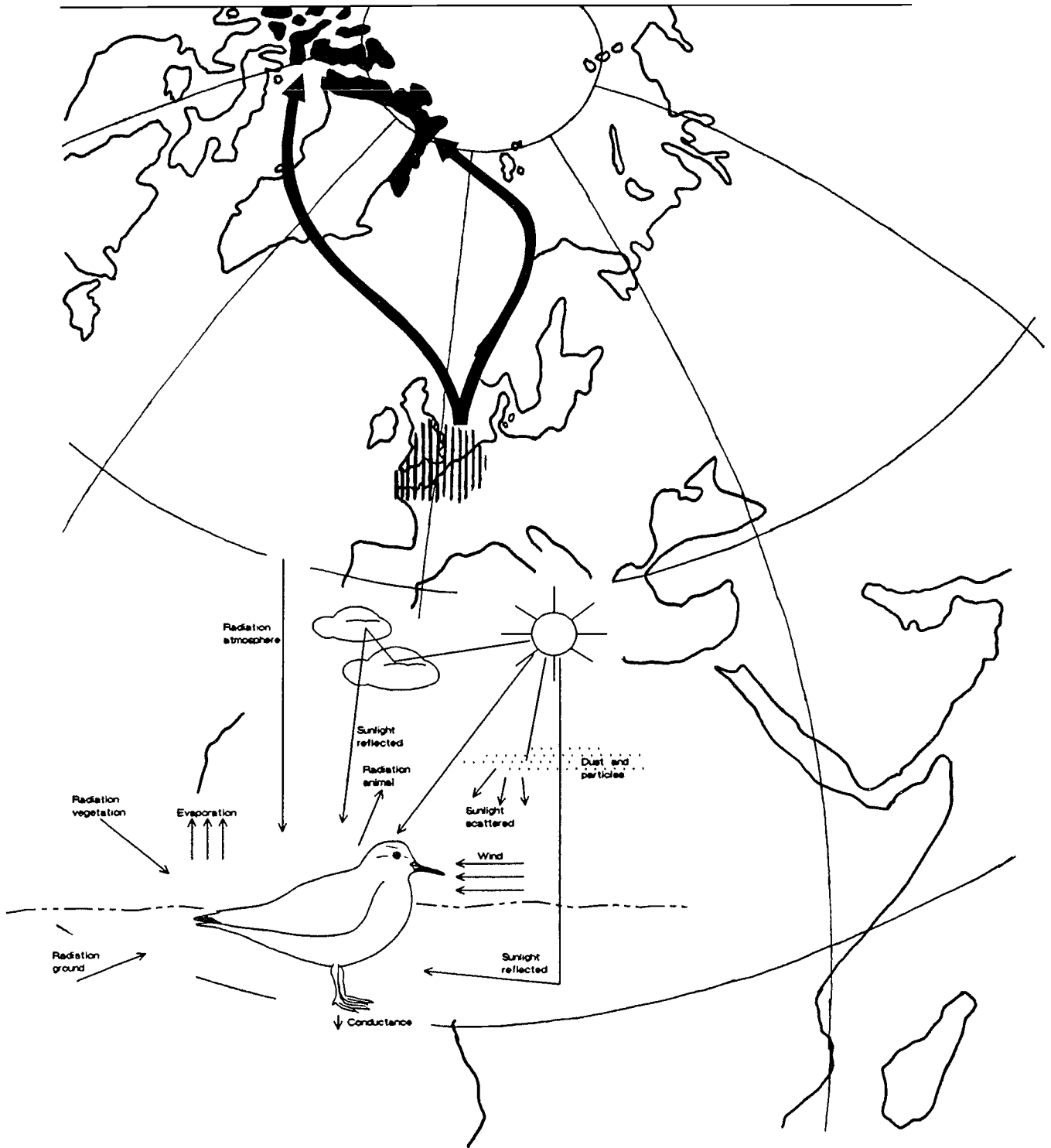


LIVING EXPOSED AND IN THE COLD

THERMOSTATIC COSTS OF NEARCTIC KNOTS (*CALIDRIS CANUTUS ISLANDICA*) AS MEASURED BY MEANS OF HEATED TAXIDERMIC MOUNTS

Popko Wiersma



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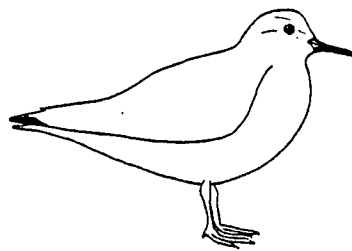
THERMOSTATIC COSTS OF NEARCTIC KNOTS (CALIDRIS CANUTUS ISLANDICA) AS MEASURED BY MEANS OF HEATED TAXIDERMIC MOUNTS

A Masters study by Popko Wiersma

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To the reader.

To improve my English writing I have written this report in that language. This will explain the many errors the reader possibly encounters. My apologies for this hindrance. For the reader not interested in detailed heat flow theory I suggest to omit a part of the chapter 'Heat flow', page 9, second paragraph, until page 11, second paragraph. P.W.

ABSTRACT.

Heated taxidermic mounts calibrated under laboratory conditions with Nearctic Knots were used to estimate the relation between thermostatic costs (TC) of Knots in the field and ambient temperature, wind speed and global radiation, as measured by meteorological stations. Microhabitat and wind speed are the most important factors defining TC. Calibrations under forced convection conditions in the case of second year birds were significantly different from calibrations at still air. This however was not so for the adults, although the trend was the same. Below the lower critical temperature TC of adult Knots was 18% higher than that of second year Knots. The possible influence of the plumage colour could not be detected. By standing 90° on the wind direction up to 13% extra energy was lost compared with Knots standing faced to the wind. Heat loss from the feet was probably neglectable. Intake of cold food could result in an extra energy loss of maximally 0.19 W. TC could differ 100% due to the microhabitat. Densely vegetated salt marsh was 'cheapest' and standing on a bare ridge on the tundra resulted in the biggest heat loss. In order to estimate mean TC over periods longer than a day, it is allowed to use mean weather registrations, except under very warm conditions when TC exceeds a critical temperature. TC of an hypothetical Nearctic Knot flying on the Afrosiberian route would be 34% lower than when flying the original route. Possibly the two subspecies follow different strategies; the Afrosiberians spending less on TC than the Nearctic one, but possibly being adapted to the warm wintering conditions, or the Nearctics being adapted to the cold. To what extent this difference is reflected in the physiology of the subspecies is unknown, although mass specific BMR of Afrosiberian Knots seems lower than that of Nearctic Knots. Climatic data from the West-African wintering grounds shows that heat stress will not occur frequently.

INTRODUCTION.

The Nearctic Knot.

Many bird species or populations migrate over large distances. The breeding grounds are left after reproduction, when the harsh winter conditions start. Then they travel to far away places with a milder climate, southward.

Knots *Calidris canutus* are an example of such a migratory bird. This wader species breeds all around the Arctic Ocean and winters on the coasts of western Europe, western and southern Africa, South America, Australia, New Zealand and East Indies (Cramp & Simmons 1983). Four subspecies are currently recognized. In this report the main attention is given to the Nearctic subspecies *C. c. islandica*. This population comprises some 345.000 specimens after numbers had decreased (Smit & Piersma 1989). They breed in northern Greenland and the north Canadian Arctic (Figure 1), profiting from the short arctic summer during which they try to raise one or more fledglings (see Pienkowski & Evans (1984) for a review on migration in the western Palearctic). Winter starts early up north and leaves them but one choice: migrating to places where food is still to be found and the climate is more friendly. In August these Knots arrive in western Europe (Cramp & Simmons 1983).

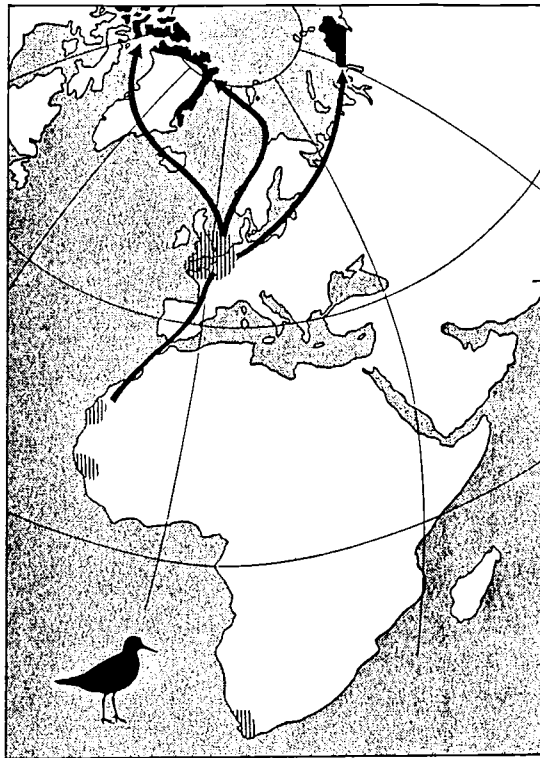


Figure 1. Migration routes of two Knot subspecies: *Calidris canutus islandica* (Nearctic Knot), breeding in the Nearctic and wintering in the European Wadden Sea and *C. c. canutus* (Afrosiberian Knot), breeding in Siberia and wintering in West-Africa and some in South-Africa. Wintering areas hatched and breeding grounds black.

The Knots flying to Europe mainly winter in the Dutch Wadden Sea and the North Sea estuaries of England (Smit & Piersma 1989; Cramp & Simmons 1983; Figure 1). Here they switch to a totally different diet consisting mainly of mollusks like *Macoma balthica*, *Mitilus edulis*, *Crastoderma edule* and *Hydrobia ulvae* and crustacea like *Corophium voluntator* (Prater 1972; Piersma et al. in prep.). By probing the mudflat with their relatively short bills of c. 3.5 cm (Prokosch 1988), they search for edible shellfish which they swallow entirely and crack in their strong stomach.

In April the adult Nearctic Knot population starts to prepare itself for a new breeding season. By accumulating fat and protein they fuel for a flight back to the breeding grounds. Prokosch (1988) found April weights of c. 130 g rising to some 190 g until begin May when they depart. Having reached their 'ready-for-take-off-weight', time is ripe. In flocks of 13 to 500 they start flying (Prokosch 1988; Piersma et al. 1990). While loudly singing they head for the tundra (Piersma et al. 1990). Iceland is used as a stopover site for about a month (Cramp & Simmons 1983). From late May to early June they arrive at the breeding grounds where they stay till August (Cramp & Simmons 1983).

It is no surprise that such a bird becomes the focus of intensive research. So many questions rise trying to see through the motives of Knot's doings. One way of solving this problem is by looking into a restricted indispensable resource: energy. Energy is the major resource for life, so it follows naturally that most questions are asked in terms of energy gain and consumption. From an evolutionary point of view energy is a force shaping nature as it is today. All this make it exciting to do research into the energy budget of animals: it might well explain some behavioural patterns, like migration.

In order to research energetics of animal life, we have to do some kind of housekeeping: What is the income and what the expended energetic currency, and how is it divided among the various behavioural components?

The energy budget.

Energy budgets can be made on different scales. A very large scale one is annual, or monthly, the summation of the amounts of incoming and expended energy, assuming no energy disappears unnoticed or is created out of the blue, conform the 'law of energy preservation'. This forms the basis of the budget. But we may subdivide the two major partitions. Figure 2 shows the items in the energy budget of an animal. The expended energy represents the consumption of the energy which is the reason for the energy intake. The energy consuming properties are: muscle movements, for external use like locomotion and for internal use like the blood flow through the body, growth: energy is converted into body tissues and last, energy is used for all kinds of chemical reactions like breakdown of food particles (digestion), information transport through the nerve system and production of hormones. Birds and mammals, which have a constant body temperature, also have to invest energy in thermo-regulation. The above classification is based on the kind of work performed using the energy. Of course all energy in fact is chemical.

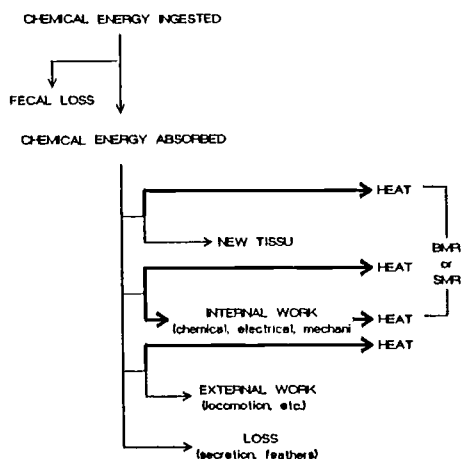


Figure 2. Flow diagram of energy through an animal, showing the constitution of basal metabolic rate (BMR) or standard metabolic rate (SMR). Bold lines show production of internal heat. From Eckart & Randall (1983).

On the income side of the budget food is the energy source. The amount of energy obtained from food depends on the composition. Fat has a very high energy content, proteins and

carbohydrates less. It also depends on the digestibility. Food may be enormously energy rich, but as long as an animal can not digest it, the energy is not usable and will be lost as faeces.

The energy budget does not look the same throughout the year. Different seasons have different energy demands, both as it relates to the absolute amounts as to the pathways of energy losses. The migratory period is very demanding. Flying is extremely expensive, so energy-rich plus supporting tissues have to be formed before a long distance non-stop journey can be undertaken (Drent & Piersma 1990). The breeding season has other claims. The female produces eggs after which one or both parents have to keep them warm, which should result in a period of chick raising, when the parent(s) have to find food for themselves and the chicks (for an extensive review see Drent & Daan 1980). During the nonreproductive stage the main pastime is survival. On top of these periodic energy costs comes the thermostatic cost. This particular energy item also changes throughout the year, due to changing weather conditions and Knot (micro)habitats in which the Knots are exposed to the elements at varying degrees.

This study deals with the thermostatic part of the energy budget of Nearctic Knots throughout the year. These costs might comprise big investments: the Knots live exposed in open and cold environments. Two months up north on the scarcely vegetated tundra, and the rest of the year on the mudflats and sand banks in the temperate zone of Europe.

Metabolic rate and heat production.

Although the state in which energy appears can vary, the total amount always stays the same. Hence, all energy a Knot takes in as food will, sooner or later, turn up in another form and at the ultimate end of the energy transformations one will always find heat. Imagine a muscle where chemical energy is transformed in kinetic energy. Already at this stage energy is lost as heat. And the movement itself produces heat as a consequence of drag. When all movements involved have stopped, the total amount of energy used by the muscle has been turned into heat. When the movement takes place inside the body the heat too will be dissipated inside the body. Heat production can also be postponed. When energy is used to make new tissues, heat is only dissipated when this tissue is broken down again. In a growing or fattening animal the energy budget will thus seem negative. Unlike growth, fattening is only temporally. So when the time scale is long enough the budget will be balanced again.

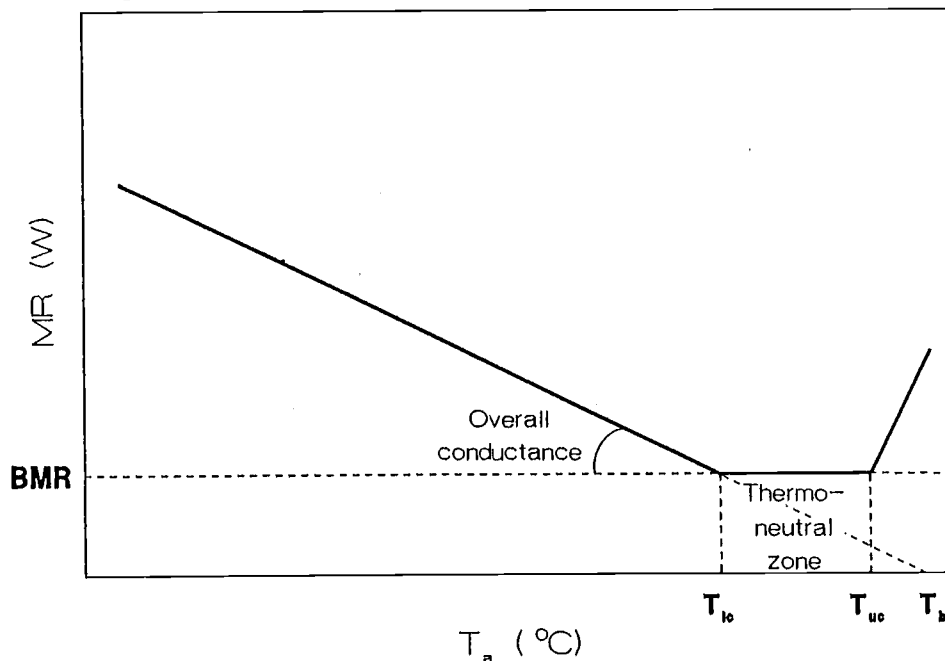


Figure 3. 'Scholander curve': metabolic rate (MR) of an inactive animal (= TC) as a function of ambient temperature (T_a). BMR: basal metabolic rate, T_{lc} : lower critical temperature, T_{uc} : upper critical temperature and T_b : body core temperature.

