layer of about 0.2 mm was deposited over the surface of the wax by connecting the graphite-covered wax mount to a DC power supply (5 V) and placing it for two days in a sulphuric acid bath containing a copper anode. The sulphuric acid solution was continuously stirred with an aquarium pump to get an even deposition of copper over the entire surface. Next, the heater wire, which was insulated by putting a silicon tube around it, was glued into the preformed groove. A second 0.2 mm copper layer was then deposited, covering the heater wire and thickening the copper cast. The beeswax was then removed by placing the mount in boiling

water and letting the wax run out through a small hole on the rear end of the cast.

The skin was then placed on the copper cast. A heat-conducting paste commonly used in electronics was put between the copper cast and the skin to avoid insulating air cushions between the two layers. The head and rear end of the skin were fixed to the copper cast with glue and the incision on the belly closed with needle and thread. Plumage was "waterproofed" with a commercial tent spray, the spray having no effect on the appearance of the plumage. Although this ensured that the models could tolerate some rain (but not more than half an hour), measurements made in rainy periods were discarded. For a second set of mounts, a ceramic mold of a skinned body was used. A total of eight mounts was produced, four of which could be used simultaneously. Seven had winter plumage skins and one a breeding plumage. In the absence of noticeable differences, we pooled the data obtained with mounts produced from different casts and with different plumage types.

The mounts had no legs. Measurements of surface temperatures of legs and feet of Red Knots showed that heat loss through these parts is negligible at air temperatures below the thermoneutral zone (Wiersma et al. 1993, L. Bruinzeel, T. Piersma and P. Wiersma, unpubl. data).

The heater wire (nickel-chromium, diameter 0.34 mm, total resistance $\pm 10 \Omega$) was connected to an electrical power supply (car battery), yielding V, which was usually 12 V DC but sometimes slightly less. We registered V at regular intervals to correct for these small variations. A thermostat (Proportional Integrated Differentiating regulator, accuracy: 1°C, TOHO Electronics Inc., Tokyo) registering T_m with a thermocouple (PT100) placed in the core of the mount, kept T_m at 41°C, close to the average T_b of Red Knots (unpubl. data). Balancing battery-life under field conditions (frequent readings greatly reducing battery-life) with consistency of the estimated power consumption of the mounts, every 20 sec a digital datalogger (Squirrel 1200, Grant Instruments, Cambridge, UK) sampled the voltage, V, over the heater wire and T_m . For the latter measurement a thermistor (NTC) was situated next to the thermocouple inside the mount. Voltage was either approximately 12 V or zero. The datalogger recorded the average values of voltage, V_m and T_m , from 90 measurements equally spread over a 30 min period. The voltage on-off patterns

were irregular and independent of the datalogger sample cycle.

The ratio V_m/V , gives the estimated proportion of time that electricity flowed through the heater wire (i.e., t_e) during the 30 min recording interval. The total resistance of the heater wire plus cable, R_m , was measured and therefore the energy consumption of the mount, H_m , can be calculated from:

$$H_m = t_e \cdot V^2/R_m \quad (1)$$

where H_m is measured in W. It would have been more elegant to separate the resistance values for model and cable. We estimate that 5% of the measured heat loss was from the cable. The calibrations of live birds to mounts with attached cables in standard laboratory environments compensated for most of this small bias.

HEAT LOSS OF LIVE BIRDS IN A STANDARD ENVIRONMENT

Oxygen consumption of adult Red Knots was measured inside an isothermal 60 liter respirometry system at a wind speed, u , of 1 m/sec (following Bakken 1976, but see Bakken 1992). The wind was generated by a fan in a closed circuit. Outside air was pumped through the respirometry unit at a rate of about 100 liter/hr. Oxygen consumption under wind-free conditions was measured in a 25 liter plexiglass box of which the walls were covered with black paper to reduce radiation effects. Outside air was pumped through the box at a rate of 100 liter/hr.

The oxygen concentration of the dried ingoing and outflowing air was measured in a calibrated oxygen analyzer (AMETEK Applied Electrochemistry Pittsburgh, PA, USA, Models S-3A and S-3A/II) with an accuracy of 0.002% (manufacturer's calibration). Flow rate was controlled and measured with a Mass Flow Controller (Brooks Instruments, Veenendaal, The Netherlands, Model 5850E) to an accuracy of 0.4% (manufacturer's calibration). The use of a mass flow meter made it unnecessary to convert the data to standard temperature and pressure. Oxygen consumption in ml/h was calculated after Hill (1972). As post-absorptive Red Knots were mainly consuming fat (RQ is approximately 0.73, unpubl. data), the energy equivalent per volume oxygen was taken as 20 kJ/liter O_2 (Schmidt-Nielsen 1975, Bartholomew 1977, Gessaman 1987, Gessaman and Nagy 1988).

The live Red Knots had been in captivity for

over a year, after being captured in the Dutch Wadden Sea in October 1988. They were fed with protein-rich trout-food pellets and showed the normal circannual cycle of changes in body mass (T. Piersma, unpubl. data). Before the oxygen measurements, which took place in complete darkness and lasted for about 18 hr, the birds were deprived of food (but not of fresh water) for 24 hr. A total starvation time of approximately 42 hr produced no ill effects in the birds. Over the period in the respirometer, they decreased in body mass from an average of 129.8 g (range 96.2–173.7 g) to 120.5 g (range 87.2–165.3 g), resulting in an average mass loss of 9.2 g (range 5.4–15.2 g).

Only one air temperature per night was used, and no values were used from the first 3 hr after a bird had entered the respirometry system. Oxygen consumption was measured every minute. Metabolic rates used here were selected as the low point of the running mean of 120 measurements. We simultaneously estimated Standard Metabolic Rate, SMR, Basal Metabolic Rate, BMR (this is the SMR-value above the lower critical temperature), overall conductance at a wind speed of 1 m/sec, K_{es} , the convection-free conductance, K_c , and the lower critical temperatures, T_{lc} , for wind speeds of 1 m/sec and 0 m/sec, according to the "Scholander"-model (Scholander et al. 1950), on the basis of a total of 86 data points using an iterative regression model (SYSTAT, Wilkinson 1990). We assumed constant values for K_{es} and K_c over the range of temperatures below T_{lc} , and zero metabolism when the metabolic rates measured below T_{lc} would be extrapolated to an air temperature, T_a , equal to T_b (41°C) (McNab 1980). SMR is related to T_a as follows:

$$SMR = K_{es}(T_b - T_a), \quad \text{when } T_a < T_{lc} \quad (2a)$$

$$SMR = BMR, \quad \text{when } T_{lc} < T_a < T_{uc}. \quad (2b)$$

As SMR is in W and the temperatures are in °C, K_{es} is in W/°C. T_{uc} is the upper critical temperature (38–40°C, N. Verboven, pers. comm.), but no measurements were taken at temperatures approaching it.

Maintenance Metabolism (M_{maint}) is defined as the metabolic rate of postabsorptive birds resting or sleeping in different microhabitats. Maintenance Metabolism is a shorthand for the residual component of the daily energy expenditure excluding activity, heat increment of feeding (HIF),

energy retention (storage) and cost of synthesis. It is the (nearly) obligatory energy expenditure covering BMR and the extra costs of thermoregulation (see Walsberg 1983b and Weathers and Sullivan 1989 for an earlier use of the term). In the laboratory-“microhabitats” SMR equals M_{maint} . We avoid the term Resting Metabolic Rate to describe our measure of energy expenditure (e.g., Gessaman 1973), since it is defined to include the energy expended on digestion and absorption of food (Bligh and Johnson 1973).

HEAT LOSS OF MOUNTS IN STANDARD ENVIRONMENTS

The energy expenditure of the heated taxidermic mounts at a range of air temperatures (-20°C to $+40^{\circ}\text{C}$) was measured in a respirometry unit with u equal to 1 m/sec, i.e., in similar conditions to which the live birds were subjected. The relation between H_m and T_a was estimated using a simple linear regression model to fit the model derived from “Newton’s law of cooling”:

$$H_m = K_{\text{esm}}(T_m - T_a) \quad (3)$$

where K_{esm} is the overall conductance of the mount in the standard environment ($\text{W}/^{\circ}\text{C}$). The value of K_{esm} varied between the mounts, and also increased with time. Mean K_{esm} of four new mounts was $0.063 \text{ W}/^{\circ}\text{C}$ (range $0.058\text{--}0.074$). After 10 months it had increased to $0.094 \text{ W}/^{\circ}\text{C}$ (range $0.077\text{--}0.104$). Consequently, K_{esm} of the different mounts had to be estimated several times during the period of usage. Calibration exercises were usually carried out just before or after the field measurements. For the few remaining field measurements made in the interval between two calibration exercises, linearly interpolated values for K_{esm} were used. All equations calculated from the different mounts and measuring periods were adjusted to a standard mount with a K_{esm} of $0.055 \text{ W}/^{\circ}\text{C}$ (this being the value for conductance measured in live birds at $u = 1 \text{ m/sec}$, see Results) and a standard core temperature of 41°C according to:

$$H_{\text{sm}} = 0.055 \cdot (41 - (T_m - H_m/K_{\text{esm}})) \quad (4)$$

where H_{sm} is the heat loss of the standard mount in W . In doing so, we assumed that the mounts’ absorptances to solar radiation varied in the same way over time as their conductances.

The manner in which the effects of air temperature, wind and radiation are combined in the mounts and in the live birds, was thus only

calibrated under a range of air temperatures at one wind speed. It is likely that the integration of the three effects on heat loss depends on the size of the bird (similar in mounts and live Red Knots) and on the pattern of surface temperatures, at the interface of animal and environment. Surface temperatures of the heated taxidermic mounts were measured with an AGEMA thermovision system (AGEMA Infrared Systems, Oberursel, Germany) at the University of Marburg, Germany. The patterns obtained were remarkably similar in the mounts and in the birds (Fig. 2). The heated mounts lost more heat from the back but less through the plumage of head and neck. The conductance of the mounts under wind-free conditions (average of the four freshly made models mentioned earlier was $0.046 \text{ W}/^{\circ}\text{C}$, range $0.043\text{--}0.051$) almost equaled that of live birds ($0.045 \text{ W}/^{\circ}\text{C}$, see Results). This suggests that similar surface temperature patterns indeed imply similar heat loss patterns. We therefore believe that the integration of the effects of temperature, wind and radiation did not differ much between mounts and live individuals.

MAINTENANCE METABOLISM IN THE FIELD

The thermal conditions for Red Knots were measured with the heated taxidermic mounts in both the nonbreeding and the breeding areas. During the nonbreeding season 1989–1990 the mounts were placed on the mudflats and high-tide roosts near the island of Griend in the Dutch part of the Wadden Sea ($53^{\circ}15'\text{N}$, $03^{\circ}15'\text{E}$). In June–July 1989 they were used in the tundra habitats on Rowley Island, Foxe Basin, Canada (69°N , 79°W), and in June 1990 on the tundra near Alert, Ellesmere Island, Canada ($82^{\circ}30'\text{N}$, 62°W). At each of the study sites the mounts were placed in the different microhabitats frequented by Red Knots. We ensured that the mounts were always facing the wind, as free-living Red Knots usually do.