The basic, internal work, performed in order to stay alive, to 'keep the engine going', during the resting phase of the day, is called the basal metabolism. The basal energy consumption is called the Basal Metabolic Rate (BMR) (Figure 2). As soon as an animal has to do more physiological and/or physical work to stay alive, the energy consumption, or Metabolic Rate (MR), rises. In 1950, Scholander et al. published curves of inactive animals' MR in relation to the air temperature. A so called 'Scholander curve' is shown in Figure 3. In a restricted temperature range the homeothermic animal does not use more than the BMR, but when the air temperature exceeds a certain minimum level the MR will go up. This particular temperature is called the Lower Critical Temperature (T_{lc}). The metabolic rate at a specific temperature is called the Standard Metabolic Rate (SMR). The extra energy needed is used to keep the body temperature constant. At the other side of the curve MR will also rise: above the Upper Critical Temperature (T_{uc}) more energy is needed to loose heat, e.g. by panting. Between T_{lc} and T_{uc} we speak of the Thermoneutral Zone (TNZ). Here the animal does not regulate its body temperature by heat production (chemical heat regulation), which is already minimal, but by varying the heat flow to the environment (physical heat regulation). To accomplish this the blood flow to the skin can be changed and the resistance to heat flow can be altered by the fur or feathers. BMR plus the additional energetic cost for thermoregulation is defined as the thermostatic cost (TC) (Piersma et al. in press). Interested in the thermostatic costs of the bird, inactive animals should be measured in the post-absorptive stage, in order to measure only the heat production, which will then equal the metabolic rate.

There are two ways to measure the MR: estimating the total energy intake minus what is lost in the faeces, or by measuring the total heat loss of the animal. In this study the energy production was estimated by estimating heat loss through indirect calorimetry. The method depends on the measurement of a related factor. At the basis of all chemical reactions is the oxidation of the food molecules and their products. The amount of heat produced in these reactions is related to the amount of work performed which is related to the amount of oxygen consumed, at least at aerobic conditions. When the oxygen consumption of the animal is known, the energy consumption (MR) can be estimated. The energy production of oxidation however depends on the kind of fuel oxidized. If carbohydrates are oxidized 21.13 kJ per litre O_2 consumed is produced. Fat and proteins produce 19.83 and 18.66 kJ/l O_2 respectively (Eckert & Randall 1983).

Heat flow.

Thermostatic costs depend on the environmental circumstances. Cold weather results in high energy demands, while warm weather does not. The words cold and warm falsely suggest that temperature is the only variable to be considered. However, the experienced temperature, or 'coldness', of a particular situation depends on ambient temperature, but also on radiation and wind speed. Radiation can warm, but also can cool the animal while wind can intensify the temperature effect considerably. Before going into any detail I will give a more specific definition of the 'experienced temperature'. It is in fact a heat flux. Own experience probably can subscribe this, as shown in an example from Campbell (1977). Imagine standing barefoot in your bath room on the tiling: you will suffer from cold feet. Standing on the mat you will experience a more comfortable temperature. To complete this experiment one should measure the real temperature of the tile floor and the mat: these actually seem to be identical. What we did experience was in fact the heat flow from our feet. A stone tile is an excellent conductor. Heat, from our feet for instance, is easily transported toward the tiling. The mat is a much worse conductor, hampering the heat flow and hence feeling warmer. Conclusion: temperature is not the only factor defining experienced temperature. What we really are interested in is the rate at which heat flows to the environment.

There are four pathways used for heat flow: conduction, convection, evaporation and radiation (Figure 4). Evaporation is energy transport caused by the expansion of a liquid to gas. Conduction is energy transported from one solid substance to another by direct transport of kinetic energy of the molecules. Convection is an energy transport from a solid substance to a gaseous one. Convective heat loss increases when the gaseous substance is moving, in that way supplying a 'fresh amount of gas' which can take up heat. This is called forced convec-

tion, in contrast to free convection. Unlike the rest, radiation does not need any use of molecules: heat flows by electromagnetic waves.

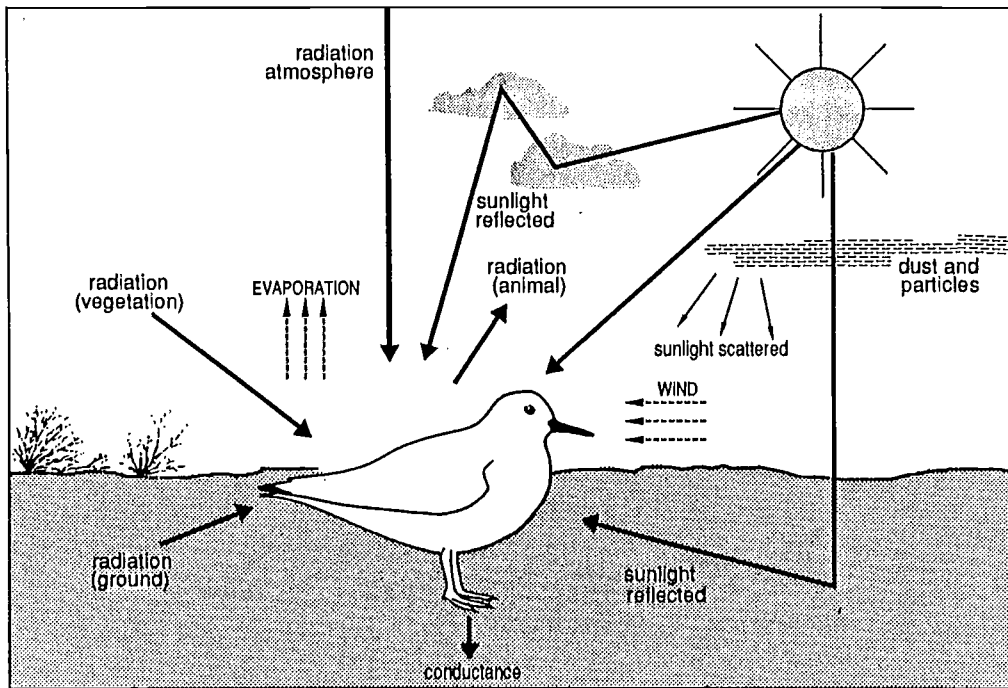


Figure 4. Channels of heat transfer between an animal and its environment. After Eckert & Randall (1983).

For better understanding heat flow can be compared to an electrical circuit (Bakken 1976). This gives good opportunities of describing the energy flow and identifying the influencing variables. Figure 5a shows a cross sectional view of a bird, and Figure 5b shows the electrical equivalent if heat flow is considered. Each layer is represented by a resistance, the energy driving potential is a temperature difference between the layers' borders. This scheme can be simplified by using the operative environmental temperature (T_e). This temperature also includes radiation. The equation describing heat flow with use of T_e is as follows:

$$H = K_e(T_a - T_e) \quad (1)$$

where H is heat flow (W/animal), K_e is the overall thermal conductance, being the reciprocal of resistance, in the general environment (W/animal $^{\circ}$ C), T_a is the ambient temperature. T_a and T_e in $^{\circ}$ C. According to Gagge and Hardy (1967, from Bakken et al. 1985) T_e can be described as:

$$T_e = T_a + \Delta T_r \quad (2)$$

and

$$\Delta T_r = (Q_a - A_e \sigma \epsilon T_a^4) / (K_c + K_r) \quad (3)$$

where ΔT_r is the temperature increment due to radiative heat flow (H_r), Q_a is the total absorbed radiation (W/animal), the total emitted radiation is equal to $A_e \sigma \epsilon T_a^4$. A_e is the effective thermal radiation area, σ is the Stefan-Boltzman constant ($= 5.67 \times 10^{-8} \text{ W/m}^2 \cdot ^{\circ}\text{C}^4$), ϵ is the thermal emittance ($0 < \epsilon < 1$), K_c is the convective conductance (W/animal $^{\circ}$ C) and K_r is the equivalent radiation conductance equal to $4A_e \sigma \epsilon T_a^3$. Equations 2 and 3 result in:

$$T_e = T_a + (Q_a - A_e \sigma \epsilon T_a^4) / (K_c + K_r) \quad (4)$$

Because T_e does not incorporate any wind effect, standard operative temperature (T_{es}) is used. T_{es} is defined as the temperature of an isothermal blackbody enclosure with a standard convection condition, e.g. a blackened wind tunnel, which would result in the same net sensible heat flow to or from the same animal with an identical body core temperature (Bakken 1976). This means that the metabolic rate of an animal in any environment with a particular T_{es} is equal to the metabolic rate in the standard environment (usually a climatic chamber) with an identical T_{es} . T_{es} can be described as:

$$T_{es} = T_b - (K_e / K_{es})(T_b - T_e) \quad (5)$$

where K_{es} is the overall thermal conductance in the standard environment (W/animal·°C).

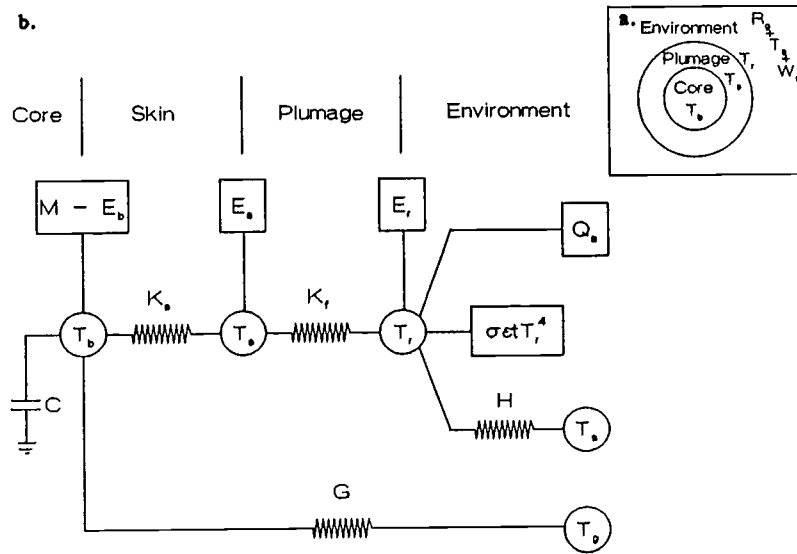


Figure 5. (a) Cross sectional view of a bird showing the relevant temperatures for heat flow. T_b : body core temperature, T_s : skin temperature and T_r : plumage temperature. (b) Basic thermal circuit of heat transfer between a simplified animal and its environment. Thermal conductance is represented by an electrical resistance symbol, temperatures by voltages, heat storage capacity by a capacitor symbol and heat flow by current flows. Circles are connection points or nodes, labeled with the corresponding temperature, square boxes are heat current sources with no relation to thermal conductance (from Bakken 1976).

Note that because T_{es} incorporates the overall conductance that it is an direct index of heat flow. Combined with equation 4 the next equation for T_{es} arises:

$$T_{es} = T_b - (K_e / K_{es})(T_b - T_a - (Q_a - A_e \sigma \epsilon T_a^4) / (K_c + K_r)) \quad (6)$$

Because it is our aim to estimate T_{es} from simple standard weather registrations, namely ambient temperature (T_a), global radiation (R_g) and wind speed (W_{sp}), it is tried to express every element in equation 6 into one of these variables. K_e is believed to be related to the square root of wind speed ($\sqrt{W_{sp}}$) (Gessaman 1972; Robinson et al. 1976; Bakken et al. 1981):

$$K_e = p + a\sqrt{W_{sp}} \quad (7)$$

with W_{sp} in m/s and p and a being constants. Here must be stated that some studies undermine the square root and show that another power than 0.5 is more appropriate (Goldstein 1983; Rogowitz & Gessaman 1990). The total absorbed radiation (Q_a) is related to the global radiation (R_g). The exact relation is not known but next one seems obvious:

$$Q_a = bR_g \quad (8)$$

with R_g in W/m^2 and b being a constant. Total emitted radiation ($A_e\sigma\epsilon T_a^4$) or R_e is related to the temperature difference between T_a and the surface temperature (T_r) in the following way (Calder & King 1974):

$$R_e = c(T_r^4 - T_a^4) \quad (9)$$

where c is a constant. Next equation of surface temperature is highly hypothetical, the linearity is an assumption.

$$T_r = d \cdot R_g \cdot T_a / (W_{sp} + 1) \quad (10)$$

where d is a constant. The convective conductance (K_c) is related to W_{sp} , but again linearity is hypothetical:

$$K_c = q + eW_{sp} \quad (11)$$

where q and e are constants. The radiative conductance is dependent of T_a^3 (Bakken et al. 1985):

$$K_r = 4A_e\sigma\epsilon T_a^3 \quad (12)$$

Now we can create the following equation:

$$T_{es} = T_b - (r + f\sqrt{W_{sp}})(T_b - T_a - (bR_g - c((d \cdot R_g \cdot T_a / (W_{sp} + 1))^4 - T_a^4)) / (q + eW_{sp} + 4A_e\sigma\epsilon T_a^3)) \quad (13)$$

Because the metabolic rate (heat production) is linearly related to T_{es} , we could, if the constants in equation 13 were known, calculate T_{es} . However, this approach leads to very obscure non-linear relations, as in equation 13. Probably this equation can be simplified by removing some variables whose influence are of minor importance in calculating the heat flow. Alas, my current knowledge is not sufficient to make this relation clearer and, what is even more important, more suitable for this study. Hence another, more 'back to earth', approach is used to relate TC to the weather variables.

First we go back to equation 1 ($H = K_e(T_b - T_e)$). Instead of T_e we now use T_a , the ambient temperature (Calder & King 1974). In this way ignoring the radiative dependent temperature difference. This results in equation 14:

$$H = K_e(T_b - T_a) \quad (14)$$

and incorporating equation 7 this results in

$$H = (p + a\sqrt{W_{sp}})(T_b - T_a) \quad (15)$$

where p and a are constants. To get free of the constant p , the equation has been reformulated by using the square root of W_{sp} plus one:

$$H = g\sqrt{(W_{sp} + 1)}(T_b - T_a) \quad (16)$$

where g is a constant. Now absorbed radiation, Q_p as in equation 6, is simply added to equation 16. Because radiation constitutes just a small part of the heat flow (Walsberg 1988) it is believed that the possible negative effect on the 'strength' of the heat transfer equation is negligible. This is also shown in the studies of Lustick (1969) and Hayes & Gessaman (1980), where artificial radiation simply seems to add a constant amount of energy to the total. This leads us to the following equation:

$$H = g\sqrt{(W_{sp} + 1)}(T_b - T_a) + bR_g \quad (17)$$

This is the equation used throughout this report. It is expected that an increasing ambient temperature results in a decreasing heat production. Increment of the global radiation should result also in a decreasing TC. Increasing wind speed on the other hand has an opposite result: TC gets higher.

Physical, physiological and behavioural responses.

Birds can minimize their energetic needs in three ways: physiological, physical and behavioural (Figure 6).

Physiological responses possible to birds are blood flow regulation toward the skin (vasoconstriction and -dilation), affecting the skin temperature and hence the heat flow between surface and environment. Second, fluffing of the feathers (ptilorection) increases the insulation. Fluffed feathers create a thicker plumage causing a higher resistance to heat flow. Evaporative cooling is stimulated during sweating and panting. Although birds do not have sweat glands they do lose water, and hence energy, through the skin (Bernstein 1971; Dawson 1982). Panting is a common feature in birds to lose excess heat (Dawson 1982). Some birds can lower their body temperature, decreasing the temperature difference between body and environment and consequently decreasing the energy flow from the bird (calder & King 1974).

Physical control includes the changes in the fat layer insulation and possibly a change in plumage structure and/or colour. Plumage colours have found to effect the radiative absorption and reflection (Lustick 1971; Walsberg et al. 1978; Morse 1980; Hüppop 1987).

Behavioural responses are microhabitat selection, body orientation and activity adaptations. Knots, being small sized, have many opportunities of selecting a habitat which would be less energetically stressing than another. Wind, being an important factor causing severe heat loss can be avoided by living in selected microhabitats (Porter & Gates 1969) or living close together in flocks (Ydenberg & Prins 1984), in that way creating their own profitable microhabitat.

By orientating towards or away from the sun radiative heat gain also can be regulated, at least in some birds. It was shown in Herring gulls *Larus argentatus* by Lustick (1980) and Hüppop (1987). This ability probably only exists in birds with contrasting plumage colours and consequently different radiative properties.

Activity regulation for thermostatic means has to be seen as regulating the heat produced by muscle activity. Because of the none existing 100% efficiency of energy transformations all work performed inside the body is accompanied by heat. This heat can probably be used to

sustain at body temperature and could in that way be useful to minimize the energy expenditure (Webster & Weathers 1990). This is only true below the thermoneutral zone. Above T_{uc} any extra heat load leads to more active heat loss. In that case the bird may have two options: 1) trying to loose heat by other behavioural, physical and/or physiological properties, or 2) by reducing its muscle activity which would practically mean walking and flying for shorter periods of time and/or at speeds energetically less expensive. On the other hand both options would probably also mean a decrease in food, and hence energy, intake, possibly resulting in an optimal choice for the activity rate at which the ratio of energy taken in, needed to loose

Behavioural	Microhabitat selection
	Body orientation
	Activity patterns
Physical	Plumage positioning
	Feather characteristics
Physiological	Body temperature
	Evaporation
	Fat layer
	Blood flow skin

Figure 6. Items of the energy budget, divided into three major parts, each subdivided into particular regulating properties.

heat, and the heat production of the muscles encountered in that same process is highest. Below the lower critical temperature the heat production by muscle activity can probably help to keep the body temperature fixed by adding it to the heat produced in the resting metabolism processes. This could then lead to a decrease in maintenance metabolism. So, on first sight one could expect a bird to be active for reasons of heat production. But is it an efficient way of producing heat? This will depend on the amount of exchangable heat produced and the costs of being active, which can be reduced by the intake of food.

The situation however changes when maintenance metabolism can not supply all heat needed, due to a further decrease of the environmental temperature. Now any extra heat production is helpful in maintaining body temperature. Again the question rises does a bird perform external work just to produce heat. The answer is probably no, because a more efficient process is available: shivering. Shivering is a fast muscle movement with the only purpose of producing heat. Thus the conclusion might be that birds do not regulate thermo-static costs by activity regulation. But further study to the possibilities of this item is needed.

METHODS.

In order to calculate the thermostatic costs of Knots under field conditions heated taxidermic mounts were used as a measuring tool for the standard operative temperature (Bakken et al. 1981). At this calculated temperature a Knot has the same thermostatic costs as it would have with an identical Ambient Temperature (T_a) in an standard laboratory environment (see Introduction and Bakken 1976). To estimate the thermostatic costs for various locations for long periods, calculated thermostatic costs from the mounts were correlated to simultaneously registered standard weather measurements, to ensure that the method could be used with large meteorological data bases existing all over the world. These parameters, which were known to be the main factors defining this part of the energy budget (see Figure 4), are ambient temperature, wind speed and global radiation. With these three weather factors and a microhabitat usage schedule for different times of the year, thermostatic costs of Knots in their natural habitat have been estimated throughout the year.

The heated taxidermic mount.

The construction of the mounts was according to the instructions as given by Bakken et al. (1983). A frozen Knot corps was used as a mould. First it was carefully skinned. To preserve the feathered skin for later usage it was cleaned from fat and dabbed with a Borax solution which also kept it flexible. The remaining 'naked' body was plastered with artificial rubber (Latex). As the rubber had dried it was pulled of, producing a mould which was filled with melted beeswax. After the beeswax had hardened the rubber mould was pulled of leaving a copy of the skinned Knot made of wax. From the venter, near the cloaca, upward trough the back a narrow tunnel was drilled in which a hollow copper tube (ϕ 5 mm) was placed. To lead the heater wire over the body a continuous serpentine groove was curved in the wax. After covering the wax mount with electrically conducting graphite, a thin copper layer of about 0.2 mm was electroformed over the surface. To accomplish this, the graphite covered wax mount was connected to a wire which made contact with the copper tube inside the mount and was connected to a power supply. The mount was placed in an acid copper sulfate bath with a copper anode in it. Continuous stirring of the solution with an aquarium pump provided a more or less equal distribution of the copper over the surface. This process of electroformation took 2 days. The next procedure was to place the insulated heater wire in the preformed groove. A quick drying two component glue helped to keep the wire at its place. A second copper layer was than electroformed to cover the insulated heater wire and thicken the deposition. To remove the beeswax the mount was placed in boiling water. The wax ran out through a small prefab hole on the rear end of the copper cast. The skin was pulled over the copper core. Head and rear end were fixed with a heat conducting glue and the incision on the belly closed with needle and thread.

A thermocouple and a thermistor were put inside the copper tube and fixed with glue. The heater wire was connected with a power supply and a thermostat via a cable. The thermocouple also was connected with the thermostat. The thermistor was connected to a data logger. All cables were fixed to a leg on which the mount stood in order to protect the connections on the mount from damaging caused by handling the mount. Four mounts were produced in this way. Three with winter plumages and one with a summer plumage.

Four other mounts were constructed after the old ones had served duty for a year. They were constructed in a slightly different way: 1) A heat conducting paste was put between the copper cast and the skin to avoid air captured between the two layers, and 2) instead of using a dead Knot as a mould, a ceramic model was used. This offered the opportunity of creating more identical mounts in a more natural shape with a smoother copper wall.

To provide the mount with energy the heater wire was connected with a 12 V DC power supply: a car battery or a 220 V AC to 12 V DC transformer. To keep the temperature of the mounts' core (T_m) constant, the power supply was regulated with a thermostat which switched the current off or on according to T_m as measured with the thermocouple inside the copper core. A digital data logger (Squirrel 1200, Grant Instruments Cambridge) recorded the 'mean voltage' (V_m) over the heater wire by taking a sample every 20 seconds and recording the 30 minutes mean. Because the voltage over the heater wire (V) was known the mean effective

voltage (V_e) over 30 minutes can be calculated as:

$$V_e = V_m \cdot V \quad (18)$$

Because the total resistance of the heater wire plus cable (R_m) was measured, energy consumption (P_m) in Watts can be calculated as being:

$$P_m = V_e^2 / R_m \quad (19)$$

To check on the mount core temperature, T_m was simultaneously recorded. With the thermostat T_m was fixed to 41 °C, probably close to the Knots body temperature (Brouwer, pers. comm.).

Locations and weather registrations.

To make measurements with the mounts they were brought to the natural habitat of Knots. We chose the small island Griend (coor: 53°15'N, 3°15'E) in the Dutch Wadden Sea where in winter large numbers of Knots can be found which made it possible to do behavioural observations as well. The island consists of a 'hockey-stick-shaped' dune and a small salt marsh with bare and overgrown areas. During low tide Knots were foraging on the surrounding mudflat. High tide roosts were most frequently situated on Richel, a sand bank 10 km north-west from Griend. Sometimes Knots were staying on the island to roost: on the salt marsh or on the beach. Probably this was due to strong winds which would make their flight to the sand bank a strenuous pursuit. Measurements during their breeding season were performed on the tundras at Rowley Island and at Alert (Arctic Canada, coor: 69°00'N, 79°00'W and 82°30'N, 62°00'W respectively). During our measurements in the Wadden Sea we did our own weather registrations. A thermograph was placed 1.8 m above the surface and a mechanical wind speed meter stood at a height of 8 meters above ground level, c. 2 m above the small warden's house on which it was fastened. Using wind speed at this height is legitimate because it is linearly related with wind speed near the surface (Wieringa & Rijkoort 1983). Global radiation was measured on 30 to 50 cm above ground level on the same spot as where the mounts were standing, using a pyranometer (Kipp en Zonen, Delft). Weather registrations of periods without complete measurement were obtained from a weather station of the Royal Netherlands Meteorological Institute (KNMI) on the island Terschelling, 10 km north of Griend. These comprised hourly data. Weather registrations in Canada, also on an hourly base, were obtained from stations situated less than a 100 m from the mounts.

Ambient temperature was measured in °C, wind speed in m/s and global radiation in W/m².

Calibration of the heated taxidermic mounts.

A mount and a Knot are not equally insulated, considering the mount does not moult, feathers are badly kept in repair and subcutaneous fat is lacking. Because the mount does not duplicate a live Knot it had to be calibrated. The energy consumption of the mount was measured under standard conditions at which also live Knots were measured. The mounts were placed in a box of 0.37 x 0.25 x 0.24 m or 0.31 x 0.22 x 0.19 m (lxwxh). The inside walls were covered with black paper to avoid any reflection of infrared radiation from the animal via the box walls which would result in an underestimate of the energy consumption (Porter 1969). It was placed in a dark climatic chamber. Ambient temperature was measured inside the box with a thermistor. Mount core temperature and mean voltage were recorded every 15 or 30 minutes, being the mean of 180 samples. T_a ranged from -20 °C up to +38 °C. On two occasions a

blackened wind tunnel was used creating a wind speed of 1 m/s, as recommended by Bakken et al. (1981). The mount was placed facing the wind as live Knots mainly do in the field (Wiersma, report in prep.).

The measurements resulted in a equation of the following form:

$$P_m = c_m(T_m - T_a) \quad (20)$$

where P_m is the power consumption of the mount (W/mount), c_m is the conductance of the mount ($\text{W}/^\circ\text{C}\cdot\text{mount}$), T_m is the core temperature of the mount ($^\circ\text{C}$).

Measuring heat production of Knots.

To measure the heat produced by Knots indirect calorimetry was used. The method depends on the measurement of a related factor: oxygen. Heat is released in the chemical reactions and the movements taking place inside the body. On the basis of all these reaction stands oxidation of the food molecules and their products. In aerobic oxidation, the amount of heat produced is related to the amount of oxygen consumed. As the oxygen consumption of the animal is known the energy consumption, or MR, can be estimated assuming an energetic equivalent of 20.08 kJ/l O₂ during the post-absorptive period (Kersten & Piersma 1986), thus assuming that mainly fat is oxidized. And because all the energy used will be converted into heat, the MR is similar to the heat production (see introduction).

To construct the temperature dependent metabolic rate curve ('Scholander curve') a Knot was placed in an airflow circuit, connected to an oxygen meter, at different ambient temperatures in a standard box. The boxes' dimensions were as described above. T_a was measured inside the box every minute with a thermistor. The first measurements were performed using three different temperatures during one session. Later on only one temperature was used to get a better idea about the metabolic 'behaviour' throughout a one day cycle within both the subjective night and day.

The Knots were selected from a group of 21 specimens living in outside cages. they were fed with artificial trout food pellets (Trouvit), consisting of 11% water, 12% fibers, 3% cellulose, 45% proteins and 8% fat. The birds were selected on the overall condition. Birds weighing less than 95 g or with injuries were never used. In total 11 animals were used, 5 of them adults and 6 early second calender year birds (old juveniles). Before and after the measurement took place the birds were weighed to the nearest 0.1 g on an electronic balance. Every week the birds were examined for moult intensity. Body moult was estimated with a 4 scale index, ranging from 0 (none) to 4 (heavy). Also wing moult and plumage stage were estimated. The body moult scores were used to check on differences in MR between moult classes.

A measurement started between 16.00 and 20.00 h and ended the next day at about 16.00 h, totalling on average 21 hours. The oxygen meter and supporting equipment were all started and kept running using the program Measure v. 11 and later on v. 12, written in Pascal programming language. The program collected the data and recorded it each minute. The variables recorded were: channel, date, time, T_a , air flow rate through system and oxygen percentage. First a reference sample was taken. During 20 minutes, inlet air of the box was measured. After an 8 min wash-out period 4 samples were taken. Again after a wash-out period of 8 min the outlet air from the box was measured for 160 min. The percentage oxygen in the inlet air was corrected by interpolation of the reference measurements before and after the 160 min period. Almost every day the system was calibrated before the measurement started by letting through two different gas mixtures with known O₂ content (20.15 and 20.90%).

In order to measure metabolism during the post-absorptive state, the birds were separated from their cage mates 24 h before the measurement started and were kept in a cage without food and with water ad libitum. Animals digesting and assimilating food are found to have a higher metabolism than post-absorptive animals (Eckert & Randall 1983).

At the end of a measurement faeces, collected on the bottom paper with known dry mass, were weighed to the nearest 0.01 g on a mechanical balance. After one day in a drying oven at

60 °C it was weighed again.

Efforts were done to estimate the evaporative water loss. Three tubes filled with a water absorbing chemical (3Å molecular filter) were placed in the circuit behind the box. For reasons unclear this did not succeed. The amount of water measured always was far under the expected value.

The collected data were afterwards converted to the essential values by using Lotus 1-2-3 r. 2 (Cambell 1986). Oxygen consumption was calculated by subtracting the O₂ percentage of the inlet air from the O₂ percentage of the outlet air, taking into account the flow rate. To correct the oxygen volume consumed for the CO₂ produced during the oxidation a respiratory quotient (RQ), which is the ratio of oxygen consumed and carbondioxide produced, of 0.75 was assumed, according to the assumption that mainly fat is oxidized (Eckert & Randall 1983). The equation used to calculate the oxygen consumption is:

$$VO_2 = VI(FIO_2 - FEO_2)/(1 - FEO_2(1 - RQ)) \quad (21)$$

VO₂ is the amount of oxygen consumed (l/h), VI is the flow rate at which air flows through the system and hence through the box containing the bird (l/h), FIO₂ is the fraction of oxygen in the inlet air and FEO₂ is the fraction of oxygen in the outlet air (Klaassen 1984; Hill 1972). The energy consumption is estimated at:

$$MR = 20.08 \cdot VO_2 / 3600 \quad (22)$$

resulting in Watts (J/s). The metabolic rate of a bird, at one temperature, was defined as the lowest mean value calculated over 120 minutes.

Theoretically anaerobe metabolism only occurs in extreme situations: when the oxygen supply is not sufficient. This is thought to take place only in extreme hard working muscles and can only last for short periods of time. The assumption was that this never occurred in the lab situations under which the measurements took place.

The Scholander curve was calculated by a non-linear method in statistical package SYSTAT. In this way the BMR, and the conductance were estimated, resulting in the following equations:

$$MR = c_k(T_b - T_a) \quad [T_a < T_{lc}] \quad (23)$$

$$MR = BMR \quad [T_{uc} \leq T_a \leq T_{lc}] \quad (24)$$

MR in W/animal, which is equal to TC, c_k the conductance of the Knots skin plus plumage (W/animal·°C). All through this report T_b is assumed to be 41 °C, according to measurements by A. Brouwer (not published).

Combining the 'copper Knot', live Knot and weather registrations.

Because both the mounts and the Knots were measured under identical standard situations, with T_a as the only changing factor for the environmental temperature inside the box, it is possible to express the power consumption of the mount in terms of energy consumption of a Knot. Combining equation 20 and 23 gives:

$$TC = c_k(T_b - T_m + P_m/c_m) \quad (25)$$

Using this equation we can convert the mount field measurement to the metabolic rate a Knot would have at that same time and place. From equation 17 we can now express the metabolic rate of a single Knot in terms of T_a , R_g and W_{sp} which were registered at the same time. Multiple regression analyses were performed to estimate the parameters of equation 26 which is identical with equation 17.

$$TC = g\sqrt{(W_{sp} + 1)}(41 - T_a) + b \cdot R_g \quad (26)$$

The multiple regression was performed on selected data sets for different (micro)habitats and body orientations. The SPSS/PC+ statistical package (Norusis 1988) was used to perform the multiple regression. Many other statistics were performed using Lotus 1-2-3 r. 2.

RESULTS.

Calibration of the heated taxidermic mounts.

The thermistors inside the climatic chambers were calibrated. Figure 7 shows the results. All temperatures measured with these thermistors were afterwards adjusted according to this calibration.

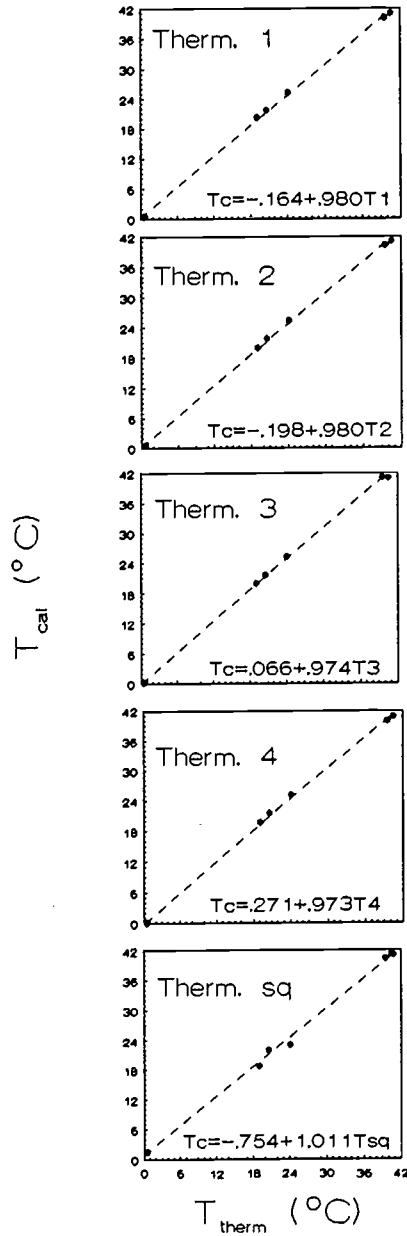


Figure 7. Calibration curves of the thermistors used in this study. Results of the linear regression shown in the boxes. T_c : corrected temperature, T_{sq} : thermistor connected to data logger.

The mounts are numbered 1 to 4, the newly produced set 1n to 4n. Mount 2n broke down very soon and was used as a cold model from the beginning. Due to the many working hours in the field (see Table 6) the mounts characteristics changed throughout the study period. This applied to the plumage as well as to the electrical circuit. Changes in the electrical circuit

were made allowance for in the further calculations by interpolating the resistances of the heater wire of different dates (Table 1). Resistances during the first three months of field measurements were considered to be constant.

Table 1. Electrical resistance of mounts (R) during period of usage. Bold numbers are real measurements, rest interpolations, except June and July 1989 and July 1990.

		Mount			
		1	2	3	4
Date		R (Ω /mount)			
Jun	89	8.9	11.1	10.8	11.9
Jul	89	8.9	11.1	10.8	11.9
Aug	89	8.9	11.1	10.8	11.9
Sep	89	8.8	11.5	11.0	11.7
Oct	89	8.7	12.0	11.3	11.5
Nov	89	8.6	12.4	11.5	11.3
Dec	89	8.6	12.8	11.7	11.2
Jan	90	8.5	13.2	11.9	11.0
Feb	90	8.4	13.7	12.2	10.8
Mar	90	8.3	14.1	12.4	10.6
Apr	90	8.2	14.5	12.6	10.4
		1n	2n	3n	4n
Jun	90	15.5	15.5	13.8	11.0
Jul	90	15.5	15.5	13.8	11.0

Mount core temperature was not as constant as expected. T_m was found to be related to the mean voltage. This means that in a cold environment the mount temperature was higher than in a warmer. Because T_m was not always recorded, due to a lack of channels of the data logger, it sometimes had to be estimated from the existing data. Table 2 gives the estimates for T_m from V_m .

Changing plumage effects the conductance. So power curves of the mounts were made regularly during their period of usage (Table 3). During the first 6 months a decrease in conductance took place, probably due to corrosion of the copper wall caused by the often damp and salt circumstances in the field. After this period conductance increased considerably. This could be the effect of worsening of the plumage condition. Figure 8 and 9 show the power curves of the four mounts as measured in August 1989 and of the new mounts as measured in May 1990 respectively. It shows that no big differences exist between the mounts' conductance properties. Figure 10 shows the linear relations of temperature and power consumption of one mount through time.

Table 2. Regression of mount core temperature and mean voltage according to the equation $T_m = c + rc \cdot V_m$. Marked ⁱ are interpolated values.