Simultaneously with the measurements made with the mounts, the relevant determinants of dry heat loss (Monteith and Unsworth 1990), were recorded according to standardized methods used by meteorological services over half-hourly, or sometimes hourly, periods. These are: air temperature, T_a (measured at a height of about 1.5 m above the ground), wind speed, u (measured in m/sec at a height of about 10 m with different instruments), and global solar radiation, R_g (measured in W/m^2 , with a Kipp solarimeter

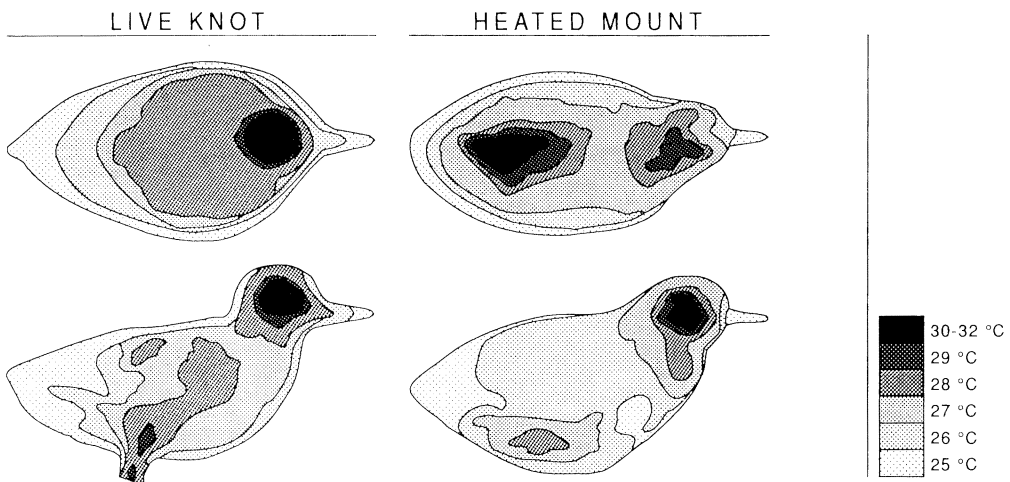


FIGURE 2. Comparison of the surface temperature of a heated taxidermic Red Knot-mount (right) and a live bird of the same species (left) at an air temperature of 24°C and no wind. This picture of surface temperatures was drawn from color photographs made by a thermovision camera at the University of Marburg.

in the Dutch Wadden Sea and on Rowley Island and with an Eppley pyranometer at the weather station at Alert). In all arctic situations and in the majority of the remaining cases, the weather data were collected at the location where the mounts were placed. In a few cases we obtained them from a weather station at a maximum distance of 10 km from our study site, but then only in the extremely flat and uniform habitat of the western Wadden Sea.

We developed a physically realistic regression model to describe the heat loss of the mount in terms of the three meteorological variables. Basically, the model follows "Newton's law of cooling," describing the linear relation between heat flow and the temperature difference between the environment and the subject (see Eq. 3). Overall conductance is a power function of wind speed, u , and measured exponents are generally in the theoretically expected order of size, i.e., about 0.5 (Goldstein 1983, Stahel et al. 1987, Chappell et al. 1989, Bakken 1990). Using an iterative regression procedure and the regression model developed in detail below, we estimated the wind speed exponent for the six main microhabitats (the first six listed in Table 1) at an average of 0.75 (range: 0.16–1.13). Given the statistical uncertainty of the microhabitat-specific estimates of the exponent, and the uncertainty about the commonly used value of 0.5 (Bakken 1991), we used the value of 0.75 when estimating the re-

maining parameters. As heat loss through forced convection depends on the temperature gradient between animal and environment (i.e., no gradient = no heat loss), wind speed and the temperature gradient are multiplicative variables. Incoming radiative energy has been taken as an additive element in our heat flow model, on the basis of the measurements reported by Lustick (1969), Gessaman (1972) and Hayes and Gessaman (1980), in spite of the possible multiplicative effect of radiation, wind speed and air temperature implied by biophysical theory (Bakken 1976). In our model, evaporation is not separately quantified in the total heat flow because in the range of weather conditions encountered in this study evaporative heat loss is small and constant in relation to air temperature (N. Verboven and T. Piersma, unpubl.). Taken together, this leads to the following model of heat loss:

$$H_{sm} = (0.045 + K_u \cdot u^{0.75}) \cdot (T_m - T_a) - K_r \cdot R_g \quad (5)$$

where $K_u \cdot u^{0.75}$ is the part of the overall conductance due to convective heat loss in the particular microhabitat and K_r the radiative conductance of the mount in that habitat (K_u and K_r in $W/^\circ C$). Measured wind speeds were always larger than zero. The value 0.045 represents the conductance of live birds measured in a convection-free environment, where $K_u \cdot u^{0.75} = 0$ (see Results). Val-

TABLE 1. Conductance parameters of adult Red Knots in different microhabitats as estimated from measurements with heated taxidermic mounts on three meteorological variables (air temperature T_a , wind speed u and global solar radiation R_g), using iterative regression, according to the model: $H_{sm} = (0.045 + K_u \cdot u^{0.75}) \cdot (T_m - T_a) - K_r \cdot R_g$. SEE is the standard error of the estimate, n stands for the number of half-hourly periods for which data were used in the regression. All estimated parameters are significantly different from zero at the 5% level (asymptotic confidence interval).

	K_u	SEE	K_r	SEE	r^2	n
Densely vegetated salt marsh	0.00294	0.00048	0.00103	0.00016	0.53	32
Vegetated salt marsh	0.00478	0.00022	0.00139	0.00006	0.90	78
Mudflat and bare salt marsh	0.00809	0.00011	0.00080	0.00004	0.59	1,923
On snow on tundra	0.00899	0.00025	0.00197	0.00010	0.88	197
Behind tundra hillock	0.00707	0.00012	0.00140	0.00004	0.78	879
On tundra hillock	0.01164	0.00018	0.00107	0.00006	0.62	1,970
Dense group	0.00358	0.00015	0.00052	0.00005	0.75	238
Open group	0.00455	0.00024	0.00063	0.00008	0.61	237
Solitary	0.00614	0.00028	0.00048	0.00010	0.57	235
Head in wind	0.00829	0.00019	0.00067	0.00007	0.46	425
Flank in wind	0.00952	0.00077	0.00062	0.00017	0.29	18

ues for K_u and K_r in Eq. 5 were estimated by iterative regression techniques in SPSS of the lumped data sets of measurements of all mounts performed in identical microhabitats.

To convert the heat loss of mounts into that of live Red Knots, heat loss values, H_{sm} , were converted to standard operative temperatures, T_{es} (°C). T_{es} is by definition equal to T_a in the standard environment (in our case the respirometry unit where $u = 1$ m/sec) at which the mount would have the same heat loss as measured in the field. T_{es} is thus a measure of the "environmental temperature," combining all factors affecting heat flow. T_{es} is calculated by combining Eqs. 3 and 4, solving for T_a ($=T_{es}$):

$$T_{es} = 41 - H_{sm}/0.055 \quad (6)$$

which through Eqs. 2a and 2b (i.e., replace T_a with T_{es}) relates maintenance metabolism of Red Knots in that particular microhabitat to the weather data. All mounts were used in all habitats.

Since the conductance and core temperature of the standardized mount were chosen to equal those of live Red Knots (so $T_b = T_m$ and $K_{es} = K_{esm}$ at a range of air temperatures and with $u = 1$ m/sec), the heat loss of the standard mount directly predicted the heat loss of a Red Knot, although only below T_{ic} . We nevertheless chose the indirect approach via equations 2a and 2b using T_{es} (Eq. 6) in order to be able eventually to substitute values other than 0.055 W/°C for

K_{es} and 41°C for T_b during analyses of other categories of Red Knots with slightly different characteristics (e.g., other subspecies or age or molt classes).

BEHAVIORAL ENERGY-SAVING MECHANISMS

Birds living in flocks create their own microhabitat and will experience less wind than solitary birds. As we failed to induce free-living Red Knots to roost around our mounts, an estimate of the energetic saving was made by measuring the heat loss of a mount standing in a flock of decoys. In the absence of a sufficient number of stuffed Red Knots, stuffed specimens of Greater Golden-Plovers (*Pluvialis apricaria*), along with a few Bar-tailed Godwits (*Limosa lapponica*), were placed in a flock with their heads pointed into the wind. These species are slightly larger than Red Knots, their lean masses being 1.47× and 2.17× that of Red Knots, respectively (van der Meer and Piersma, in press). A mount was placed in the center of the flock. The average distance between the decoys in two flocks was either 15 or 30 cm, similar to 0.75 and 1.5 bird lengths, the latter being the measure used in the field. Flock sizes were 52 and 31 specimens, respectively. As a control, one mount was placed alone in the same barren field.

The effect on heat loss of body orientation to wind was estimated with mounts placed perpendicular to the wind direction. This experiment was conducted in an open habitat.

Field observations of free-living Red Knots were collected throughout the nonbreeding season at various locations in the Dutch Wadden Sea: on the mudflats near Texel (53°08'N, 04°56'E), Griend, and Schiermonnikoog (53°28'N, 06°10'E). During the breeding season Red Knots were studied on Rowley Island and near Alert, Ellesmere Island, in the Canadian Arctic. Flocks, or parts thereof, were scanned systematically while recording the behavior of each focal bird. Our ethogram included the following categories: feeding, preening, standing, sleeping (with the bill tucked between the scapulars), walking, running, bathing and standing. In addition, scans were made to record the body orientation of birds with regard to the wind axis (recognizing six categories: 0° [headwind], 45°, 90° [sidewind], 135° and 180° [tailwind]), and to assess flock density in terms of the average nearest-neighbor distance (in bird lengths = about 20 cm). Simultaneously collected meteorological data were usually measured in the study area or sometimes obtained from the nearest weather station (within a radius of 10 km).

RESULTS

MEASUREMENTS IN THE STANDARD LABORATORY ENVIRONMENT

The Scholander-model fitted to the metabolic rate measurements described the data well (Fig. 3). Basal metabolic rate of the Red Knots was estimated to be 0.95 W (SE = 0.037) (Fig. 3), 83% of the value of 1.14 W predicted by Kersten and Piersma (1987) for a 130 g wader (average starting mass during the oxygen measurements). Note that the values of BMR measured under the wind conditions in the respirometry unit and under wind-free conditions in the standard black plexiglass box did not differ (F -test, $P > 0.05$, Fig. 3). The simultaneously estimated values of K_{es} (at $u = 1$ m/sec) was 0.055 W/°C and of K_e (without wind) was 0.045 W/°C (Fig. 3), the difference being statistically significant (F -test, $P < 0.05$). This resulted in T_{ic} s of 23.7 and 19.9°C, respectively.

MAINTENANCE METABOLISM IN THE FIELD

The microhabitat-dependent values for K_u and K_r (Eq. 5) are shown in Table 1. The percentage of the total variation explained by Eq. 5 is 53% or more for all microhabitats. As an illustration of the goodness of fit between measurements and

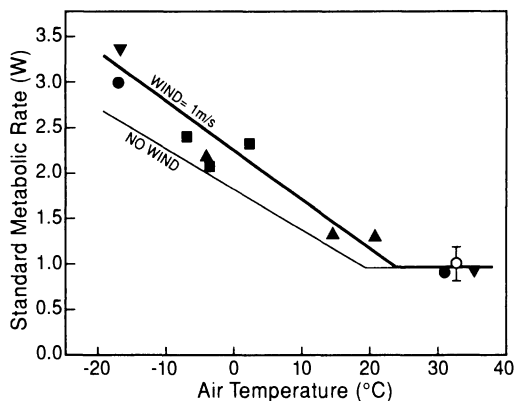


FIGURE 3. Standard Metabolic Rate (SMR) of post-absorptive adult Red Knots in a dark respirometry unit with a wind speed of 1 m/sec in relation to air temperature. The four different individuals used in the measurements are indicated by different symbols. A "Scholander"-model was fitted with iterative regression techniques and the result is indicated by the straight lines. The average metabolic rate of five Red Knots measured under wind-free conditions in a pitch-black plexiglass box at air temperatures above a T_{ic} of 23.7°C is indicated by the open circle (average ± 1 SD). The line at left summarizes the level of SMR at zero wind speed (the measurements of which were published in full by Wiersma et al. 1993:fig. 4).

resulting models, plots of predicted M_{maint} on heat loss values measured with mounts are given in Fig. 4. These indicate that the derived equations are robust under the range of climatic conditions over which values were collected. Figure 5 indicates that regression models to predict M_{maint} on the basis of single weather variables give much poorer predictions than the use of the compound measure incorporating all three in a physically realistic way.

There is a clear relationship between K_u and the extent of shelter offered by vegetation and/or relief, with the highest conductance experienced by birds which are standing exposed on a bare hillock and the lowest for birds roosting in the dense vegetation of a salt marsh (Table 1). It is likely that microhabitat-related differences in K_u can be explained by differences in relative air temperature and, especially, relative wind speed (i.e., air temperature and wind speed in microhabitats relative to the values of the standard meteorological data measured under a different but standardized regime). The effects of microhabitat and flock mates on windspeed as experienced by the individual bird can be described as "habitat shelter" and "mutual shelter," re-

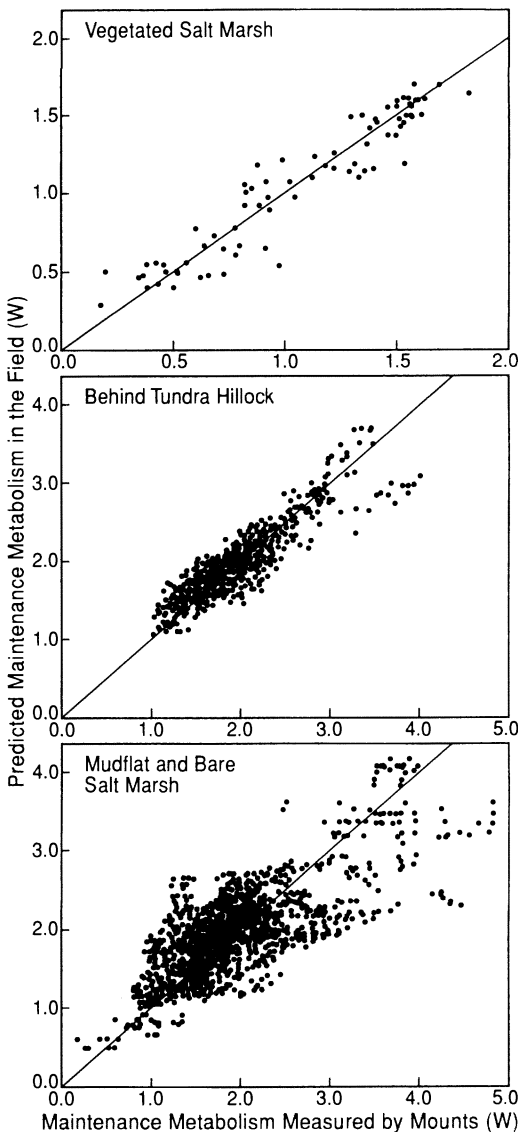


FIGURE 4. The extent to which complete regression equations predicting Maintenance Metabolism (M_{maint}) of Red Knots in different microhabitats (Table 1) fit the actual measurements. As examples, we show predicted M_{maint} as a function of measured values for three important microhabitats.

spectively (after Whitlock 1979). These indices indicate the extent of the reduction in wind speed inside the particular habitat or flock relative to a reference situation (Appendix 1). Figure 6 shows the degree of habitat and mutual shelter as estimated for all situations used in our calculations

of M_{maint} . The biggest difference is found between the densely vegetated habitat and the tundra hillock. Birds on a hillock experienced a wind speed $6 \times$ higher than birds in the vegetation.

K_r varies by a factor of 2.5 in different microhabitats (Table 1). Maximum radiative energy gain is about 1.6 W (on snow on tundra at a global solar radiation of 800 W/m^2), indicating that solar radiation reflected by snow may be of use to shorebirds. However, under most circumstances radiation will have a relatively small effect on M_{maint} .

BEHAVIORAL ENERGY-SAVING MECHANISMS

Red Knots in the temperate nonbreeding areas live in very large flocks averaging 7,000–8,000 birds (Piersma et al. 1993b), and the effect of spending time in the periphery of a flock must be rather small. Most Red Knots therefore experience a reduction in M_{maint} relative to solitary birds. In a dense flock with an average nearest-neighbor distance of 0.75 bird lengths, wind speed is reduced by 51%, compared to a solitary bird. In an open flock with an average nearest-neighbor distance of 1.5 bird lengths, wind speed is reduced by 33% (Fig. 6, Appendix 1). These reductions should be applicable for all wind speeds.

Red Knots standing with their flanks in the wind would experience up to 17% more heat loss than when standing with their heads facing the wind, depending on wind speed (Table 1, Appendix 1). Our estimate may be slightly biased because the susceptibility of individual contour feathers to be moved by the wind must have been affected by the preservation of the bird skins and the absence of ptilomotor responses. Red Knots standing more than 90° from the wind direction, more or less with their tail to the wind, would experience greater heat loss because their feathers are blown apart.

The average nearest-neighbor distance of foraging Red Knots observed on the Dutch nonbreeding grounds was 4.4 bird lengths, ranging between 0.5 and 20 bird-lengths in different observed flocks. When T_{es} decreases, the absolute energetic advantage of living in a flock will increase. For the purpose of reducing energy expenditure, we expected Red Knots to form denser flocks with an increasing potential energetic advantage. Figure 7 shows the frequency distribution of the nearest-neighbor distances per flock divided into four “energetic advantage” cate-

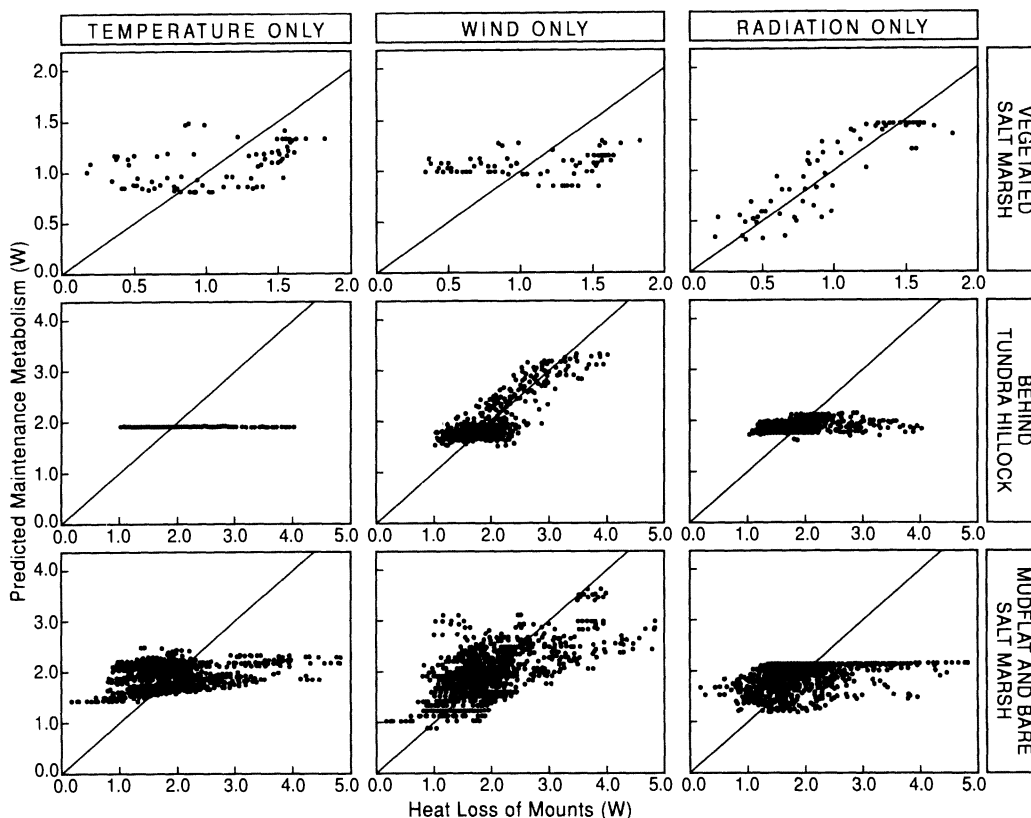


FIGURE 5. The performances of incomplete regression models based on one weather variable only (structured as in Eq. 5, but leaving out the two others) (three columns at right). As in Figure 4, we show predicted M_{maint} as a function of measured values for three important microhabitats (top row: “vegetated salt marsh,” middle row: “behind tundra hillock” and bottom row: “mudflat and bare salt marsh”).

gories (expressed as M_{maint} of solitary bird minus M_{maint} of a bird in a flock, see Appendix 1). Our prediction is borne out, since the four categories are significantly different (Kruskal-Wallis ANOVA, $\chi^2 = 12.2$, $P < 0.01$) and a negative correlation exists between the nearest-neighbor distance and the energetic advantage (Spearman’s rank correlation coefficient, $r_s = -0.10$, $P < 0.05$).