Mount	Date	c (S.E.) 'C	rc (S.E.) 'C/V _m	r ²	n
1	Aug 89	37.56 (.17)	23.43 (.18)	.996	66
	Nov 89	37.42 (.44)	23.59 (.25)	.969	283
	Dec 89	37.89 (.80)	19.34 (.46)	.904	186
	Feb 90	38.49 ⁱ (-)	15.39 ⁱ (-)	.-	-
	Apr 90	39.09 (.15)	11.43 (.69)	.958	14
2	Aug 89	37.67 (.25)	21.81 (.25)	.992	66
3	Aug 89	36.97 (.39)	28.66 (.39)	.988	66
	Nov 89	37.41 (.44)	17.50 (.23)	.952	286
	Dec 89	37.73 (.46)	16.61 (.15)	.927	971
	Feb 90	37.11 (.19)	16.34 (.25)	.976	107
	Apr 90	37.09 (.28)	12.42 (.15)	.960	302
4	Aug 89	37.68 (.98)	23.90 (.85)	.925	65
	Nov 89	37.88 ⁱ (-)	9.04 ⁱ (-)	.-	-
	Dec 89	38.07 (.18)	-5.82 (.09)	.878	555
	Feb 90	37.69 (.06)	-5.18 (.10)	.961	106
	Apr 90	37.62 (.09)	-4.54 (.04)	.977	330
1n	May 90	42.14 (.58)	-4.05 (.36)	.493	130
	Aug 90	41.62 (.13)	-4.31 (.08)	.963	113
2n	May 90	41.85 (.21)	-4.04 (.13)	.884	128
3n	May 90	41.62 (.13)	-4.46 (.08)	.966	113
	Aug 90	41.47 (.18)	-4.09 (.12)	.901	125
4n	May 90	41.29 (.02)	-3.54 (.02)	.997	127
	Aug 90	41.68 (.14)	-4.40 (.09)	.958	113

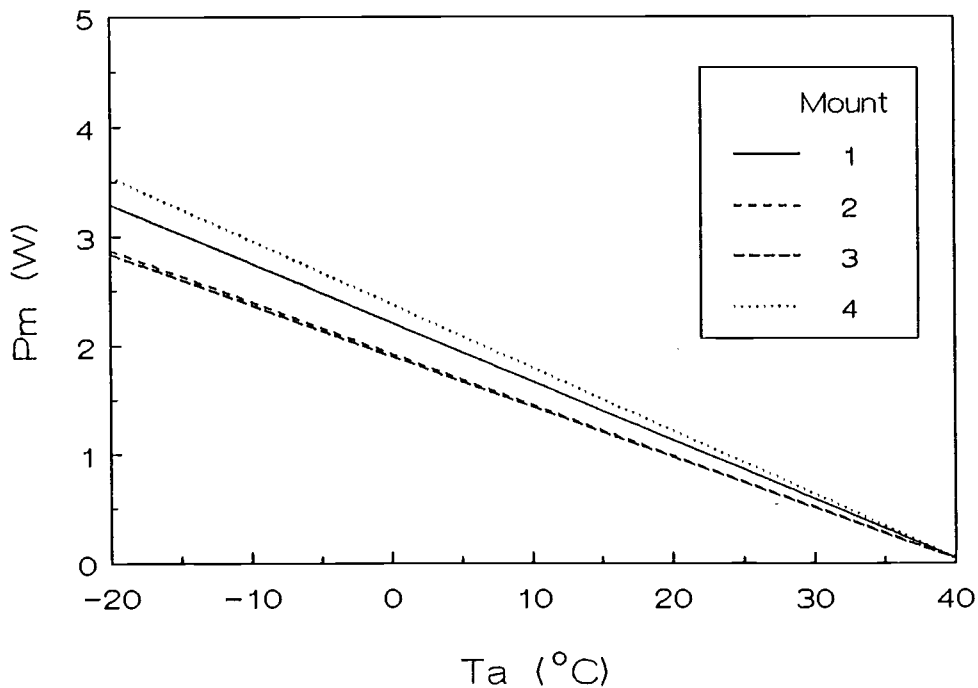


Figure 8. Power curves of heated taxidermic mounts as measured in august 1989. Mounts were standing in the climatic chamber (box 0). See Table 3 for detailed information.

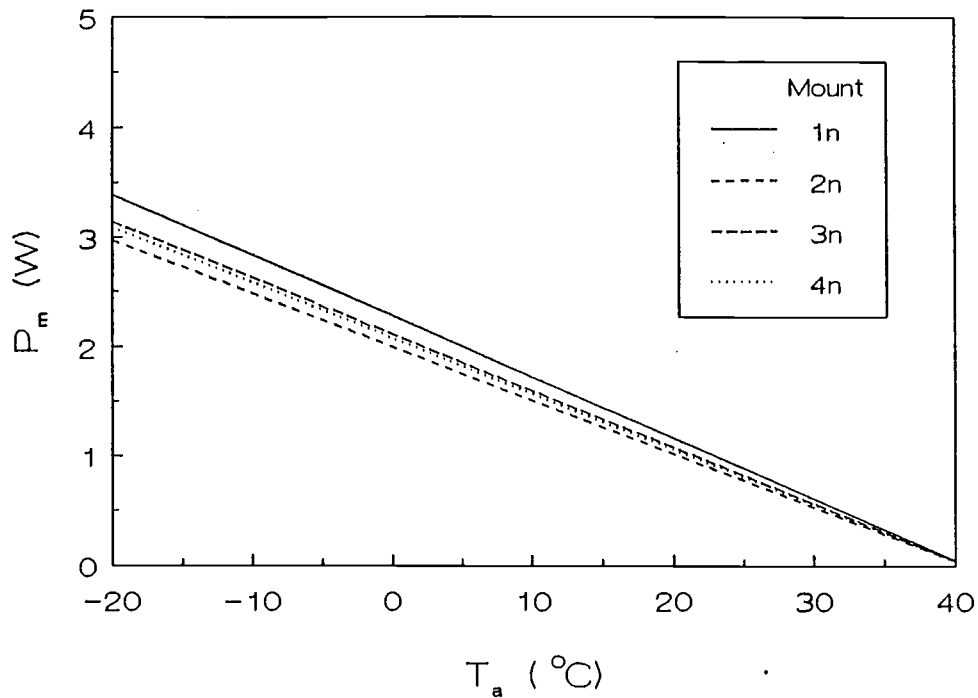


Figure 9. Power curves of latest heated taxidermic mounts as measured in May 1990. Mounts were standing in the climatic chamber (box 0). See Table 3 for detailed information.

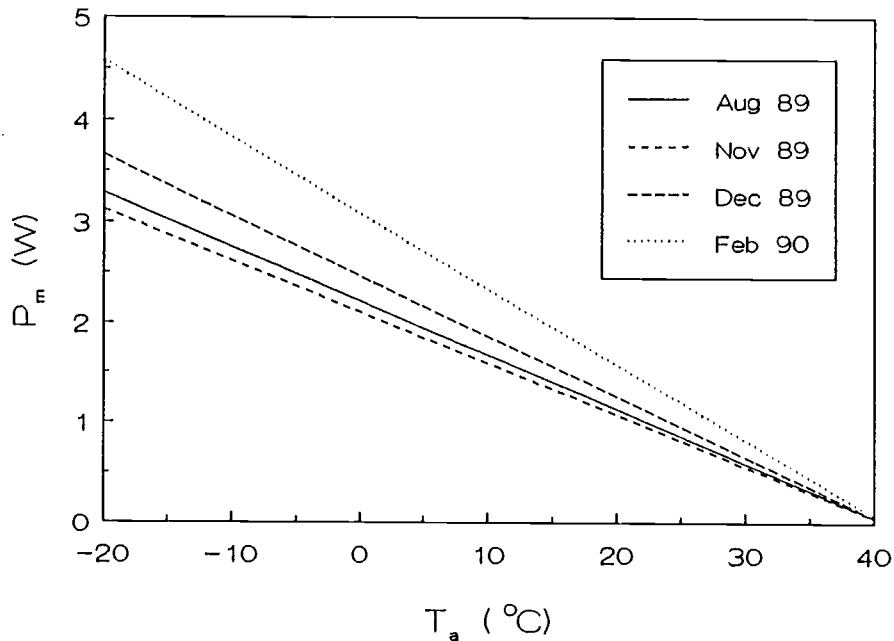


Figure 10. Power curves of mount 1 through time. All measurements were performed in the climatic chamber (box 0). See Table 3 for detailed information.

Most calibrations were not performed under the standard conditions under which the Knots were measured (box 1 or 2) but in the climatic chamber (box 0). Due to different conditions, conductances were not identical at these measurements (Figure 11). Since the conductances in box 0 and 1, and box 1 and 2 differed significantly (t-test of regression coefficient, $p < 0.01$), adjustments had to be made afterwards, derived from the December 1989 data. During that period the mounts were measured both in and outside the standard situation. Correction factors are shown in Table 4. The conductances used for further calculations are shown in Table 5 and 6.

Table 3. Power curves of the mounts according to equation 20 ($P_m = c_m \cdot (T_m - T_a)$) including standard error of the origin. Box 0: climatic chamber, outside blackened box. Box 1: small blackened box. Box 2: blackened wind tunnel (c. 1 m/s). Each sample is a 20 minutes measurement.

Mount	box	Date	n	S.E. origin	c_m (S.E.) W/°C	r^2
1	0	Aug 89	66	.0656	.0540 (.0003)	.997
	0	Nov 89	147	.0513	.0471 (.0003)	.975
	0	Dec 89	439	.1724	.0601 (.0003)	.933
	1	Dec 89	91	.0990	.0533 (.0005)	.965
	2	Dec 89	530	.0719	.0719 (.0001)	.992
	0	Feb 90	107	.1033	.0752 (.0002)	.986
	2	Apr 90	129	.1197	.1040 (.0004)	.985
2	0	Aug 89	65	.0633	.0471 (.0003)	.996
3	0	Aug 89	66	.0967	.0465 (.0004)	.992
	0	Nov 89	149	.1922	.0438 (.0004)	.958
	0	Dec 89	269	.1125	.0448 (.0002)	.975
	1	Dec 89	262	.0822	.0423 (.0001)	.981
	2	Dec 89	206	.0780	.0569 (.0001)	.990
	0	feb 90	107	.1071	.0585 (.0002)	.975
	2	Apr 90	43	.1454	.0751 (.0006)	.993
4	0	Aug 89	58	.0851	.0581 (.0003)	.996
	0	Nov 89	147	.2953	.0494 (.0006)	.921
	0	Dec 89	440	.1512	.0605 (.0002)	.968
	1	Dec 89	77	.1216	.0535 (.0004)	.971
	0	Feb 90	106	.0969	.0731 (.0002)	.981
	2	Apr 90	154	.1035	.1034 (.0003)	.989
1n	0	May 90	121		.0556 (.0006)	.988
	2	May 90	9		.0661 (.0003)	1.000
	0	Aug 90	103	.0702	.0491 (.0002)	.988
2n	0	May 90	109		.0487 (.0006)	.985
	2	May 90	19		.0599 (.0006)	.998
3n	0	May 90	120		.0516 (.0006)	.985
	2	May 90	5		.0685 (.0006)	1.000
	0	Aug 90	103	.0893	.0546 (.0004)	.984
4n	0	May 90	122		.0507 (.0005)	.987
	2	May 90	5		.0707 (.0009)	1.000
	0	Aug 90	103	.1950	.0544 (.0008)	.932

Table 4. Conductances of the mounts (c_m) and the correction factors (cf) in order to convert measurements of conductance of the mounts performed in box 0 (climatic chamber, outside blackened box) and box 2 (blackened wind tunnel, c. 1 m/s), respectively, to box 1 (small blackened box) and box 2. When data not available, mean value is used (rest, including new mounts).

Mount	box 0	box 1	box 2	$cf_{0 \rightarrow 1}$	$cf_{2 \rightarrow 1}$	$cf_{0 \rightarrow 2}$
1	.06009	.05325	.07190	.8862	.7406	1.197
3	.04476	.04225	.05687	.9439	.7429	1.270
4	.06045	.05354	.-	.8857	.-	.-
rest	.-	.-	.-	.9053	.7418	1.233

Table 5. Conductances of the mounts in box 1 (small blackened box). According to equation 20: $P_m = c_m(T_{m0} - T_a)$. Real measurements from box 1 are typed bold, marked ⁱ: interpolated, ⁰: estimated from box 0, ^w: estimated from wind tunnel and ^m: estimated using mean course of the other mounts' resistances. Correction factors are given in table 4.

		Mount			
		1	2	3	4
Date		c_m (W/°C)			
Jun 89		.04786 ⁱ	.04266 ⁱ	.04391 ⁱ	.05149 ⁱ
Jul 89		.04786 ⁱ	.04266 ⁱ	.04391 ⁱ	.05149 ⁱ
Aug 89		.04786 ⁰	.04266 ⁰	.04391 ⁰	.05149 ⁰
Sep 89		.04707 ⁱ	.-	.04304 ⁱ	.04890 ⁱ
Oct 89		.04628 ⁱ	.-	.04218 ⁱ	.04631 ⁱ
Nov 89		.04549 ⁰	.-	.04131 ⁰	.04372 ⁰
Dec 89		.05325	.-	.04225	.05354
Jan 90		.05996 ⁱ	.-	.04874 ⁱ	.05916 ⁱ
Feb 90		.06667 ⁰	.-	.05522 ⁰	.06478 ⁰
Mar 90		.07190 ⁱ	.-	.05552 ⁱ	.07078 ⁱ
Apr 90		.07712 ^w	.-	.05581 ^w	.07678 ^w
		1n	2n	3n	4n
May 90		.05035 ⁰	.04412 ⁰	.04668 ⁰	.04592 ⁰
Jun 90		.04839 ⁱ	.04419 ^m	.04760 ⁱ	.04703 ⁱ
Jul 90		.04642 ⁱ	.04426 ^m	.04851 ⁱ	.04814 ⁱ
Aug 90		.04446 ⁰	.04433 ^m	.04943 ⁰	.04925 ⁰

Table 6. Conductances of the mounts in box 2 (blackened wind tunnel) at c. 1 m/s wind speed. According to equation 20: $P_m = c_m(T_m - T_a)$. Real measurements from box 2 are typed bold, ⁱ: interpolated, ⁰: estimated from box 0, and ^m: estimated using mean course of the other mounts' resistances. Correction factors are given in table 4.

Date		Mount			
		1	2	3	4
		c_m (W/°C)			
Jun	89	.0646 ⁱ	.0581 ⁱ	.0591 ⁱ	.0716 ⁱ
Jul	89	.0646 ⁱ	.0581 ⁱ	.0591 ⁱ	.0716 ⁱ
Aug	89	.0646 ⁰	.0581 ⁰	.0591 ⁰	.0716 ⁰
Sep	89	.0635 ⁱ	.-	.0579 ⁱ	.0680 ⁱ
Oct	89	.0625 ⁱ	.-	.0568 ⁱ	.0645 ⁱ
Nov	89	.0614 ⁰	.-	.0556 ⁰	.0609 ⁰
Dec	89	.0719	.-	.0569	.0746
Jan	90	.0809 ⁱ	.-	.0656 ⁱ	.0824 ⁱ
Feb	90	.0899 ⁰	.-	.0743 ⁰	.0901 ⁰
Mar	90	.0970 ⁱ	.-	.0747 ⁱ	.0968 ⁱ
Apr	90	.1040	.-	.0751	.1034
		1n	2n	3n	4n
May	90	.06605 ⁰	.05990 ⁰	.06854 ⁰	.07068 ⁰
Jun	90	.06348 ⁱ	.06000 ^m	.06989 ⁱ	.07239 ⁱ
Jul	90	.06089 ⁱ	.06009 ^m	.07123 ⁱ	.07410 ⁱ
Aug	90	.05832 ⁰	.06019 ^m	.07258 ⁰	.07581 ⁰

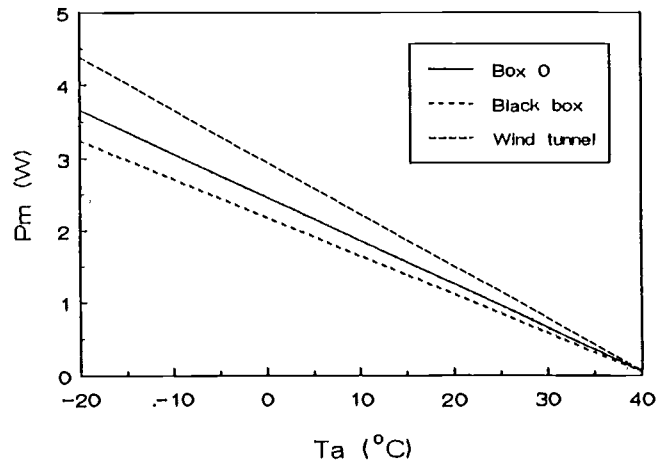


Figure 11. Power curves of mount 1 as measured in December 1989. Box 0 represents the climatic chamber, small black box is box 1. Wind tunnel (box 2) measurement were performed at wind speed of c. 1 m/s.

Field data.

Table 7 tells where the heated mounts were used. All data was collected between June 1989 and June 1990. Weather varied considerably during that period. Mean, minimum and maximum values of the weather parameters as experienced during the measurements are shown in Table 8. Ambient temperatures during field measurements never were extreme. Minimum T_a was -3.2 and maximum 24.2 °C. Wind speed ranged from 0.0 to 19.4 m/s, the

latter being identical to 8 Beaufort (almost 9). Global radiation ranged from 0 to 799 W/m², the latter being an average value of a Dutch cloudless midday in August.