For body orientation with regard to the wind axis, the percentage of birds standing with their heads from 0° to about 67° relative to the wind direction was plotted against the standard operative temperature, T_{es} (Fig. 8), yielding a significant negative correlation ($r = -0.60$, $P < 0.001$). Below a T_{es} value of 5°C , the average percentage of time that birds spent facing the wind is 92%, much higher than the randomly expected percentage (37.5%) (one-tailed Student’s t -test, $T = 32.5$, $P < 0.0005$).

THE ANNUAL CYCLE OF MAINTENANCE METABOLISM

Weather data are often made available as daily, weekly or monthly averages. Estimates based on these data do not incorporate the diurnal and day-to-day fluctuations in the weather variables. Since the relationship between M_{maint} and wind speed is a power function, the use of wind speed averaged over long time intervals causes overestimates of M_{maint} . In contrast, if T_{es} exceeds T_{ic} for periods shorter than the averaging interval, M_{maint} is underestimated. These biases do not necessarily cancel each other out.

Hourly weather data were averaged on a daily and a monthly basis, to investigate these potential biases empirically. Calculations are based on Red Knots behaviorally adjusting to their thermal environment in ways outlined above, and

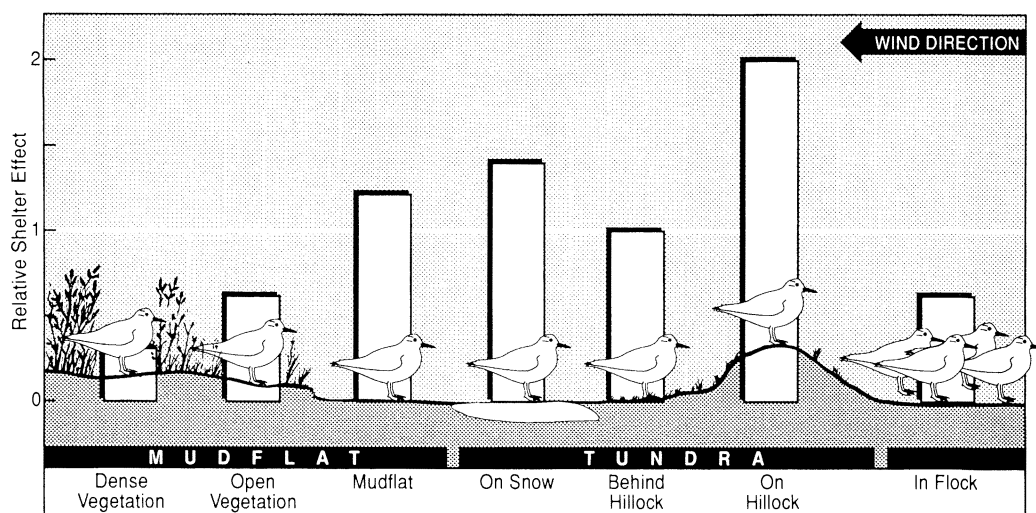


FIGURE 6. Reduction in wind speed in the microhabitats used most by Red Knots (expressed as relative heat loss, “habitat shelter,” see Appendix 1) and in flocks with average nearest-neighbors distances of 0.5 and 1.0 bird lengths (“mutual shelter,” Appendix 1). The line indicates the average value for all microhabitats.

staying in the Dutch Wadden Sea and in the Canadian Arctic. The estimates on the use of different microhabitats are given below. On average, monthly estimates are 1–2% higher than hourly estimates. Figure 9 shows that this deviation from hourly estimates is related to T_{es} . Since the probability that Red Knots encounter thermoneutral conditions is correlated to the amount of shelter that a microhabitat offers, the deviation also depends on microhabitat use. With high T_{es} s the deviations change quite abruptly, due to the increasing probability of achieving thermoneutral conditions. The relationships shown in Figure 9 have been used below to correct the presented data.

We estimated seasonality in M_{maint} of Red Knots using the regression model (Eq. 5) together with the microhabitat-dependent conductances (Table 1). Birds observed on the Dutch nonbreeding and Icelandic staging grounds spent about 50% of the time foraging (Alerstam et al. 1992, Wiersma and Piersma, unpubl. data). The rest of the time was mainly devoted to sleeping and preening (with at most 4% spent in flight; this includes the flights to and from the high-tide roosts). The time expenditure in the different microhabitats is therefore assigned as follows: 75% on mudflat and bare saltmarsh (50% of which is spent foraging), and 25% roosting on vegetated saltmarsh. On the breeding grounds the birds were considered to occur only solitarily, spending 50% in

dense vegetation (nest), 25% in open vegetation, and 25% standing exposed on top of a hillock (T. Piersma, unpubl. data).

To estimate heat loss reductions for Red Knots due to their habit of living in flocks, data collected with solitarily standing heated taxidermic mounts had to be converted to the predicted values as if measurements had been performed in a flock, as outlined in Appendix 1. At an average nearest-neighbor distance of 4.4 bird lengths in foraging flocks, the average decrease in M_{maint} compared to solitary standing birds works out at 6%. Since the nearest-neighbor distances showed only a weak decrease with an increase in the potential saving on M_{maint} (Fig. 7), the value of 6% was used throughout all calculations.

The extra heat loss incurred by not consistently facing the wind was estimated on the basis of equations presented in Appendix 1, and the behavioral data presented in Figure 8. For a given thermal advantage, the expected percentage of time spent not facing the wind was estimated and the resulting extra heat loss calculated by using the measurements of mounts standing with their flanks into the wind (Table 1). M_{maint} would increase by 2–9%, depending on microhabitat and weather conditions. Finally, the monthly estimates were adjusted for biases due to averaging-intervals according to the method outlined above (Fig. 9).

Combining all this information resulted in an-

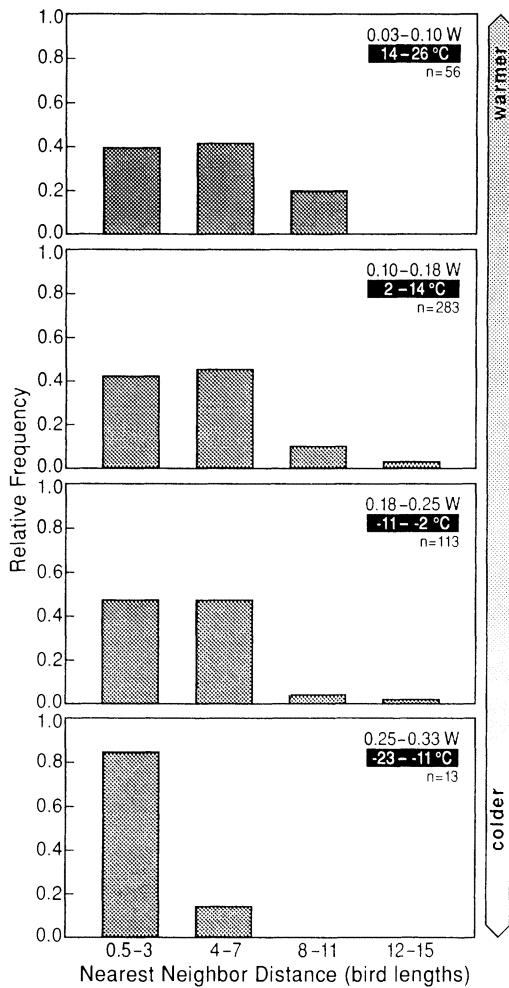


FIGURE 7. A breakdown of nearest-neighbor distances of Red Knots foraging on intertidal flats in the Dutch Wadden Sea in the nonbreeding season for different degrees of potential savings on maintenance metabolism. The potential saving on maintenance metabolism by heading into the wind instead of standing perpendicular to it indicated in W (Appendix 1), is inverse to standard operative temperature (T_{es}) in the group indicated in $^{\circ}\text{C}$, and was estimated on the basis on local meteorological data and the equations in Table 1 (ANOVA, $F = 3.89$, $P < 0.01$, $n = 464$). n gives the number of separate flocks for which a nearest-neighbor estimate was made.

nual cycles in M_{maint} as shown in Figure 10. The average monthly M_{maint} ranges from 1.64 W in August to 2.93 W in January in the Dutch Wadden Sea. M_{maint} in the High Arctic during the breeding season is relatively low compared to those estimated for the rest of the year. This is partly caused by a shift to more sheltered habitats

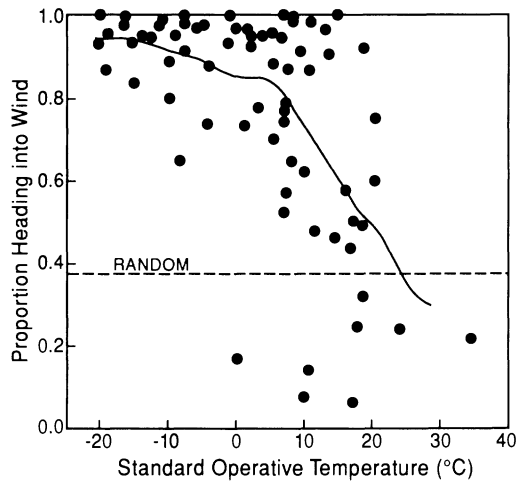


FIGURE 8. The proportion of foraging Red Knots facing the wind (i.e., -67° to $+67^{\circ}$) in relation to the standard operative temperature (T_{es}) on intertidal flats in the Dutch Wadden Sea. Each data point stands for a scan of at least 50 Red Knots in a flock. To lead the eye, a running regression line was fitted with the LOWESS routine of SYSTAT (tension = 0.5, Wilkinson 1990).

by breeding Red Knots (Fig. 10C). The annual M_{maint} averages 2.32 W. The total annual energy expenditure on M_{maint} is thus 73.0 MJ, of which 41% (30.0 MJ) is devoted to BMR, and 59% (43.0 MJ) to thermoregulation.

DISCUSSION

Two issues warrant discussion: (1) the accuracy of the prediction of M_{maint} levels and the possible use of alternative methods, and (2) the biological implications of different M_{maint} regimes at different potential nonbreeding areas.

SENSITIVITY ANALYSIS OF THE REGRESSION EQUATIONS

Figure 11 shows the effects of deviations from the estimated values of K_u , K_r , and the time spent in different microhabitats during the nonbreeding season. Although the time spent in different microhabitats also affects the prediction of M_{maint} (by $\pm 3\%$ with microhabitat use varying with $\pm 20\%$ of the stated use), it is obvious that K_u has the strongest effect (by $\pm 9\%$ with K_u varying with $\pm 20\%$ of the estimated value). A $\pm 20\%$ change in K_r resulted in a $\pm 1\%$ change in predicted M_{maint} . Recall that several heated mounts were used to characterize the “thermal parameters” (K_u and K_r) of each microhabitat and that

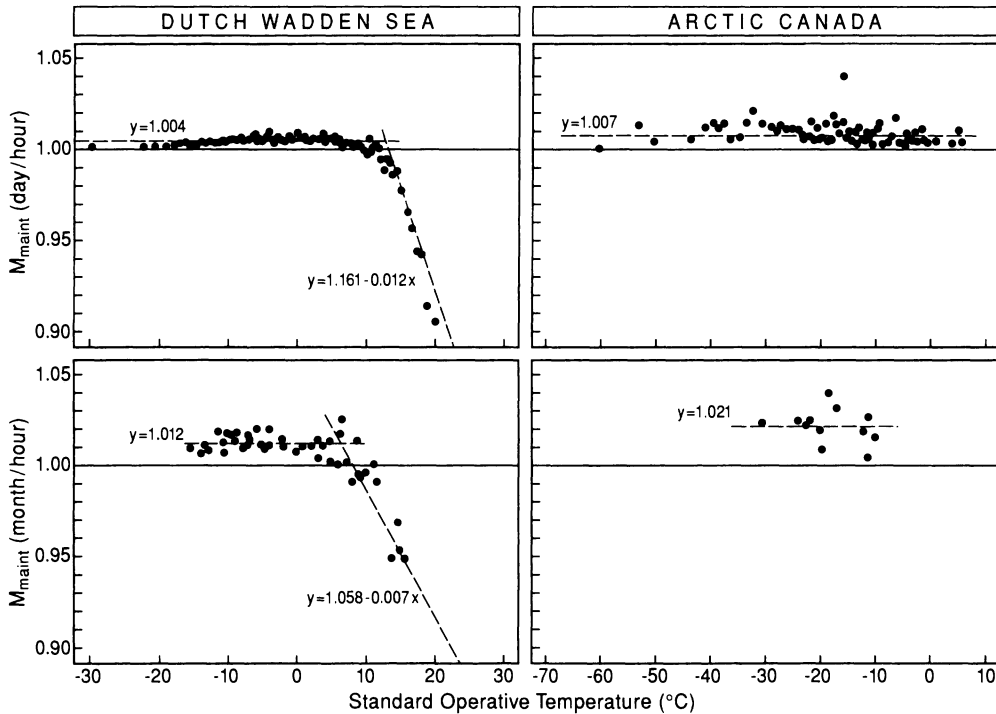


FIGURE 9. Effects of averaging the weather data over different time intervals (hour, day, month) on the average predicted maintenance metabolism of Red Knots in relation to the standard operative temperature, in the Dutch Wadden Sea (left panel) and on the Canadian Arctic tundra (right panel). The climatic data for the Dutch Wadden Sea were collected at station De Kooy ($52^{\circ}56'N$, $04^{\circ}48'E$) in the western part of the Dutch Wadden Sea. The data for the Canadian Arctic were collected at Alert, Ellesmere Island, by the Atmospheric Environment Service, Environment Canada.

the mounts were rotated among habitats, which should make the equations more robust.

THE USE OF HEATED TAXIDERMIC MOUNTS (MEASURING T_{es}) INSTEAD OF SIMPLER ALTERNATIVES (T_{e} or T_{a})

Heated taxidermic mounts are fragile and variable measurement devices, which require a constant power source. This makes them difficult to work with in the field. A simpler and more robust measuring device such as a hollow copper sphere would be the favored alternative to measure the thermal environment, if it could function as well (Bakken et al. 1985, Walsberg and Weathers 1986, Bakken 1992). The temperature of such a sphere (or, as an intermediate solution, of an unheated taxidermic mount) approximates operative temperature (T_{e}). This is the integrated temperature of the environment which combines the effects of air temperature and radiation, but does not completely account for convective effects. Due to the low surface temperature of the "cold"

sphere or mount, wind has only a minor effect on T_{e} . This will result in a large underestimate of the equivalent blackbody temperature at strong winds in wind-exposed microhabitats (Fig. 5). Klaassen (1992) showed the same effect by comparing cold and heated tern chick-mounts in sheltered and open habitats.

Figure 5 indicated that air temperature, wind speed or global solar radiation on their own can not consistently predict the heat loss of the mounts over the range of studied microhabitats (wind speed does rather well in the "behind tundra hill-ock" and "mudflat and bare saltmarsh" habitats, radiation rather well in the "vegetated salt marsh" habitat). Predicting M_{maint} in various microhabitats from the regression of SMR on T_{a} (the Scholander model) yields even poorer results for this species and for the open habitats it uses. Therefore, the quantification of M_{maint} of birds living exposed and in the cold can only be done the more difficult way, using either heated taxidermic mounts, or unheated mounts or spheres while

reconstructing wind effect taking simultaneous microclimatic wind measurements, including shelter and near-ground effects, into account (see Weathers et al. 1984; Weathers and Sullivan 1989, 1993; Bakken 1990 for examples). The latter approach has the clear disadvantage that it does not allow generalized empirical relationships to be derived between standard weather variables and M_{maint} . This means that habitat- and site-specific evaluations of climate as it affects heat loss always have to be based on an (complicated) array of local measurements. Apart from the need to establish a continuous program of measurements, it precludes the opportunity to exploit the massive worldwide meteorological data archive.

HEAT LOSS IN OTHER SHOREBIRD SPECIES

Because development of predictive equations of heat loss in different microhabitats is necessarily labor-intensive, it would be helpful for comparative studies in shorebird distribution patterns (Castro et al. 1992, Piersma, in press) if the equations developed here could be applied to smaller and larger species. The steps to adapt the equation for the other shorebird species are outlined in Appendix 2. For example, M_{maint} of Eurasian Oystercatchers (*Haematopus ostralegus*, with a lean mass of 4–5 × that of Red Knots) in mid-winter in the Dutch Wadden Sea is 95% higher than a prediction based on air temperature only (Wiersma et al. 1993).

VARIABILITY OF MAINTENANCE METABOLISM IN THE NONBREEDING SEASON

To this point, our predictions of M_{maint} were based on long-term average climatic data. Since birds have to cope with the prevailing weather conditions and not with long-term averages, we estimated the variability in M_{maint} during the winter season in open habitats in the Dutch Wadden Sea by using a 31-year set of monthly average climatic data, from the period 1960 to 1991 (Fig. 12). M_{maint} over the 31 different nonbreeding seasons (September to April) in the Dutch Wadden Sea varied between 2.36 W and 2.74 W, the coefficient of variation ($CV = SD/\text{mean} \cdot 100$) being $0.10/2.57 \cdot 100 = 3.9\%$. The average monthly minimum was 1.87 W, varying from 1.69 to 2.15 W in different years ($CV = 5.3\%$), and the average monthly maximum cost was 3.05 W, varying from 2.72 to 3.44 W ($CV = 5.9\%$). Figure 12 also indicates that over the last 31 years, M_{maint} of Red Knots spending the winter in the Dutch

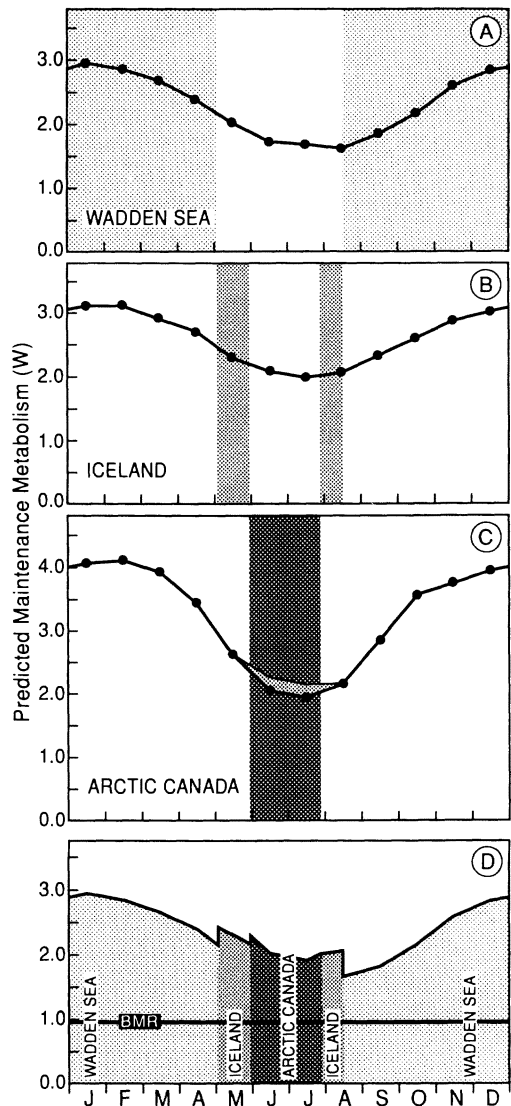


FIGURE 10. Seasonal variation in Maintenance Metabolism (M_{maint}) of European-wintering Red Knots. (A) gives M_{maint} in the nonbreeding area (Dutch Wadden Sea), (B) in the spring and fall staging area (south-west Iceland), (C) in the northeast Canadian breeding area (Alert, Ellesmere Island) and (D) gives the summary of the cycle in M_{maint} of individual Red Knots based on average timing of migratory movements as outlined by Piersma and Davidson (1992). Climatic data are from Einarsson (1976) and Müller (1980). The hatched area in (C) indicates the saving due to the use of relatively sheltered microhabitats during breeding.

Wadden Sea has decreased. This effect, totalling 0.3 W, is significant ($r = -0.73$, $P < 0.001$). The same trend is found in the yearly monthly minimum ($r = -0.34$, $P = 0.06$) and in monthly

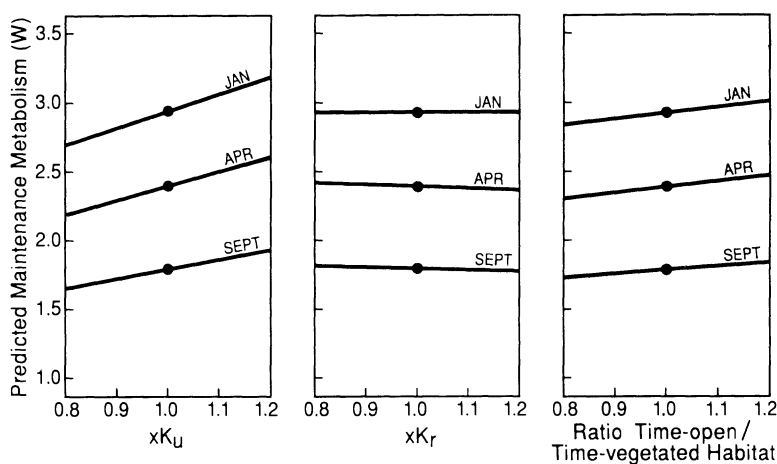


FIGURE 11. Effects of deviations in the exponents K_u and K_r in the equations for estimating Maintenance Metabolism (M_{maint}) of Red Knots (Table 1) on predicted M_{maint} during the winter season in the Dutch Wadden Sea (A and B). (C) shows the effects of biases in assigning the time spent in different habitat categories. All three panels show the predicted average M_{maint} in September, January, and April.

maximum M_{maint} ($r = -0.36$, $P = 0.05$.) The decrease in winter-average M_{maint} is due more to a decrease in wind speed ($r = -0.79$, $P < 0.001$) than to an increase in temperature ($r = 0.52$, $P < 0.001$). This shows the potential of our approach to evaluate predicted patterns of climate change from a bird's, and therefore a conservation, viewpoint.