Table 7. Details of field measurements grouped per mount per location. Including locations (Loc), orientation to wind (Ori), sample size (n, one sample is 30 minutes), mean ambient temperature (T_a), wind speed (W_{sp}), global radiation (R_g) and energy consumption (P_m), minimum and maximum values between brackets. Locations defined as follows: 1: Mudflat, 2: Bare salt marsh, 3: Vegetated salt marsh, 4: Densely vegetated salt marsh, 5: Bare ridge on tundra, 6: Nest cup on tundra, 7: In snow bank on tundra, 8: On ridge on tundra, 9: On snow on tundra.

Mnt	Loc	Ori	n	T _a (range) °C	W _{sp} (range) m/s	R _g (range) W/m ²	P _m (range) W/mount
1	1	0	290	12.6 (1.0-24.2)	6.8 (.5-19.4)	170 (0-793)	3.6 (.1-9.2)
	2	0	121	18.0 (15.0-20.8)	8.0 (5.5-12.0)	195 (1-799)	2.6 (1.5-3.9)
	3	0	21	20.3 (18.9-21.1)	5.9 (3.5- 8.5)	405 (2-767)	.9 (.0-1.8)
	4	0	16	21.1 (20.4-21.8)	12.6 (1.5-15.0)	342 (40-630)	1.2 (.8-1.9)
	5	0	317	7.9 (.9-19.6)	4.7 (.0- 9.8)	319 (0-778)	3.1 (.0-6.2)
2	1	0	61	20.0 (16.9-24.2)	5.9 (1.0- 9.5)	365 (0-793)	1.5 (.4-2.2)
	2	0	143	19.3 (16.9-21.8)	7.7 (1.5-15.0)	178 (0-767)	1.6 (.8-2.3)
	6	0	317	7.9 (.9-19.6)	4.7 (.0- 9.8)	319 (0-778)	2.0 (.6-3.4)
3	1	0	461	11.3 (1.0-24.2)	5.9 (.5-18.9)	178 (0-793)	2.3 (.0-5.2)
	2	0	75	17.4 (15.0-18.9)	7.8 (5.5-11.5)	212 (1-799)	1.8 (1.2-2.6)
4	1	0	456	11.3 (1.0-24.2)	5.9 (.5-18.9)	180 (0-793)	2.5 (.3-5.6)
	2	0	86	18.5 (16.9-20.8)	7.5 (4.5-11.5)	122 (0-555)	2.3 (1.6-3.3)
	3	0	60	19.4 (17.1-21.1)	7.6 (3.5-12.0)	231 (1-767)	1.4 (.0-2.4)
	4	0	16	21.1 (20.4-21.8)	12.6 (1.5-15.0)	342 (40-590)	1.1 (.5-1.7)
	5	0	317	7.9 (.9-19.6)	4.7 (.0- 9.8)	319 (0-778)	2.9 (.0-5.1)
	2	1	18	16.2 (15.0-16.8)	7.6 (6.0- 8.5)	459 (90-799)	2.7 (2.3-3.3)
1n	7	0	98	2.8 (-3.2- 5.8)	5.3 (.5-17.5)	364 (214-528)	2.3 (1.4-4.3)
	8	0	879	1.9 (-1.9- 8.0)	3.3 (.4-17.0)	311 (53-681)	2.3 (1.2-4.6)
2n	6	0	94	1.3 (-.5- 7.4)	3.1 (.9-16.3)	354 (200-592)	1.8 (1.3-2.6)
	8	0	269	3.1 (-.6- 8.0)	5.1 (.4-17.0)	359 (186-544)	2.1 (.9-4.4)
	9	0	98	2.8 (-3.2- 5.8)	5.3 (.5-17.5)	364 (214-528)	2.3 (1.3-5.1)
3n	6	0	515	1.3 (-1.9- 5.9)	2.4 (.4-16.8)	278 (53-681)	2.1 (1.1-4.0)
	8	0	363	2.7 (-.6- 8.0)	4.6 (.4-17.0)	358 (186-592)	2.4 (1.3-4.2)
	9	0	99	2.8 (-3.2- 5.8)	5.4 (.5-17.5)	363 (214-528)	2.6 (1.4-4.7)
4n	5	0	977	2.0 (-3.2- 8.0)	3.5 (.4-17.5)	317 (53-681)	3.6 (1.2-8.3)

One mount out of four was not connected with the battery most of the time. Core temperature of this mount, or operative temperature (T_g; see Bakken 1976) was measured along with the other mount measurements. Data from these 'cold models' have not yet been examined. Due to malfunctioning sometimes only one or two mounts were used simultaneously.

Power consumption of the mounts was calculated using equations 18 and 19. Although all mounts were connected to one and the same electricity source, Voltage V was not equal for all mounts, due to their slightly different electrical properties. A car battery, a car battery charger and a transformer were used. Voltages are given in Table 9. During March 1990 a battery and a charger were used at various moments. An estimate of V is made, assuming 2/3 of the time a battery was used and a charger the remaining time.

Table 8. Weather conditions at the locations (Loc) during measurements. Including mean ambient temperature (T_a), mean wind speed (W_{sp}) and mean global radiation (R_g). Also shown mean energy consumption (P_m), minimum and maximum values and sample size (n). Each sample is equal to 30 minutes measuring time. Locations defined as in table 6.

Loc	n	T_a (range) 'C	W_{sp} (range) m/s	R_g (range) W/m ²	P_m (range) W/mount
1	1286	12.0 (1.0-24.2)	6.1 (.5-19.4)	186 (0-793)	2.6 (.0-9.2)
2	245	18.4 (15.0-21.8)	7.8 (1.5-15.0)	178 (0-799)	2.0 (.8-3.9)
3	81	19.6 (17.1-21.1)	7.2 (3.5-12.0)	176 (1-767)	1.3 (.0-2.4)
4	32	21.1 (20.4-21.8)	12.6 (1.5-15.0)	342 (40-630)	1.1 (.5-1.9)
5	1294	3.4 (-3.2-19.6)	3.8 (.0-17.5)	317 (0-779)	3.5 (.0-8.3)
6	926	3.6 (-1.9-19.6)	3.2 (.0-16.8)	299 (0-778)	2.0 (.0-4.0)
7	98	2.8 (-3.2- 5.8)	5.3 (.5-17.5)	364 (214-528)	2.3 (1.4-4.3)
8	1511	2.3 (-1.9- 8.0)	3.9 (.4-17.0)	331 (53-681)	2.3 (0.9-4.6)
9	197	2.8 (-3.2- 5.8)	5.3 (.5-17.5)	364 (214-528)	2.5 (1.3-5.1)

Table 9. The voltages (V) as used in equation 18 ($V_e = V_m/V$). V_{bat} : car battery, V_{ch} : battery charger, V_{tr} : transformer.

Mount	V_{bat}	V_{ch}	V_{tr}
1	9.5	9.0	10.5
2	10.0	9.5	11.0
3	10.0	9.5	11.1
4	11.8	11.2	13.0
1n	10.05	--	--
2n	9.96	--	--
3n	10.31	--	--
4n	9.52	--	--

'Scholander curves'

All Standard Metabolic Rates of the individual Knots are given in Table 10. Because the 'Scholander curves' of adults and second years differed significantly ($p < 0.05$) they are calculated separately. Measurements in the wind tunnel also are significantly different from the standard measurements (t-tests of regression coefficient, $p < 0.05$). 'Scholander curves' of these four categories are shown in the Figures 12a and 12b. BMR of the adults and the second year birds were identical: 0.95 W. The adults' insulation was worse than the second years': under standard conditions a conductance of 0.045 and 0.035 W/°C·animal respectively. At a wind speed of 1 m/s overall conductance increases to 0.055 and 0.045 W/°C·animal for an adult and second year bird respectively. Lower critical temperature was 13.9 and 19.9 °C for second year birds in the standard box and the wind tunnel respectively. T_{lc} of the adults was 19.9 and 23.7 °C respectively. T_{uc} is estimated to be close to 38 °C because this was the highest temperature used and no increment of the MR was shown. This results in the next four equations for the standard situation:

$$TC_b = 0.045(41 - T_a) \quad [T_b < 19.9] \quad (27)$$

$$TC_a = 0.95 \quad [19.9 \leq T_a \leq 38] \quad (28)$$

$$TC_{sy} = 0.035(41 - T_a) \quad [T_a < 13.9] \quad (29)$$

$$TC_{sy} = 0.95 \quad [13.9 \leq T_a \leq 38] \quad (30)$$

In forced convection conditions (1 m/s) equations are:

$$TC_{aw} = 0.055(41 - T_a) \quad [T_a < 23.7] \quad (31)$$

$$TC_{aw} = 0.95 \quad [23.7 \leq T_a \leq 38] \quad (32)$$

$$TC_{syw} = 0.045(41 - T_a) \quad [T_a < 19.9] \quad (33)$$

$$TC_{syw} = 0.95 \quad [19.9 \leq T_a \leq 38] \quad (34)$$

The subscriptions a, sy, aw and syw stand for adult, second year, adult plus wind and second year plus wind.

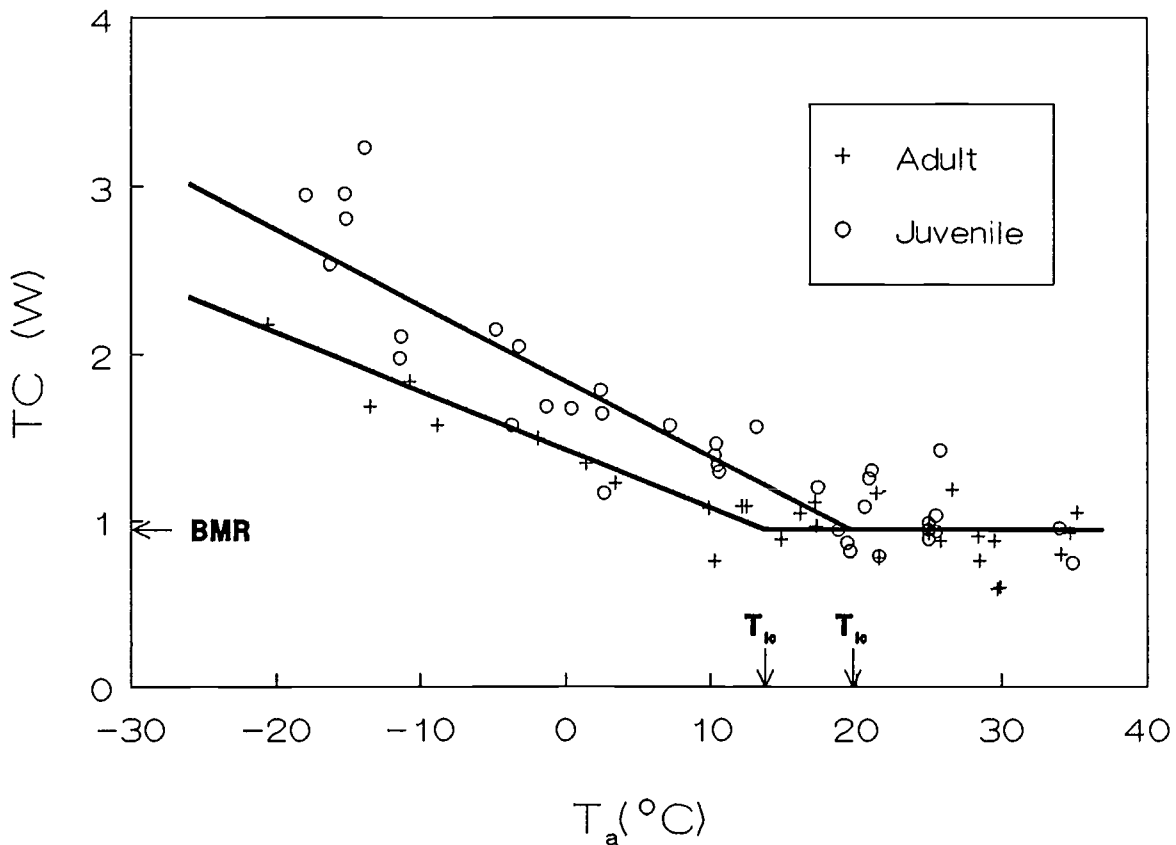


Figure 12 a. 'Scholander curves' of adult and early second year (postabsorptive) Nearctic Knots. Measurements performed in box 1 (small blackened box). BMR equals 0.95 W. T_{lc} of adult bird is 19.9 and of second year bird 13.9 °C.

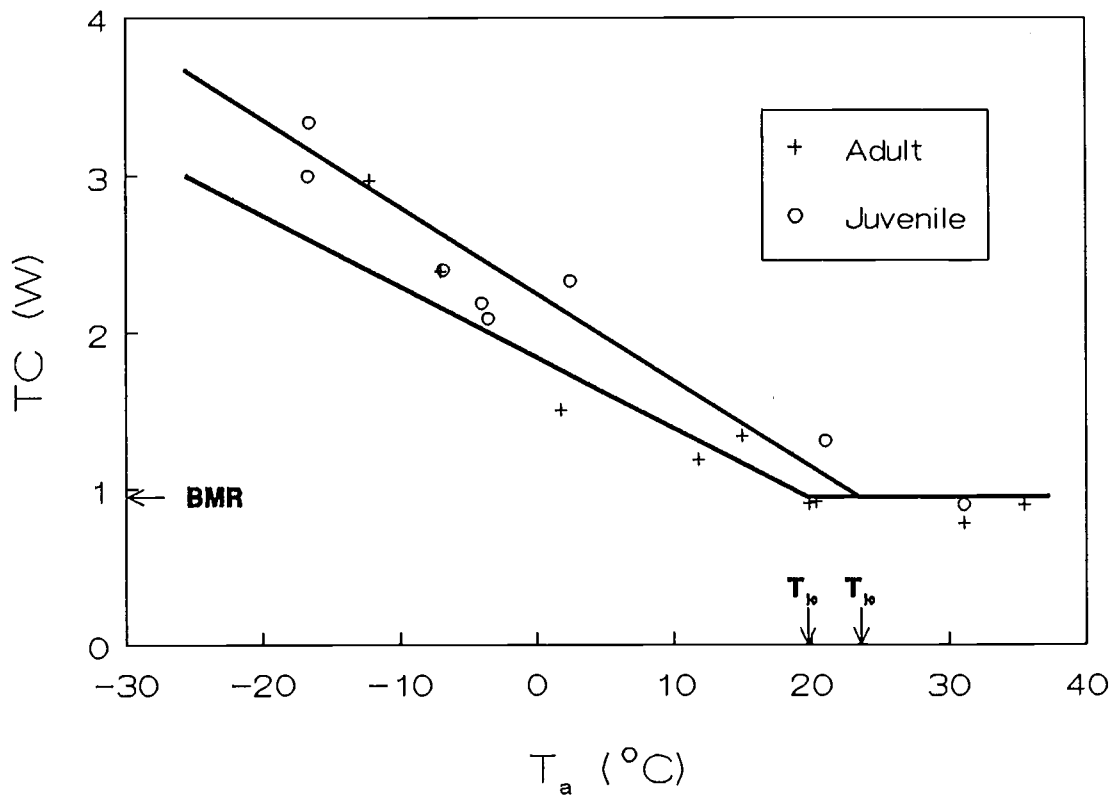


Figure 12 b. 'schölander curves' of adult and early second year (postabsorptive) Nearctic Knots. Measurements performed in wind tunnel at wind speed of c. 1 m/s. BMR equals 0.95 W. T_{lc} of adult bird is 23.7 and of second year bird 19.9 °C.

Table 10. Specifications of the Nearctic Knots measured in the calorimeter. Ind. stands for the identification number of the bird involved. Mass gives mean value of mass before and after the measurement. Age class 'a' is adult, 's' early second year. Pl/M is the plumage and moult score, first number gives breast moult (score 0, no moult, to 2, heavy moult), second number extent of summer plumage (score 0, winter plumage, to 7, summer plumage) and third number primary and secondary flight feathers moult (score 0, no moult, to 1, moult). T_a is ambient temperature in the box. Wind indicates use of forced convection (c. 1 m/s) or not (1 and 0, respectively). SMR is Standard metabolic rate.

Date	Ind.	Mass (g)	Age	Pl/M	T_a (°C)	wind	SMR (W)
Nov 88	k406	128.0	a	1 1 0	25.0	0	0.99
	k405	153.0	s	0 1 0	25.0	0	0.93
	k409	138.0	a	0 1 1	25.8	0	1.43
	k408	134.0	a	0 1 0	25.0	0	0.95
	k410	124.0	a	0 1 1	25.5	0	1.03
	k405	139.0	s	0 1 0	25.0	0	0.98
	k406	149.0	a	0 1 0	25.5	0	0.94
	k408	137.0	a	0 1 1	25.0	0	0.89
Dec 89	k411	115.0	s	1 1 0	21.4	0	1.17
	k409	124.4	a	0 1 0	-11.3	0	2.11
	k371	112.1	s	2 1 1	17.2	0	1.12
	k409	139.5	a	0 1 0	-15.3	0	2.96
	k371	114.9	s	1 1 0	17.3	0	0.97
	k371	112.1	s	2 1 1	35.2	0	1.05
	k414	107.5	a	0 3 1	17.4	0	1.21
	k405	106.4	s	2 1 0	1.4	0	1.35
	k414	107.5	a	0 3 1	18.8	0	0.95
	k407	122.4	a	0 3 1	2.5	0	1.65

Table 10. Continued.

Date	Ind.	Mass (g)	Age	Pl/M			T _a (°C)	wind	SMR (W)
	k373	101.5	s	1	1	0	28.5	0	0.76
	k405	104.9	s	0	1	1	34.1	0	0.80
	k407	114.9	s	0	3	0	28.4	0	0.91
	k405	103.0	s	2	1	0	9.9	0	1.08
	k409	152.0	a	0	1	0	20.6	0	1.09
	k407	119.8	a	0	3	0	10.3	0	1.40
	k407	139.8	a	0	3	1	20.9	0	1.26
	k409	129.0	a	0	1	0	10.5	0	1.34
	k373	108.6	a	0	1	1	10.6	0	1.30
	k407	139.8	a	0	3	1	-13.9	0	3.23
	k407	123.1	a	0	3	1	34.0	0	0.96
	k414	122.0	a	0	3	1	13.2	0	1.57
	k405	106.4	s	2	1	0	-20.6	0	2.18
	k373	108.6	s	0	1	1	16.2	0	1.05
	k409	120.5	a	0	1	0	21.6	0	0.79
	k409	129.0	a	0	1	0	0.4	0	1.68
	k411	91.7	s	0	1	0	21.6	0	0.78
	k373	108.6	s	0	1	1	34.7	0	0.93
	k409	139.5	a	0	1	0	-4.8	0	2.15
	k405	104.9	s	0	1	1	10.3	0	0.76
	k371	112.1	s	2	1	1	26.6	0	1.19
	k405	106.4	s	2	1	0	12.5	0	1.09
	k411	101.2	s	0	1	0	-10.7	0	1.84
	k409	129.0	a	0	1	0	-15.2	0	2.81
	k414	122.0	a	0	3	1	-18.0	0	2.95
	k409	139.5	a	0	1	0	7.2	0	1.58
	k414	109.9	a	0	3	1	-16.3	0	2.54
	k411	115.0	s	1	1	0	29.5	0	0.88
	k407	139.8	a	0	3	1	10.4	0	1.47
	k414	122.0	a	0	3	1	2.4	0	1.79
	k373	108.6	s	0	1	1	25.8	0	0.88
Feb 90	k407	127.1	a	3	2	1	21.1	0	1.31
Mar 90	k408	125.5	a	0	1	0	-3.7	0	1.58
	k408	129.4	a	1	2	1	-16.6	1	3.34
	k412	117.1	s	1	1	0	-12.2	1	2.97
	k409	128.0	a	1	2	0	-11.4	0	1.98
	k372	133.3	s	1	1	0	-7.0	1	2.39
	k373	105.1	s	3	1	0	-8.8	0	1.58
	k409	123.3	a	1	2	0	-6.8	1	2.40
	k406	120.1	a	0	1	0	19.4	0	0.87
	k407	119.4	a	2	2	1	-4.0	1	2.19
	k373	102.1	s	1	1	0	29.7	0	0.59
	k409	129.2	a	2	2	0	-3.5	1	2.09
	k412	117.4	s	1	1	0	12.2	0	1.09
	k411	109.7	s	1	1	0	1.8	1	1.51
	k408	142.5	a	1	2	1	2.6	0	1.17
	k409	144.3	a	0	1	0	2.5	1	2.33

Table 10. Continued.

Date	Ind.	Mass (g)	Age	Pl/M		T _a (°C)	wind	SMR (W)	
	k408	130.6	a	0	1	1	-1.3	0	1.69
	k373	102.3	s	1	1	0	11.8	1	1.19
	k371	102.0	s	0	1	1	-13.5	0	1.69
	k407	120.8	s	1	3	1	15.0	1	1.34
	k407	118.3	a	2	3	1	19.6	0	0.82
	k371	103.9	s	0	1	0	19.9	1	0.91
	k371	108.9	s	0	1	0	29.9	0	0.60
	k372	120.8	s	1	1	0	20.4	1	0.92
	k409	125.9	a	2	2	0	34.9	0	0.75
	k372	125.3	s	1	1	0	-1.9	0	1.50
	k407	123.4	a	2	2	1	-3.2	0	2.05
	k406	126.9	a	0	1	0	31.1	1	0.90
	k412	133.1	s	1	1	0	3.4	0	1.23
	k371	125.9	s	0	1	0	14.9	0	0.89
	k406	118.1	a	0	1	0	-16.7	1	3.00
	k412	120.6	s	1	1	0	31.1	1	0.78
	k408	125.9	s	0	1	1	35.5	1	0.90

Thermostatic costs of Knots.

According to equation 25, the MR of a Knot was estimated from the power consumption of the mount as recorded in the field, with use of the data from equations 27 to 34 (the 'Scholanders') and Table 5 and 6 (power curves). Estimated metabolic rates below BMR were not adjusted, but used as valid data points in the multiple regressions. The outcome of these multiple regressions (through the origin) are shown in Table 11a to 11d. All adjusted r²s exceed 0.94 and most estimated variables are highly significant. For microhabitats 7 and 8 global radiation did not significantly improve the equation (p > 0.05). This was probably due to the narrow range of the R_g data (see Table 7).

Table 11 a. Constants of equation 26 ($TC = g/(W_{sp} + 1)(41 - T_a) + bR_g$), estimating thermostatic costs of a single adult Nearctic Knot. Calibrations performed in small blackened box (1), without wind. Locations (loc) and Orientation to wind (Ori) as defined in table 6. Each sample is a 30 minutes measurement. All mounts were used in the multiple regression analysis. All variables significant (p < .001 and marked *: .001 < p < .005), except marked 'n.s.' (p > .05).

Loc	Ori	n	g (S.E.)		b (S.E.)		r ²
1	0	1296	.03087	(2.42E-4)	-7.05819E-4	(6.417E-5)	.943
2	0	425	.03165	(3.25E-4)	-7.87821E-4	(8.055E-5)	.972
2	1	18	.03785	(1.45E-3)	-8.98576E-4	(2.080E-4)	.994
3	0	84	.02543	(7.11E-4)	-1.51120E-3	(1.120E-4)	.948
4	0	33	.01916	(1.31E-3)	-1.09031E-3	(2.454E-4)	.940
5	0	1611	.04050	(4.17E-4)	-9.25608E-4	(9.368E-5)	.945
6	0	926	.03086	(2.89E-4)	-1.10044E-3	(6.331E-5)	.970
7	0	98	.02267	(3.59E-4)		n.s.	.976
8	0	879	.02560	(1.12E-4)		n.s.	.972
9	0	197	.02847	(6.96E-4)	-5.09737E-4*	(1.763E-4)	.985

Table 11 b. Constants of equation 26 ($TC = g/(W_{sp} + 1)(41 - T_a) + bR_g$) estimating thermostatic costs of a single second year Nearctic Knot. Calibrations performed in blackened box (1), without wind. Locations (loc) and Orientation to wind (Ori) as defined in table 6. Each sample is a 30 minutes measurement. All mounts were used in the multiple regression analysis. All variables significant ($p < .001$ and marked *: $.001 < p < .005$), except marked 'n.s.' ($p > .05$).

Loc	Ori	n	g (S.E.)		b (S.E.)		r ²
1	0	1296	.02401	(1.89E-4)	-5.48660E-4	(4.996E-5)	.943
2	0	425	.02462	(2.52E-4)	-6.13285E-4	(6.263E-5)	.972
2	1	18	.02945	(1.13E-3)	-7.02355E-4	(1.618E-4)	.994
3	0	84	.01980	(5.47E-4)	-1.17984E-3	(8.606E-5)	.949
4	0	33	.01492	(1.01E-3)	-8.48807E-4	(1.905E-4)	.940
5	0	1611	.03149	(3.25E-4)	-7.21466E-4	(7.304E-5)	.945
6	0	926	.02400	(2.25E-4)	-8.54583E-4	(4.925E-5)	.970
7	0	98	.01763	(2.79E-4)	n.s.		.976
8	0	879	.01991	(8.74E-5)	n.s.		.972
9	0	197	.02215	(5.41E-4)	-3.99237E-4*	(1.372E-4)	.985

Table 11 c. Constants of equation 26 ($TC = g/(W_{sp} + 1)(41 - T_a) + bR_g$) estimating thermostatic costs of a single adult Nearctic Knot. Calibrations performed in blackened wind tunnel (2), wind c. 1 m/s. Locations (loc) and Orientation to wind (Ori) as defined in table 6. Each sample is a 30 minutes measurement. All mounts were used in the multiple regression analysis. All variables significant ($p < .001$ and marked *: $.001 < p < .005$), except marked 'n.s.' ($p > .05$).

Loc	Ori	n	g (S.E.)		b (S.E.)		r ²
1	0	1296	.02787	(2.13E-4)	-6.16081E-4	(5.639E-5)	.946
2	0	425	.02826	(2.94E-4)	-6.76082E-4	(7.302E-5)	.972
2	1	18	.03307	(1.26E-3)	-7.81787E-4	(1.810E-4)	.994
3	0	84	.02248	(6.30E-4)	-1.29895E-3	(9.913E-5)	.948
4	0	33	.01714	(1.17E-3)	-9.49204E-4	(2.206E-4)	.941
5	0	1611	.03355	(3.33E-4)	-7.91328E-4	(7.466E-5)	.949
6	0	926	.02646	(2.47E-4)	-9.17490E-4	(5.415E-5)	.971
7	0	98	.02114	(3.34E-4)	n.s.		.977
8	0	879	.02298	(1.05E-4)	n.s.		.969
9	0	197	.02477	(6.39E-4)	-4.59304E-4*	(1.162E-4)	.983

Table 11 d. Constants of equation 26 ($TC = g\sqrt{(W_{pp} + 1)}(41 - T_p) + bR_p$) estimating thermostatic costs of a single second year Nearctic Knot. Calibrations performed in blackened wind tunnel (2), wind c. 1 m/s. Locations (loc) and Orientation to wind (Ori) as defined in table 6. Each sample is a 30 minutes measurement. All mounts were used in the multiple regression analysis. All variables significant ($p < .001$ and marked *; $.001 < p < .005$), except marked 'n.s.' ($p > .05$).

Loc	Ori	n	g (S.E.)		b (S.E.)		r ²
1	0	1296	.02280	(1.74E-4)	-5.04768E-4	(4.617E-5)	.946
2	0	425	.02311	(2.41E-4)	-5.52075E-4	(5.974E-5)	.972
2	1	18	.02706	(1.03E-3)	-6.40319E-4	(1.479E-4)	.994
3	0	84	.01840	(5.17E-4)	-1.06398E-3	(8.146E-5)	.948
4	0	33	.01403	(9.60E-4)	-7.72362E-4	(1.803E-4)	.941
5	0	1611	.02746	(2.72E-4)	-6.47307E-4	(6.105E-5)	.949
6	0	926	.02165	(2.02E-4)	-7.50437E-4	(4.430E-5)	.971
7	0	98	.01729	(2.73E-4)	n.s.		.976
8	0	879	.01880	(8.59E-5)	n.s.		.969
9	0	197	.02027	(5.22E-4)	-3.78059E-4*	(1.324E-4)	.983

DISCUSSION.

Forced or free convection during calibration.

Because under conditions of free convection a layer of still air can be formed around the bird or mount, an extra insulation can be created, which of course does not exist in the field. Bakken et al. (1981) concluded that the mounts and live birds should be measured in a wind tunnel, at low wind speeds, e.g. 1 m/s. Because this report presents both methods this assumption is investigated. To test if the two methods lead to statistical different results, equation 20 and 23 were used, in which the energy consumption of both a mount and a Knot is related to the temperature difference of mount or Knot respectively and ambient temperature. These equations are combined, resulting in equation 35, considering $(T_m - T_a)$ equals $(T_b - T_a)$:

$$TC = (c_k/c_m)P_m \quad (35)$$

To test if forced and free convection during measurements give different results, the ratio of c_k to c_m should be compared for the two situations. The December 1990 data gives this opportunity because mounts were measured at these two situations. In adult birds there is no significant difference ($p > 0.05$) while in second year birds there is ($p < 0.01$); both with a t-test after log-transforming equation 35. Because there is in both a trend to the same direction and one of them is significant, only calibrations at forced convection conditions are used.

Changing BMR of captive birds.

When the Knots used in this study were measured they had been in captivity for a good year. There is evidence however that BMR changes during captivity (Warkentin & West 1990). Measurements taking place at this moment suggest this is also happening in captive Knots (N. Cadée, pers. comm.). This new data suggests a BMR of 0.8 W. Overall conductance is not likely to be different. If this number is valid the thermostatic costs as estimated here would be too high, but only when T_{es} is higher than T_{lc} . As will be shown later this does not occur frequent, so TC will not be very different not considering this BMR change.

BMR throughout the year.

The MR measurements took place in a three months period during the winter of 1989/90 (Table 10). There is however the possibility of a changing BMR during a one year cycle, which would limit the use of the TC estimates. So far no evidence is found that BMR is variable. But during the fattening period of the Knots BMR could well be different. During that period fat and protein is stored. Organs are adapted to the long flight they are about to undertake. Because BMR is related to (structural) mass of the bird (Aschoff & Pohl 1970; Kersten & Piersma 1986), it is likely it has a higher value in the fattening period, caused by the extra muscle tissue. Consider a body mass rise from 130 to 190 g during fattening and suppose 50% of this deposit is added as 'structural' mass as found in Bar Tailed Godwits *Limosa lapponica* by Piersma & Jukema (1990), (see Piersma (1990) about protein and fat deposition), then 'structural' body mass rises to 160 g. Using the equation of Kersten & Piersma (1986) this predicts a change in BMR of 17% from 0.95 to 1.11 W during fattening. Consequently T_{lc} would shift from 23.7 to 20.8 °C. Hence fattening could increase the thermostatic costs. To what extent fat is used as extra insulation should also be taking into consideration. Note that this change in BMR only affects TC of Knots in an environment

where it experiences standard operative temperatures above the lower critical temperature. To what extent this occurs will be discussed later on.

Are the thermostatic costs age dependent?

The data shows significant differences between adult and early second year birds. Although BMR for these two categories are identical, $0.95 W$, their insulation is significantly different. Adult Knots have an overall conductance of $0.055 W/^\circ C$ and second year Knots of $0.045 W/^\circ C$, both at forced convection conditions. Consequently the lower critical temperature is 23.7 and 19.9 $^\circ C$ respectively.

Following this finding, body mass of the two groups were compared. A t-test concluded that the mean mass of the second year Knots differed significantly from the adults' mass (113.5 and 127.9 g resp., $p < 0.001$). If body mass is related to the structural size of the bird this might give a clue to the difference in conductances. Suppose that mass is related to body surface area according to the overall relation between surface area and mass (see Walsberg & King 1978):

$$S = M^{2/3} \quad (36)$$

where S is the surface area and M the body mass. Surface area of a second year Knot would be 8% less than the adult. If there is a linear relation between surface area and conductance, the latter also would be 8% less for second years. This difference however is 18% and thus seems not fully explained by structural size.

Another approach to explain the difference in conductance between the two age classes is by using the data from Aschoff (1981). Using existing data, not only size dependent changes in the ratio 'surface:volume', as described earlier, are incorporated, but also the dependance of fur thickness on size (Scholander et al. 1950) and the dependance of the thickness of the boundary layer on the radius of the curvature which changes with size (Aschoff 1971; Hardy 1949, both from Aschoff 1981). He gives an equation describing the differences in weight dependent conductance for various groups of animals. For non-passerine birds measured during the resting phase the equation is as follows:

$$\log C/W = \log .947 - .583 \log W \quad (37)$$

where C/W is the conductance ($ml O_2/g \cdot h \cdot ^\circ C$) and W the body mass (g). Using this equation together with the mean body masses of the two age classes, a difference of 5% in their overall conductances would be expected. Together with the 'surface:volume' ratio approach the conclusion is that only 5 to 8% of the difference in overall conductance between adults and early second year birds can be explained from structural differences.

To examine another physical factor possibly causing the difference in conductances, body moult is tested as a variable in the non-linear regression together with T_b and age. Moult did not significantly improve the regression ($p > 0.05$). The conclusion so far is that the difference in conductance between adults and second year birds is probably due to the quality of the plumage. Adults may have less feathers or feathers of inferior quality.

The result implies that a second year Knot has an energetic advantage, under cold conditions below T_{lc} , of some 18%. This would probably make a big difference regarding mortality during cold spells and predicts the possibility of differentiated migration of these two age classes. During winter flocks of Knots however look well mixed concerning age. Another possibility explaining the difference is the intra-flock distribution of age classes. Second year birds may be found more at the edges of the flock, more exposed to wind.

To what extent TC of early second year Knots equals TC of juveniles can not be told. No juveniles have been measured so far. But since second year Knots are better insulated it seems likely it also applies to juveniles. Maybe second year birds insulation is only a remnant of juveniles'. But why should juveniles be better insulated than adults? When they are more

exposed to the elements, or living in an colder environment it seems obvious. Juveniles however live in the same environment as the adults. Only in summer this is not true. When the adults are leaving for the arctic tundra, juveniles stay behind and summer on the North Sea coasts (Cramp & Simmons 1983). But is it colder there than in the arctic? Probably this is not the case, as will be shown later on. This leaves us with the question if they are living in more open flocks. No clear evidence exists to support this.

Another explanation for the possible better insulation of juveniles might be to compensate for a decreased energy intake. If they are not able to have the same intake rate as the adult Knots they would be better off being better insulated. But this would give rise to the question as to why adults are not better insulated.

This problem needs more study. Along with structural size, plumages of juvenile and adult Knots should be compared, considering feather density and quality.

Summer and winter plumage.

Because one of the four 'old' mounts was in summer plumage it was possible to investigate the effect on plumage colour on the heat flow. It is expected that light winter feathers reflect more of the incoming radiation than the darker summer feathers. This would then lead to higher thermostatic costs in birds with a winter plumage.