On the basis of published climatic data for stations which provide alternative nonbreeding areas for the Wadden Sea (Smit and Piersma 1989, Davidson and Wilson 1992) (the Wash, eastern England, 53°N, linear distance to Wadden Sea is 350 km; Morecambe Bay, western England, 54°N, 550 km; and the Vendée coast, west-central France, 46°N, 900 km), we calculated average M_{maint} of Red Knots spending their time there instead of the Wadden Sea. During the nonbreeding period September–April, the two English sites (where most *islandica* Red Knots spend November through January) were marginally cheaper in energy expenditure than the western Wadden Sea, whereas Red Knots moving onto the French Vendée coast incur a 24% lower M_{maint} , a saving that varied little with time of the year. Therefore, under average circumstances, Red Knots can substantially reduce their maintenance requirements only by moving almost 1,000 km southwards. Red Knots wintering in western Europe are well-known for their inter-estuarine movements (Davidson and Wilson

1992). An analysis of the energetic advantages that may accrue by selective movements to areas with more congenial weather conditions is outside the scope of this paper.

That the rate of energy expenditure in hard-working parent birds rarely exceeded a level of four times BMR led to Drent and Daan (1980) to infer a “maximum sustained working level” or “metabolic ceiling” above which birds would incur a fitness penalty (e.g., reduced survival). The fairly constant ratio between BMR and maximum sustained energy expenditure of parent birds (Drent and Daan 1980) and between BMR and maximum metabolizable energy intake in birds and mammals (4.5 times BMR, Kirkwood 1983), is easily explained if BMR is a reflection of the mass of organs (the “metabolic machinery”) necessary to support peak levels of energy expenditure. This is the “energetic margin hypothesis” (Kersten and Piersma 1987), which has recently found considerable empirical support (Masman et al. 1989, Hammond and Diamond 1992; reviews in Peterson et al. 1990, and Weiner 1992).

Assuming a metabolic ceiling of 4.5 times BMR (i.e., $4.5 \cdot 0.95 = 4.225$ W for Red Knots), and an average *net* cost of activity (i.e., excluding any activity costs that substitute for heat loss) of 1.5 W (Piersma et al. 1991), the maximum sustained maintenance metabolism for a Red Knot must be close to $4.2 \cdot 1.5 = 2.7$ W. The probability of

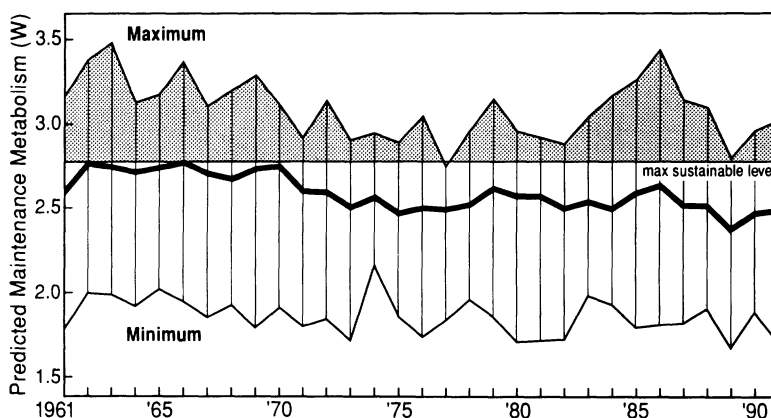


FIGURE 12. Long-term variability in predicted average Maintenance Metabolism (M_{maint}) of Red Knots staying in open habitats in the Dutch Wadden Sea during the entire nonbreeding season (September–April). The lower and the upper lines show minimum and maximum monthly M_{maint} encountered during the particular season. This analysis was based on a long series of meteorological data from station Den Helder/De Kooy in the western part of the Wadden Sea, except for the global radiation which was collected at stations Vlissingen or De Bilt until October 1964 (51°27'N, 03°34'E and 52°06'N, 05°11'E), and at De Kooy from then onwards (KNMI 1960–1991).

Red Knots to reach this inferred metabolic ceiling in winter is substantial (Fig. 12). Red Knots remaining in the Dutch Wadden Sea in the coldest month would exceed it in 30 of the 31 years. This suggests that some shorebirds may winter under more severe climatic conditions than some passerines, where the northern boundary in mid-winter coincided with a maintenance metabolic rate of 2.45 times BMR (Root 1988), or 2.3 W for Red Knots. Root's measure did not take wind and radiation effects into account, but they are likely to be of lesser importance for passerines living in sheltered habitats than for Red Knots.

Of course, we need more experimental information on actual maximum sustained energy expenditure (e.g., Dawson and Marsh 1989) in this species, and on the importance of exercise-generated heat in substituting for thermoregulatory expenditures (e.g., Paladino and King 1984, Zerbe and Walsberg 1991, Bakken and Lee 1992). We also need to explore the ways in which Red Knots respond to differences in M_{maint} relative to the quality of the feeding grounds and the distance to alternative nonbreeding areas.

A SIMULATED PROLONGED MIGRATION

Red Knots spend the nonbreeding season at a wide range of latitudes and climates (Piersma and Davidson 1992). Indeed, most subspecies winter predominantly in the tropics. To under-

stand the evolution of this pattern it would be of interest to know the energetic repercussions of differences in nonbreeding latitude (cf. Drent and Piersma 1990). A first step is an analysis what M_{maint} would be if *islandica* Red Knots wintered in the much warmer tropics of West Africa instead of the Wadden Sea.

Figure 13 compares M_{maint} of Red Knots spending the period September to April in the Dutch Wadden Sea and on the Banc d'Arguin in Mauritania on the West African coast. On average, M_{maint} is 1.38 W in West Africa, 1.13 W less than in the Wadden Sea. The maximum monthly cost is only 1.50 W in Africa, against 2.93 W in Europe.

Empirical evidence of such large differences in maintenance requirements of shorebirds wintering in temperate and tropical coastal areas is provided by Castro et al. (1992) in their study of Sanderlings, a species less than half the size of Red Knots. Here, daily energy expenditure varied by a factor of two over a range of 30°C in air temperatures.

A full evaluation of the energetic saving of wintering in the tropics necessitates incorporation of the cost of travelling from and back to the high arctic breeding grounds (Summers et al. 1989, Piersma et al. 1991). Based on population-average changes in body mass and composition of Red Knots in Europe and West Africa during

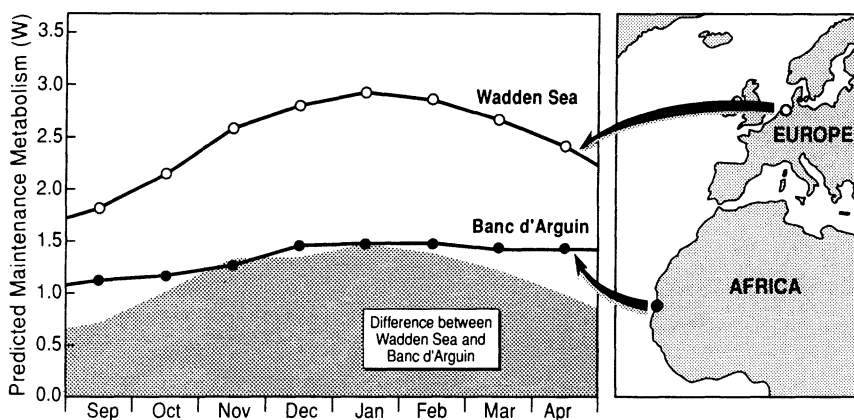


FIGURE 13. Effects on Maintenance Metabolism of a simulated prolonged migration of *islandica* Red Knots from the temperate Dutch Wadden Sea (53°N) to the tropical Banc d'Arguin, Mauritania, West Africa (20°N). Climatic data are from the KNMI-archives (KNMI 1960–1991), Müller (1980) and Wolf and Smit (1990).

migrations, Piersma et al. (1991) estimated the cost of travelling between the Wadden Sea and West Africa at 0.3–0.5 kJ/km. With a round-trip flight distance of 9,200 km, Red Knots moving to West Africa would have to spend an extra 2,760–4,600 kJ. Averaged over the period September–April this equals an overall travel cost of 0.13–0.22 W. Comparison with the estimated saving of 1.13 W on M_{maint} indicates that wintering in West Africa would make life energetically less expensive for *islandica* Red Knots, provided that the energy requirements for activity are of similar magnitude in the two nonbreeding areas.

CONCLUSIONS

Heated taxidermic mounts are a powerful tool for converting standard laboratory measurements of energy expenditure to an ecologically and behaviorally important parameter, the maintenance metabolism of free-living birds in their natural environment. Obtaining measurements by using heated taxidermic mounts in different natural microhabitats to arrive at microhabitat-specific equations to predict M_{maint} on the basis of standard weather variables, allows for analyses of habitat, climate and behavior as they affect the energy expenditure of birds in the field. They also allow the behavioral adjustments made by birds in flocks and in different microhabitats in relation to weather to be modelled.

The calculations presented here suggest that M_{maint} of Red Knots wintering in temperate Eu-

ropean coastal areas may have decreased by more than 10% over the last 30 years. Nevertheless, the overall average M_{maint} is 83% higher than that of those wintering in the West African tropics. Moreover, there is a strong indication that Red Knots wintering in the Dutch Wadden Sea, the north-eastern edge of the winter range, are operating close to their metabolic maximum.

Attempts to explain the current distribution and migration patterns of a species, and the timing of its seasonal movements, are usually limited by our inability to explore the consequences of options not currently prevailing, such as those only available in the past. The equations presented here offer tools to do just that with respect to a major component of the total energy expenditure of a long-distance migrant bird. As the energy intake of Red Knots can also be estimated from foraging time and potential food intake on the basis of empirical functional response curves (Zwarts et al. 1992), the construction of a fully empirical annual energy budget model to evaluate the economics of decisions on when and why to move from one site to another is now within reach. Such a budget model allows a first comparison of predicted levels of energy expenditure with the seasonal flux of food availability. It is our conviction that when similar data become available for other populations of Red Knots, a realistic scenario for considering energetic costs and benefits world-wide will enable us to understand how their seemingly extravagant transequatorial migration system (Piersma and Davidson 1992) has evolved.