All data consisting of paired measurements with mount 4 (summer plumage) and an other mount were again analyzed by a multiple regression according to equation 17. Power consumptions of the mounts were thereafter recalculated to reveal the radiative effect in the total heat flow by subtracting the heat loss caused by forced convection, resulting in:

$$H - g\sqrt{(W_{sp} + 1)(41 - T_a)} = b \cdot R_g \quad (38)$$

Again a (single) regression analysis was performed. Differences in the regression coefficients of measurements by mount 4 and the other were then analyzed using a t-test for regression coefficients. Differences ranged from -19 to +118% in 7 data sets. No, except one, data set revealed a significant difference ($p < 0.05$), although there is a trend showing the global radiation is more effective in the winter plumages (c. 15%). Only in the comparison of mount 4 with mount 1 on location 2 (bare salt marsh) a significant difference was found. The conclusion will be that there might well be a difference in radiative properties of summer and winter plumages, but it is probably too small to detect by this method. Clustering all data, including the measurements with mount 4, seems permitted and has been done throughout the rest of the report.

Heat loss from the feet.

The temperature of the ground was not incorporated in the estimation of heat loss. The possible error caused by this shortcoming of the heated taxidermic mount is discussed here. When ground temperature is equal to ambient temperature no error will occur because that particular heat flow is incorporated in the calibration of the mounts versus the Knots. When T_g and T_a do differ, the altered heat flow through the feet will not be measured. But since waders are assumed to reduce heat loss from the feet this error is probably small. This reduction can be achieved by altering the blood flow pattern to the feet and/or by a counter-current blood flow system cooling down blood flowing to the extremities. Kilgore & Schmidt-Nielsen (1975) found only 3 to 6.6% of the total heat loss in a Mallard *Anas platyrhynchos* was from the feet at temperatures above 0 °C. Because the mallards had their feet totally immersed, which in Knots does not happen often, heat loss in the feet of Knots can probably be neglected. When T_g differs much from T_a and is below 0 °C bigger errors could arise. But note that birds can decrease this heat loss by drawing in one leg.

Microhabitat selection.

As stated earlier the structure of the microhabitat influences the thermostatic costs enormously. By placing the mounts in different microhabitats the effect has been quantified. Table 11a to 11d give the variables for equation 26, which estimates TC from the weather variables, for

Table 12. Relative values of the non-radiative conductance constant (g : $W/\sqrt{(m/s)} \cdot ^\circ C$) and the negative value of the radiative conductance constant ($-b$: m^2) of equation 26 ($TC = g\sqrt{(W_{sp} + 1)}(41 - T_a) + bR_v$) for a single adult Nearctic Knot, as estimated using forced convection conditions (c. $1 m/s$) during calibrations. Mean values are set to 1.

Loc	Ori	Description	g	b
4	0	Densely vegetated salt marsh	.67	1.17
7	0	In snow bank on tundra	.82	n.s.
3	0	Vegetated salt marsh	.87	1.60
8	0	Ridge on tundra	.89	n.s.
9	0	On snow on tundra	.96	.57
6	0	Nest cup on tundra	1.03	1.13
1	0	Mudflat	1.08	.76
2	0	Bare salt marsh	1.10	.83
2	1	Bare salt marsh, not facing wind	1.28	.96
5	0	Bare ridge on tundra	1.30	.98

all microhabitats used in this study. Mean non-radiative conductance constant (g) for the adult is $0.02577 W/\sqrt{(m/s)} \cdot ^\circ C$ and mean radiative conductance constant (b) is $-8.11278E-4 m^2$. Table 12 and Figure 13 show the relative values of these two constants. It is obvious that

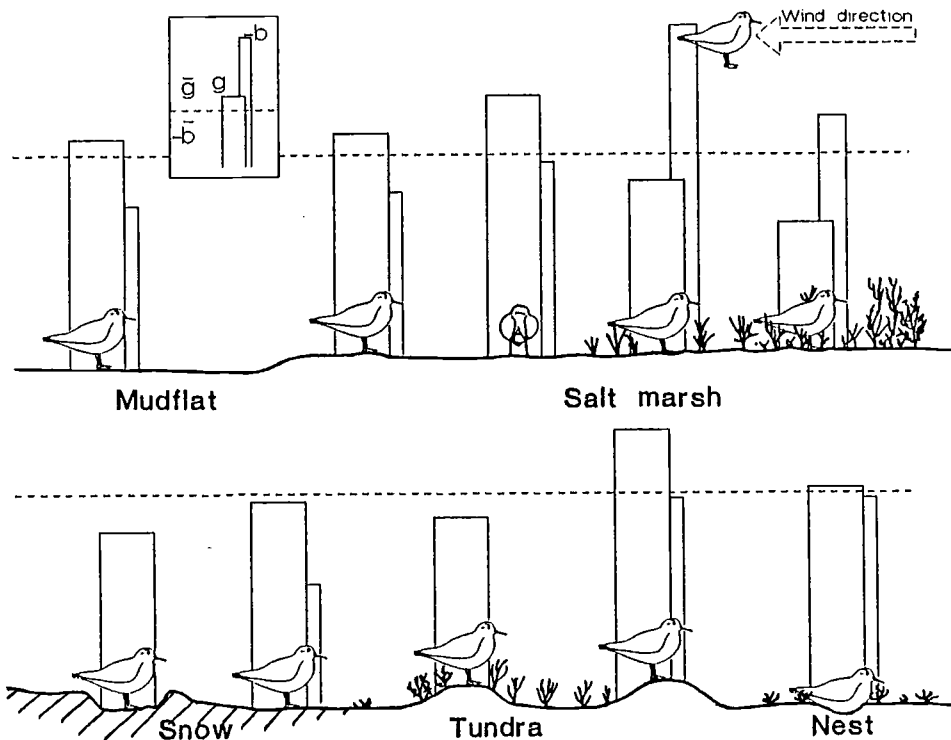


Figure 13. Relative value of non-radiative conductance constant (g) and the negative value of radiative conductance constant ($-b$) of a single adult Nearctic Knot in different microhabitats.

the vegetated habitats are less sensitive to wind than are the open habitats like bare salt marsh and mudflat. It also shows that living close to the ground has a big advantage concerning TC: Standing on top of a bare ridge (location 5) results in the highest amount of energy lost by forced convection. TC of a single Knot in a particular situation can now be calculated from equation 26 and the variables from Table 11c and 11d (using the calibrations at forced convection conditions). For a few microhabitats it has been visualized in Figure 14a to c, showing the TC isolines of an adult Knot in a 'weather landscape' for a few microhabitats. Important TC isolines are the 4 BMR line and the 6 BMR line. The first is the level of long sustainable energy expenditure according to Drent & Daan (1980). When the weather circumstances result in a MR above 4 BMR, Knots would not work on an efficient level anymore and might take precautions, like roosting in more sheltered habitats, or feeding in denser flocks. The 6 BMR ceiling is the result of the limited digestion rate (Kirkwood 1983). When exceeding this limit a Knot can not survive for a long period of time, but has to break into its reserves. To avoid the risk of starvation he should take more extreme precautions like migrating to better places.

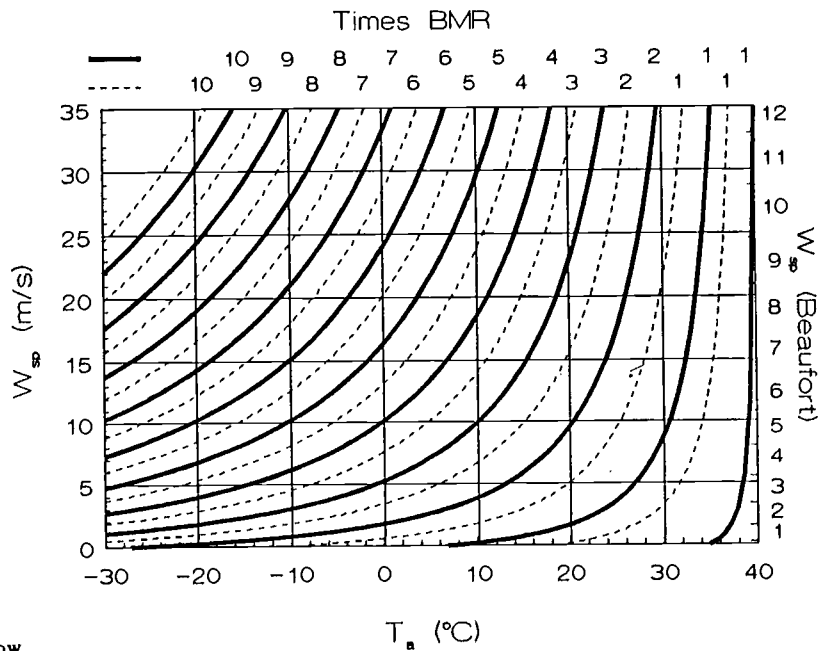


Figure 14 a. see below.

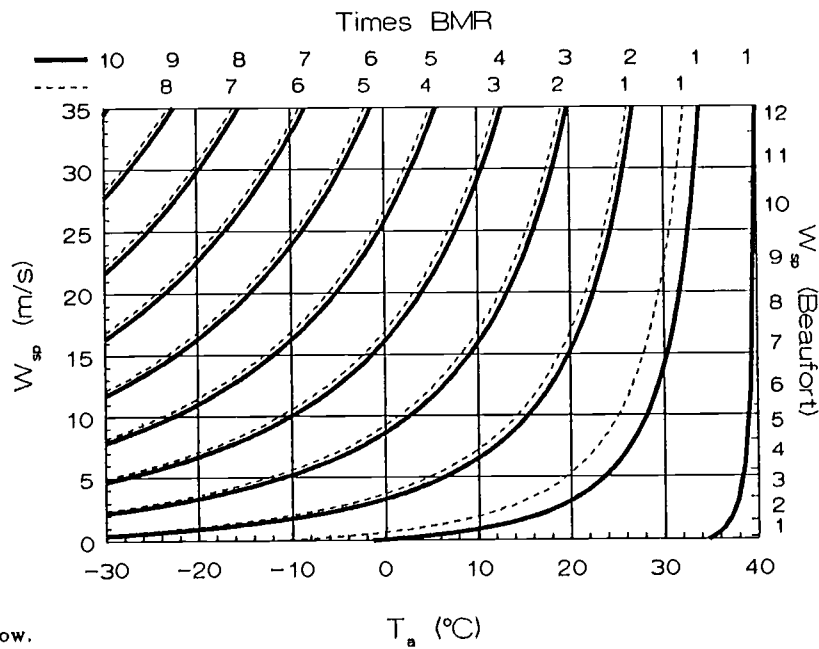
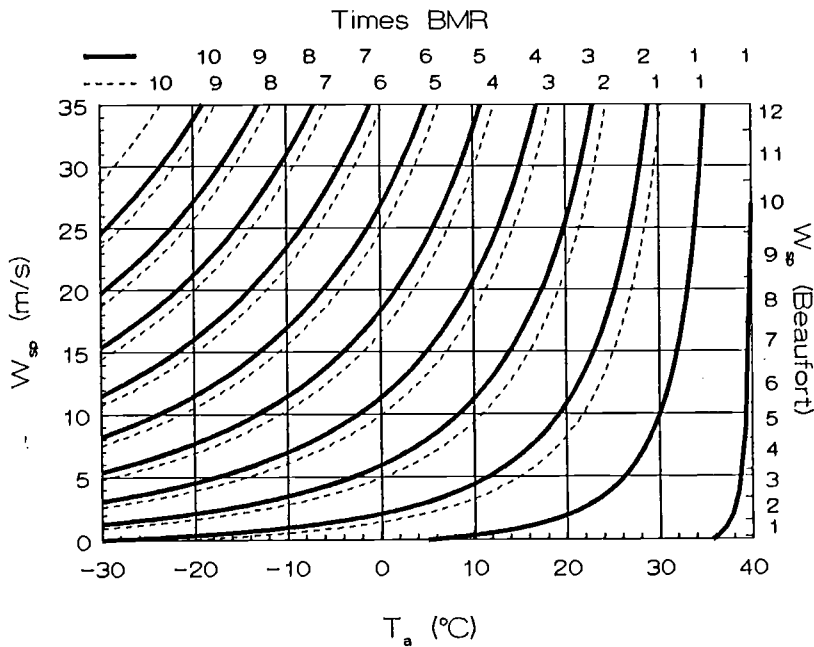


Figure 14 b. see below.



c.

Figure 14. TC isolines of a single adult Nearctic Knot in relation to three weather parameters: ambient temperature (T_a), wind speed (W_{sp}) and global radiation (W/m^2). Bold lines represent TC without radiation, broken lines TC with global radiation of $800 W/m^2$. Thermoneutral zone is between the two 1xBMR lines. Locations: (a) Mudflat, loc. 1. (b) Vegetated salt marsh, loc. 3. (c) Nest cup on tundra, loc. 6.

One example of Knot migration during a cold spell will be examined now. In October 1990 Knots were observed on the mudflat of the island Schiermonnikoog in the Dutch Wadden Sea (coor: $53^{\circ}28'N$, $6^{\circ}10'E$) by M. Poot & B. Roelen (pers. comm.). Until 14 October 10 to 15 thousand had been counted, but numbers decreased rapidly after this period (Figure 15). On 15 October the weather changed. A hard eastern wind, together with low temperatures made the environmental temperature drop considerably. Figure 15 shows the estimated thermostatic

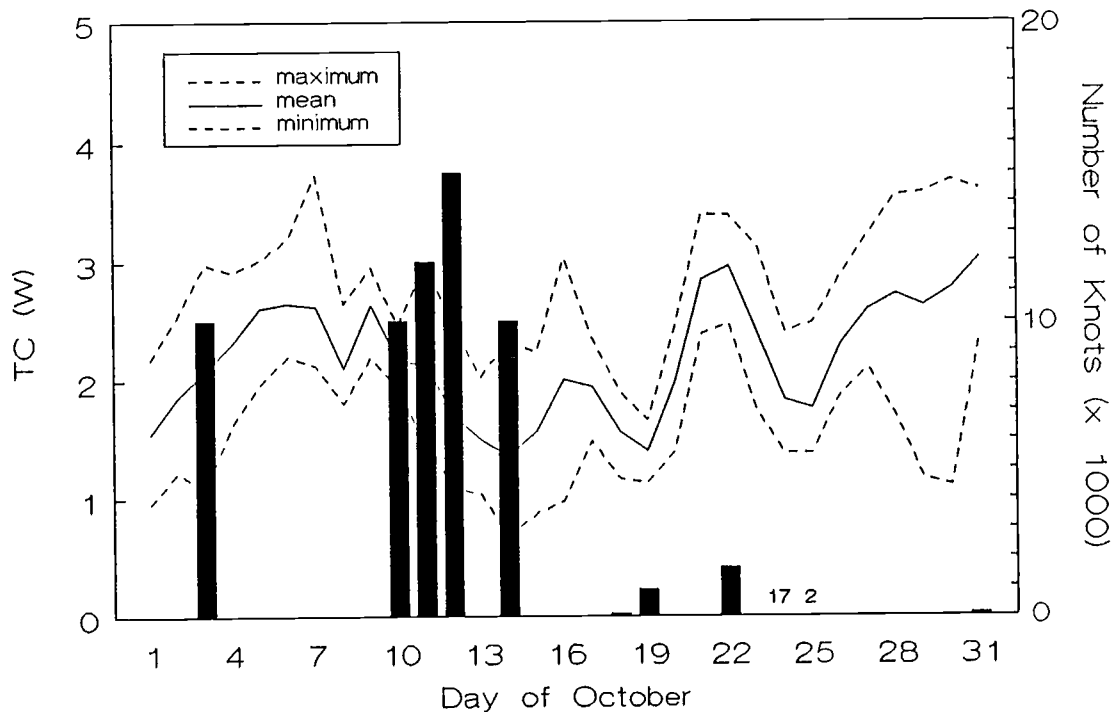


Figure 15. Minimum, mean and maximum thermostatic costs (TC) of a single adult Nearctic Knot on the mudflat of the island Schiermonnikoog in October 1990. Numbers of Knots counted are shown by the bars and the numbers above the x-axis.

costs of an adult Knot during that period. It is obvious this cold spell was not extreme; On 7 October it was possibly colder. The Figure shows the minimum ('best case scenario'), mean and maximum ('worst case scenario') TC as calculated from the daily meteorological registrations. The exact TC must be somewhere between the outer limits. So it is possible that the environmental temperature was in fact lower on 15 October than on 7 October. To investigate this, weather registrations on a smaller time scale are needed. Another possibility is that the wind direction on 15 October was the main factor triggering the migration of the Knots. It is very likely the Knots left in a western direction, in which case the south-south-east wind at that day was very useful. On 7 October the wind came from the north-west, which might have kept the Knots on the ground, implying that the environmental temperature was not severe enough to leave the area and face the unprofitable wind. A second exodus, although less extensive, took place between 22 and 24 October. It also coincided with a drop in environmental temperature. The wind direction did not change but already was south-east since the 19th, but the wind force was highest on 22 October. This migration could be a simple TC effect, but again also the effect of a profitable wind. These examples show that thermostatic costs is only one of the possible factors by which Knots have to make their 'decisions'. Wind direction and food availability are others. When the food intake and the thermostatic costs can not be balanced anymore, they have to decide on looking for better places or staying, in the hope circumstances will change for the better soon. Oystercatchers are found to behave in that way (Hulscher 1989). During a cold spell they migrate only after some days, in the mean time waiting for the cold to go.

Orientation to wind direction.

Birds feathers are directed backward. Wind blowing from the front can penetrate the plumage only with difficulty. Wind blowing from other directions penetrates to the skin much easier. This will destroy the insulating air layer between the feathers and the skin and increase the heat flow to the environment.