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LITERATURE CITED

- ALERSTAM, T., G. A. GUDMUNDSSON, AND K. JOHANNESSON. 1992. Resources for long distance migration: intertidal exploitation of *Littorina* and *Mytilus* by knots *Calidris canutus* in Iceland. *Oikos* 65:179-189.
- ASCHOFF, J. 1981. Thermal conductance in mammals and birds: its dependence on body size and circadian phase. *Comp. Biochem. Physiol.* 69A:611-619.
- ASCHOFF, J., AND H. POHL. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und des Körpergrösse. *J. Ornithol.* 111:38-47.
- BAKKEN, G. S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* 60:337-384.
- BAKKEN, G. S. 1980. The use of standard operative temperature in the study of the thermal energetics of birds. *Physiol. Zool.* 53:108-119.
- BAKKEN, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. *Auk* 107:587-594.
- BAKKEN, G. S. 1991. Wind speed dependence of the overall thermal conductance of fur and feather insulation. *J. Therm. Biol.* 16:121-126.
- BAKKEN, G. S. 1992. Measurement and application of operative and standard operative and standard operative temperatures in ecology. *Am. Zool.* 32:194-216.
- BAKKEN, G. S., W. A. BUTTEMER, W. R. DAWSON, AND D. M. GATES. 1981. Heated taxidermic mounts: a means of measuring the standard operative temperature affecting small animals. *Ecology* 62:311-318.
- BAKKEN, G. S., D. J. ERSKINE, AND W. R. SANTEE. 1983. Construction and operation of heated taxidermic mounts used to measure standard operative temperature. *Ecology* 64:1658-1662.
- BAKKEN, G. S., AND K. F. LEE. 1992. Effects of wind and illumination on behavior and metabolic rate of American Goldfinches (*Carduelis tristis*). *Auk* 109:119-125.
- BAKKEN, G. S., W. R. SANTEE, AND D. J. ERSKINE. 1985. Operative and standard operative temperature: tools for thermal energetics studies. *Am. Zool.* 25:933-943.
- BARTHOLOMEW, G. A. 1977. Energy metabolism, p. 57-110. *In* M. S. Gordon [ed.], *Animal physiology principles and adaptations*. Macmillan, New York.
- BIRKEBAK, R. C. 1966. Heat transfer in biological systems, p. 269-343. *In* W.J.L. Felts and R. J. Harrison [eds.], *International review of general and experimental zoology*, Vol. 2. Academic Press, New York.
- BLIGH, J., AND K. G. JOHNSON. 1973. Glossary of terms for thermal physiology. *J. Appl. Physiol.* 35:941-961.
- BUTTEMER, W. A. 1985. Energy relations of winter roost-site utilization by American Goldfinches (*Carduelis tristis*). *Oecologia* 68:126-132.
- CAMPBELL, G. S. 1977. *An introduction to environmental biophysics*. Springer-Verlag, New York.
- CASTRO, G., J. P. MYERS, AND R. E. RICKLEFS. 1992. Ecology and energetics of Sanderlings migrating to four latitudes. *Ecology* 73:833-844.
- CHAPPELL, M., K. R. MORGAN, S. L. SOUZA, AND T. L. BUCHER. 1989. Convection and thermoregulation in two Antarctic seabirds. *J. Comp. Physiol.* 159B:313-322.

- DAVIDSON, N. C., AND J. R. WILSON. 1992. The migration system of European-wintering Knots *Calidris canutus islandica*. Wader Study Group Bull. 64, Suppl.:39–51.
- DAWSON, W. R., AND R. L. MARSH. 1989. Metabolic acclimatization to cold and season in birds, p. 83–94. In C. Bech and R. E. Reinertsen [eds.], Physiology of cold adaptation in birds. Plenum Press, New York.
- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252.
- DRENT, R., AND T. PIERSMA. 1990. An exploration of the energetics of leap-frog migration in arctic breeding waders, p. 399–412. In E. Gwinner [ed.], Bird migration: physiology and ecophysiology. Springer-Verlag, Berlin.
- EINARSSON, M. A. 1976. Vedurfar á Íslandi. Idunn, Reykjavik.
- GATES, D. M. 1980. Biophysical ecology. Springer-Verlag, New York.
- GESSAMAN, J. A. 1972. Bioenergetics of the Snowy Owl (*Nyctea scandiaca*). *Arctic Alpine Res.* 4:223–238.
- GESSAMAN, J. A. 1973. Methods of estimating the energy cost of free existence, p. 3–31. In J. A. Gessaman [ed.], Ecological energetics of homeotherms: a view compatible with ecological modeling. Utah State Univ. Press, Logan, UT.
- GESSAMAN, J. A. 1987. Energetics, p. 289–320. In G. A. Giron Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird [eds.], Raptor management techniques manual. National Wildlife Federation, Washington, DC.
- GESSAMAN, J. A., AND K. A. NAGY. 1988. Energy metabolism: errors in gas exchange conversion factors. *Physiol. Zool.* 61:507–513.
- GOLDSTEIN, D. L. 1983. Effect of wind on avian metabolic rate with particular reference to Gambel's Quail. *Physiol. Zool.* 56:485–492.
- HAMMOND, K. A., AND J. DIAMOND. 1992. An experiment test for a ceiling on sustained metabolic rate in lactating mice. *Physiol. Zool.* 65:952–977.
- HAYES, S. R., AND J. A. GESSAMAN. 1980. The combined effects of air temperature, wind and radiation on the resting metabolism of avian raptors. *J. Therm. Biol.* 5:119–125.
- HILL, R. N. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *J. Appl. Physiol.* 33:261–263.
- KENDEIGH, S. C. 1972. Monthly variations in the energy budget of the House Sparrow throughout the year. In S. C. Kendeigh and J. Pinowski [eds.], Proceedings of general meeting of the working group of granivorous birds. IBP, PT Section, Warszawa.
- KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GAVRILOV. 1977. Avian energetics, p. 127–204. In J. Pinowski and S. C. Kendeigh [eds.], Granivorous birds in ecosystems. Cambridge Univ Press, Cambridge, England.
- KERSTEN, M., AND T. PIERSMA. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea* 75:175–187.
- KIRKWOOD, J. K. 1983. A limit to metabolisable energy intake in mammals and birds. *Comp. Biochem. Physiol.* 75A:1–3.
- KLAASSEN, M. 1992. The naive proficient: metabolic responses of chicks to problems of climate and food availability. Ph.D.thesis, Univ. of Groningen, The Netherlands.
- KNMI. 1960–1991. Jaaroverzicht van het weer in Nederland. KNMI, De Bilt. (In Dutch)
- LUSTICK, S. 1969. Bird energetics: effects of artificial radiation. *Science* 163:387–390.
- MASMAN, D., S. DAAN, AND H.J.A. BELDHUIS. 1988. Ecological energetics of the Kestrel: daily energy expenditure throughout the year based on time-energy budget, food intake and doubly labelled water methods. *Ardea* 76:64–81.
- MASMAN, D., C. DIJKSTRA, S. DAAN, AND A. BULT. 1989. Energetic limitation of avian parental effort: field experiments in the Kestrel (*Falco tinnunculus*). *J. Evol. Biol.* 2:435–455.
- MENAB, B. K. 1980. On estimating thermal conductance in endotherms. *Physiol. Zool.* 53:145–156.
- MONTEITH, J. L., AND M. H. UNSWORTH. 1990. Principles of environmental physics, second edition. Edward Arnold, London.
- MUGAAS, J. N., AND J. R. KING. 1981. Annual variation of daily energy expenditure by the Black-billed Magpie: a study of thermal and behavioral energetics. *Stud. Avian Biol.* 5:1–78.
- MÜLLER, M. J. 1980. Handbuch ausgewählter Klimastationen der Erde, second edition. Gerold Richter, Trier.
- PALADINO, F., AND J. R. KING. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion by White-crowned Sparrows *Zonotrichia leucophrys gambelii*. *Physiol. Zool.* 57:226–236.
- PEARSON, O. P. 1954. The daily energy requirements of a wild Anna Hummingbird. *Condor* 56:317–322.
- PETERSON, C. C., K. A. NAGY, AND J. DIAMOND. 1990. Sustained metabolic scope. *Proc. Natl. Acad. Sci. USA* 87:2324–2328.
- PIERSMA, T. In press. Energetic constraints on the nonbreeding distribution of coastal shorebirds. Wader Study Group Bull., Special Issue.
- PIERSMA, T., AND N. C. DAVIDSON. 1992. The migrations and annual cycles of five subspecies of Knots in perspective. Wader Study Group Bull. 64, Suppl.:187–197.
- PIERSMA, T., R. DRENT, AND P. WIERSMA. 1991. Temperate versus tropical wintering in the world's northernmost breeder, the Knot: metabolic scope and resource levels restrict subspecific options. *Acta XX Congr. Internat. Ornithol. (Christchurch)*:761–772.
- PIERSMA, T., P. DE GOEIJ, AND I. TULP. 1993a. An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. *Neth. J. Sea Res.* 31:503–512.
- PIERSMA, T., R. HOEKSTRA, A. DEKINGA, A. KOOLHAAS, P. WOLF, P. BATTLE, AND P. WIERSMA. 1993b. Scale and intensity of intertidal habitat use by Knots *Calidris canutus* in the western Wadden Sea in

- relation to food, friends and foes. *Neth. J. Sea Res.* 31:331–357.
- PORTER, W. P., AND D. M. GATES. 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* 39:227–244.
- PRINZINGER, R. 1990. Temperaturregulation bei Vögeln. I. Thermoregulatorische Verhaltensweisen. *Luscinia* 46:255–302.
- ROOT, T. 1988. Energy constraints on avian distributions and abundances. *Ecology* 69:330–339.
- SCHOLANDER, P. F., R. HOCK, V. WALTERS, F. JOHNSON, AND L. IRVING. 1950. Heat regulation in some arctic birds and tropical mammals and birds. *Biol. Bull.* 99:237–258.
- SCHMIDT-NIELSEN, K. 1975. Animal physiology: adaptation and environment. Cambridge Univ. Press, Cambridge, England.
- SMIT, C. J., AND T. PIERSMA. 1989. Numbers, mid-winter distribution, and migration of wader populations using the East Atlantic Flyway, p. 24–63. *In* H. Boyd and J.-Y. Pirot [eds.], *Flyways and reserve networks for water birds*. IWRB Spec. Publ. No. 9, Slimbridge, England.
- STAHEL, C. D., S. C. NICOL, AND G. J. WALKER. 1987. Heat production and thermal resistance in Little Penguin *Eudyptula minor* in relation to wind speed. *Physiol. Zool.* 60:413–423.
- SUMMERS, R. W., L. G. UNDERHILL, C. F. CLINNING, AND M. NICOLL. 1989. Populations, migrations, biometrics and moult of the Turnstone *Arenaria i. interpres* on the East Atlantic coastline, with special reference to the Siberian population. *Ardea* 77:145–168.
- VAN DER MEER, J., AND T. PIERSMA. In press. Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. *Physiol. Zool.* 67.
- VISSER, G. H. 1991. Development of metabolism and temperature regulation in precocial birds: patterns in shorebirds (Charadriiformes) and the domestic fowl (*Gallus domesticus*). Ph.D.thesis, Univ. of Utrecht, The Netherlands.
- WALSBERG, G. E. 1983a. Ecological energetics: what are the questions? p. 135–158. *In* A. H. Brush and G. A. Clark, Jr. [eds.], *Perspectives in ornithology*. Cambridge Univ. Press, New York.
- WALSBERG, G. E. 1983b. Avian ecological energetics, p. 161–220. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*, Vol. 7. Academic Press, New York.
- WALSBERG, G. E., AND W. W. WEATHERS. 1986. A simple technique for estimating operative environmental temperature. *J. Therm. Biol.* 11:67–72.
- WARKENTIN, I. A., AND N. H. WEST. 1990. Ecological energetics of wintering Merlins *Falco columbarius*. *Physiol. Zool.* 63:308–333.
- WEATHERS, W. W., W. A. BUTTEMER, A. M. HAYWORTH, AND K. A. NAGY. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk* 101:459–472.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1989. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monog.* 59:223–246.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1993. Seasonal patterns of time and energy allocation by birds. *Physiol. Zool.* 66:511–536.
- WEINER, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. *Trends Ecol. Evol.* 7:384–388.
- WHITLOCK, R. J. 1979. The ecological significance of energy conservation during roosting for wading birds. B.A.(Hons.)thesis, Univ. of Stirling, Scotland.
- WHITTOW, G. C. 1986. Regulation of body temperature, p. 221–252. *In* P. D. Sturkie [ed.], *Avian physiology*, fourth edition. Springer-Verlag, New York.
- WIERSMA, P., L. BRUINZEEL, AND T. PIERSMA. 1993. (Energy savings in waders: studies on the insulation of Knots.) *Limosa* 66:41–52. (In Dutch with English summary)
- WILKINSON, L. 1990. SYSTAT: the System for Statistics. SYSTAT Inc., Evanston, IL.
- WIJNANDTS, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* 72:1–92.
- WOLFF, W. J., AND C. J. SMIT. 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. *Ardea* 78:17–38.
- ZERBA, E., AND G. E. WALSBERG. 1991. Exercise-generated heat contributes to thermoregulation by Gambel's Quail in the cold. *J. Exp. Biol.* 171:409–422.
- ZWARTS, L., A.-M. BLOMERT, AND J. H. WANINK. 1992. Annual and seasonal variation in the food supply harvestable by Knot *Calidris canutus* staging in the Wadden Sea in late summer. *Mar. Ecol. Prog. Ser.* 83:129–139.

APPENDIX 1

ESTIMATING MAINTENANCE METABOLISM IN FLOCKS OF DIFFERENT DENSITY AND WITH RESPECT TO POSITION INTO THE WIND

Maintenance Metabolism, M_{maint} , of singly standing Red Knots in different microhabitats was estimated as outlined in the Results. Since individual birds made behavioral adjustments such as flocking to different densities (Fig. 7) and positioning in the wind (Fig. 8), the microhabitat-specific equations (Table 1) must be adjusted to take these effects into account.

To incorporate the effect of flocking on M_{maint} , the mutual shelter (MS) gained at different flock densities was estimated. Mutual shelter is the effect of flock members on the wind speed as experienced by the individual in that flock (u_{flock}) relative to the wind speed that a non-flocking bird would have experienced in the particular microhabitat (u_{solo}). MS is expressed as follows:

$$MS = 1 - (u_{\text{flock}}/u_{\text{solo}}).$$

To estimate MS in dense and in open flocks, we calculated the extent to which wind speed had to be adjusted in order for M_{maint} of birds in flocks to equal that of solitary birds ($M_{\text{maint/solo}}$):

$$MS = \{1 - [(M_{\text{maint/solo}} - K_r \cdot R_a)/K_u \cdot (41 - T_a) - 0.045/K_u]^{1/0.75}\}/u.$$

By filling in the specific parameters for a dense and an

open flock (Table 1) and assuming no radiation (i.e., $R_g = 0 \text{ W/m}^2$; an effect of radiation on MS is unlikely), we derived values for MS of 0.51 and 0.33, respectively.

In the field we encountered flocks with an average nearest-neighbor distance of 4.4 bird lengths. Since this is outside the range of nearest-neighbor distances offered in our experiments, the MS of birds in the field had to be estimated by extrapolation. Following Whitlock (1979), MS was logarithmically transformed to linearize the MS–nearest-neighbor distance relationship. This resulted in an estimated average MS of 0.06. This 6% reduction in wind speed was used for all situations where Red Knots were known to occur in flocks (i.e., always, outside the breeding season), according to the following equation:

$$M_{\text{maint/habitat, flock}} = (0.045 + K_u \cdot (u - 0.06 \cdot u)^{0.75}) \cdot (41 - T_a) - K_c \cdot R_g.$$

The effect of body orientation into the wind was estimated from the change in M_{maint} (due to a changing overall conductance) when moving from heading into the wind (0°) to standing sideways in the wind (90°). M_{maint} of a Red Knot standing perpendicular to the wind in an open habitat was adjusted by multiplying microhabitat-specific M_{maint} by the ratio between M_{maint} for 90° and 0° on the basis of the last two equations of Table 1:

$$M_{\text{maint/habitat, } 90^\circ} = M_{\text{maint/habitat}} \cdot (M_{\text{maint}/90^\circ} / M_{\text{maint}/0^\circ}).$$

The multiplication factor was only measured for an open habitat. As its effect is mainly due to changes in wind speed as experienced by the bird in a particular microhabitat, we have further refined the adjustment by estimating the degree of habitat shelter (HS), which is the reduction in wind speed in a particular microhabitat relative to a reference microhabitat. HS was derived in the same way as MS. As the reference we used the equation to predict M_{maint} of birds facing the wind (the penultimate one in Table 1). For the six main habitats listed first in Table 1, HS was estimated as follows: 0.75, 0.52, -0.12 , 0.19, 0.03 and -0.58 . M_{maint} of a bird standing sideways in the wind in a particular habitat can be estimated as:

$$\begin{aligned} M_{\text{maint/habitat, } 90^\circ} &= M_{\text{maint/habitat}} \cdot [(0.045 + 0.00952 \cdot (u - \text{HS} \cdot u)^{0.75}) \\ &\quad \cdot (41 - T_a) - 0.00062 \cdot R_g] \\ &\div [(0.045 + 0.00829 \cdot (u - \text{HS} \cdot u)^{0.75}) \\ &\quad \cdot (41 - T_a) - 0.00067 \cdot R_g]. \end{aligned}$$

The two behavioral effects on M_{maint} can be combined in an equation where $M_{\text{maint/habitat, flock}}$ (which incorporates the effect of mutual shelter) is multiplied by above ratio to estimate the effect of standing sideways in the wind in a particular habitat.

APPENDIX 2

ESTIMATING MAINTENANCE METABOLISM OF SHOREBIRD SPECIES OTHER THAN RED KNOT

Maintenance Metabolism (M_{maint}) of shorebird species which differ from Red Knots in their Basal Metabolic

Rate and/or body size can be predicted using the results of the heated taxidermic Red Knot mounts. The simplest way would be to predict the standard operative temperature, T_{es} , for Red Knots and then use this value in the Scholander curve of the particular species. However, since the effect of wind speed on heat loss is great, we should take into account the size of the species. A big bird standing high above ground level experiences higher wind speeds than one living closer to the ground. There is also an effect of body height on the experienced ambient temperature. The latter effect depends on ground surface temperature, and if this value is unknown, as it usually is, we cannot make estimates of its effect. Fortunately, a sensitivity analysis, under the assumption that surface temperatures are 5° above ambient temperature at 1.5 m, showed that the effect of height-related temperature differences is negligible.

To use the results of this study for other species two adjustments have therefore to be made: (1) of the basal metabolism and the conductance for the particular bird species and (2) of the wind speed effect for the appropriate body size, in particular the height from ground level, or “body height.”

Basal metabolism and conductance are given in literature for many species. If not, it should be measured in live birds (see Gessaman 1987 for an overview of methods) or estimated on the basis of the most relevant allometric equation reported in literature (Kersten and Piersma 1987 for shorebirds, and see Aschoff and Pohl 1970, Aschoff 1981, Kendeigh et al. 1977). Since we have to use the overall conductance under the standard conditions, K_{es} , where $u = 1 \text{ m/sec}$ (Eq. 2a), we predict K_{es} by multiplying K_c with 1.2 (i.e., the ratio $K_{es}/K_c = 0.055/0.045$, as reported in this paper for Red Knots). K_c is the convection-free conductance, which is the commonly measured and published value. After adjusting the lower critical temperature, T_{ic} , for this other conductance value, we can describe the Scholander curve of the particular species under the standard conditions (Eqs. 2a and 2b). For an Eurasian Oystercatcher, for example, BMR is 2.9 W and K_{es} is $0.12 \text{ W/}^\circ\text{C}$ (i.e., $1.2 \cdot 0.103$) (Kersten and Piersma 1987), and T_{ic} is therefore 16.8°C .

The difference in the experienced wind speed, due to the bird’s body height, can be compensated for by the theoretical shape of the height-dependent wind speed curve. The shape of this curve is dependent on the resistance of the specific habitat, z_o . The ratio between the wind speeds at two different heights is

$$u(h_1)/u(h_2) = \ln(h_1/z_o)/\ln(h_2/z_o),$$

where $u(h_1)$ and $u(h_2)$ are the wind speeds at heights h_1 and h_2 respectively. For body height we take the distance between the ground and the most protruding point of the birds’ breasts. For Red Knots we estimated this at 0.09 m. For an Eurasian Oystercatcher, with a body height of ca. 0.14 m, the experienced wind speed would be 1.15 times that of a Red Knot, filling in 0.005 for z_o , which is a value appropriate for a mudflat (R. Hutjes, pers. comm.):

$$\begin{aligned} u(0.14)/u(0.09) &= \ln(0.14/0.005)/\ln(0.09/0.005) \\ &= 1.15. \end{aligned}$$

The wind speed variable in the model estimating

heat loss of the standard Red Knot mount (Eq. 5) has to be adjusted by this species-specific experienced wind speed, resulting in:

$$H_{sm} = (0.045 + K_u \cdot [u \cdot u(h_i) / u(0.09)]^{0.75}) \cdot (T_m - T_a) - K_r \cdot R_g$$

For an Eurasian Oystercatcher this would result in:

$$H_{sm} = (0.045 + K_u \cdot [u \cdot 1.15]^{0.75}) \cdot (41 - T_a) - K_r \cdot R_g$$

From Eq. 6 we can estimate the standard operative temperature, T_{es} , for the bird species. Having estimated

T_{es} , we can predict M_{maint} by filling in this value in the Scholander curve of this species, as described above.

We emphasize that the results of this method should be treated with caution, especially if the bird species is much bigger or smaller than a Red Knot. Deriving K_{es} from K_e by multiplying with 1.2 gives a rather crude estimate since the factor may depend on body size and shape. Furthermore, the effect of wind on heat loss is probably also dependent on body size and shape. If no alternatives are available our method seems appropriate. It has the advantage of being straightforward with only a small number of parameters to estimate.