In one case a mount was placed not with its head in the wind but with the body turned 90°. The thermostatic costs calculated with this mount are much higher than from the mounts placed in the ordinary way. This means that a Knot standing or walking with its head in the wind uses less energy than otherwise. The energetic saving for a mount are 15% (Table 11c; Figure 13), not considering the 13% disadvantage for global radiation. Because the plumage of a mount has a lower resistance to heat flow than Knots, it is likely the effect is smaller in the latter. Suppose the effect is linearly correlated with the overall conductance the energetic disadvantage for standing 90° on the wind direction would be 13%. In the field Knots are standing with their heads in the wind most of the time, thus saving energy. Foraging flocks are always walking into the wind and roosting flock also are orientated in that same direction. Individual birds moving to the back of the flock, often, if not always, run fast to arrive at the desired spot, as to be able to stand pointed in the wind as soon as possible. When temperature rises and the wind drops the Knots follow this rule less strictly. When wind is totally lacking they walk in all directions, although they stay in a flock (Wiersma, report in prep.).

Heat loss by warming up food.

Knots eat poikilothermic prey. Knots wintering in western Europe loose heat by taking in this cold food which will be warmed to 41 °C inside the stomach and/or intestine track. When prey composition and the heating capacity is known, heat loss (H_f) can be estimated by equation 39.

$$H_f = (8.5 \times 10^2 + 3.08 \times 10^3 \cdot F_w) DI \cdot dT \quad (39)$$

with H_f in J, DI (daily intake) in kg and temperature difference (dT) in K (or °C). F_w is the

fraction water of the prey. Heat capacity of sea water is 3.93×10^3 J/kg·K and that of the remaining components of the prey is estimated by calculating the mean of 22 selected solid substances (from NVON 1977) which resulted in 8.5×10^2 J/kg·K. Figure 16 shows the estimated heat loss as a function of the fraction of sea water, daily intake and the difference between prey and body core temperature. Intake, temperature difference and fraction water all increase H_f linearly. Daily intake of a Knot is c. 0.15 kg (T. Piersma, pers. comm.), which of course can vary greatly. Their prey will have a temperature close to water temperature. The fraction water of the prey is probably c. 0.6 (J. de Leeuw, pers. comm.). For a maximum estimation of H_f , a temperature difference of 40 °C was used, resulting in an H_f of 16 kJ or 0.19 W. Assuming a mean prey temperature of 10 °C and a mean daily intake of 0.1 kg, H_f would be 0.1 W.

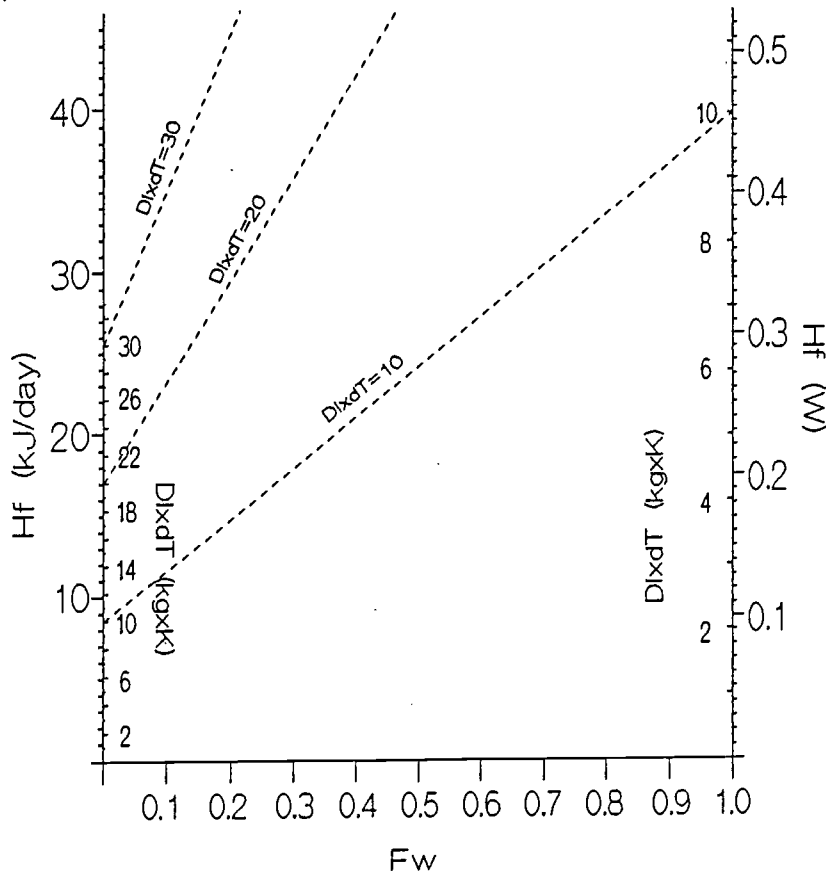


Figure 16. Heat loss by intake and warming up of cold food as a function of sea water fraction (F_w), daily intake (DI) and temperature difference between prey and predator body core (dT). The intersection of F_w with the line connecting $DI \times dT$ on the inner y-axes shows the heat loss on the outer y-axes.

Using climatic data for TC calculations.

The data presented so far were all from measurements taken per 30 or 60 minutes. However, most climatic data published, and hence easy to lay hands on, are not on this time basis but on a daily, 10 daily or monthly one. The problem rising when using this method is that it is important how T_a , W_{sp} and R_g are combined on a particular moment. Mean global radiation can be used for estimating TC_g , but the range of global radiation throughout the day should be taken into account. R_g at midday could result in an environmental temperature above T_{lc} or even T_{uc} , respectively decreasing and increasing TC as estimated using mean R_g . This also counts for temperature and wind. When using periodical means it is recommended to calculate the smallest possible TC, using maximum T_a , minimum W_{sp} and maximum R_g to check on the possibility of exceeding the critical temperatures. As an example the hourly weather data as used in this report is compared with calculations on larger time bases. As comparison TC was

calculated from all available data, averaged per day. The difference between these two is 0.7% (totaling 3.49×10^6 J and 3.51×10^6 J for the original and the averaged weather data respectively). The original data set however contains TC values below the critical value. When adjusting these values to 0.95 W (BMR) the difference becomes 0.1% (totaling 3.52×10^6 J for the adjusted original data). Conclusion: under temperate climatic conditions the mean TC calculations based on daily weather data are very much the same when based on hourly data. However, if interested in more exact TC values, a shorter time scale is necessary to reveal the exact course of TC, including the extremes.

The possible errors engaged with the use of long period weather data has been further analyzed. When only interested in mean TC over long periods (more than a day) leveling of gives no important discrepancies with the more exact approach. This is checked by comparing the calculated TC on different time scales (daily to monthly) for weather data of 1990 (Figure 17). The differences are very small. Daily calculations result in a mean value of 2.02 W, 10-daily in 2.04 W and monthly in 2.02 W. So for long period TC calculations it does not matter very much on which time scale they are based. Again, when interested in the exact course and the extremes, hourly data should be used, or the minimum and maximum weather data should be used in order to calculate a 'worst case TC' and a 'best case' one.

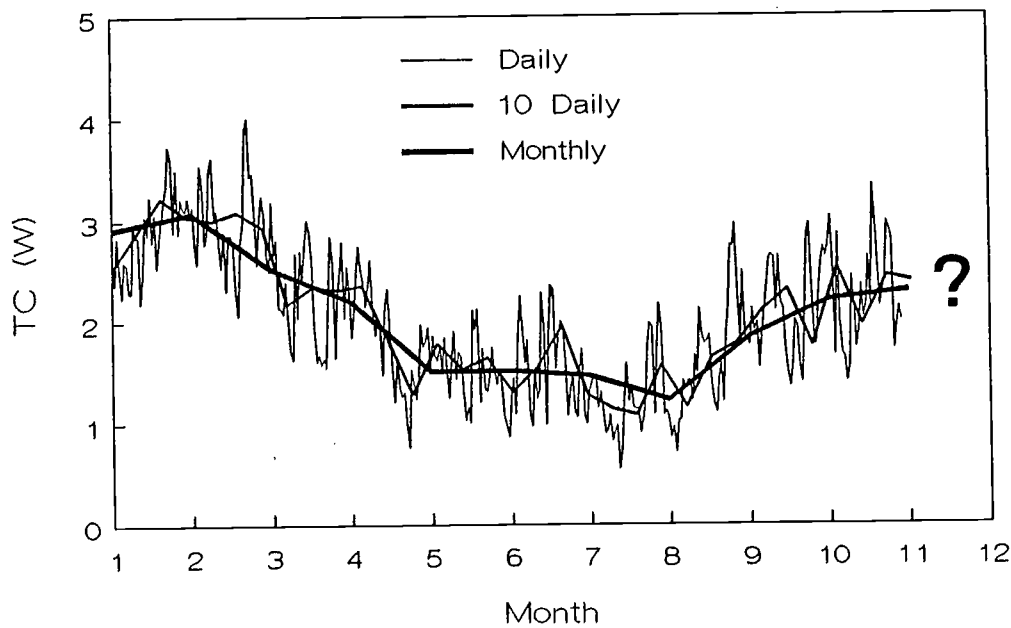


Figure 17. Thermostatic costs (TC) of a single adult Nearctic Knot in the Dutch Wadden Sea during 1990. Calculations based on three different time scales: daily, 10-daily and monthly.

In warmer climates more caution should be taken in using mean weather data. For the West-African coast, where the *C. c. canutus* population mainly winters, extreme values should be taken into account, for they might cause environmental temperatures to exceed the critical temperatures.

Thermostatic costs a year round.

To calculate the annual thermostatic budget of a Nearctic Knot, first the travel plan should be constructed. From Cramp & Simmons (1983) next schedule is extracted:

early August - April:	Wadden Sea
May:	Iceland

June - last July: Canada

last July - early August: Iceland

From monthly weather data for the relevant regions (Orvig 1970; Müller 1980) mean monthly TC for a single adult Nearctic Knot has been estimated, which is shown in figure 18. It has been assumed that during wintering 60% of the time was spent on the mudflat, 20% on the open and 20% on the vegetated salt marsh. At the breeding grounds it was assumed 30% of the time was spent on the nest and the rest divided among the other microhabitats. For Iceland time was divided among the tundra habitats excluding nest cup. The year round energy requirements for thermoregulation are 7.9×10^7 J/y or 2.50 W. Thermostatic costs are highest during wintering.

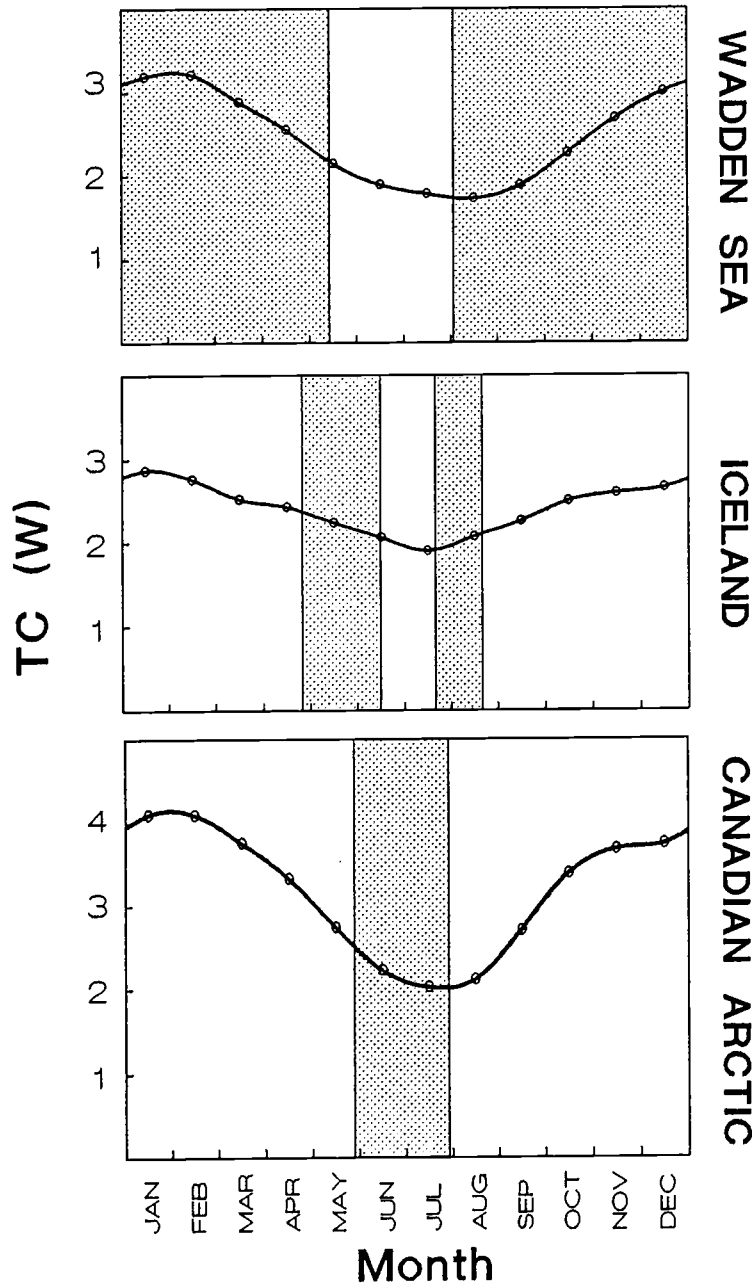


Figure 18. Thermostatic costs (TC) during a year of a single adult Nearctic Knot. Calculations based on monthly climatic data of nearby weather stations. Periods of presence are represented by shaded boxes.

The Afrosiberian Knot.

Suppose a Nearctic Knot flies the route of an *Islandica*, the other subspecies occurring in West-Europe (Figure 1). What would be its TC? Because it winters on the African coast it is expected to be lower. From Cramp & Simmons (1983) the time schedule has been extracted:

- second half August - April: West-Africa
- May - early June: Wadden Sea
- early June - late July: Siberia
- late July - first half August: Wadden Sea

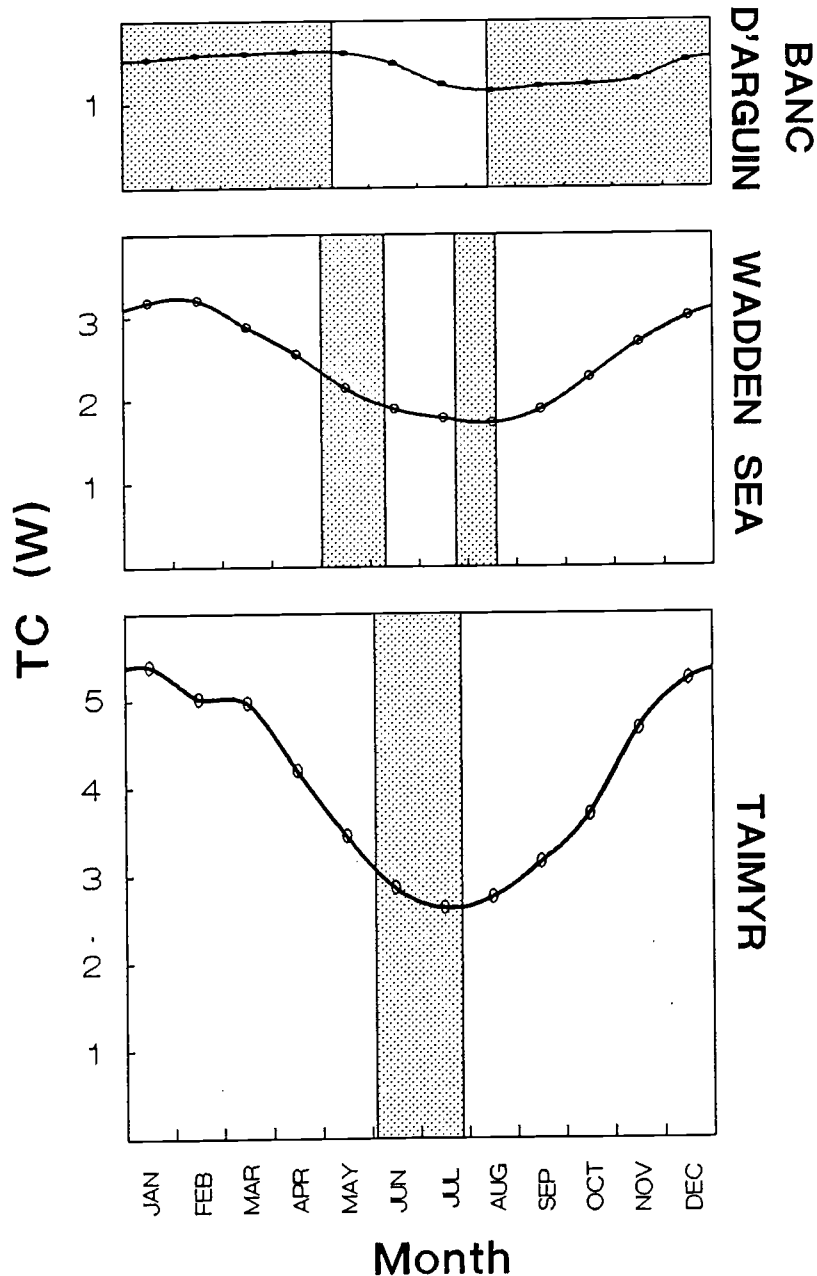


Figure 19. Thermostatic costs (TC) during a year of a single adult Nearctic Knot while on the Afrosiberian route. Calculations based on monthly climatic data of nearby weather stations. Periods of presence are represented by shaded boxes.

From the monthly weather data (Orvig 1970; Müller 1980) TC was calculated, resulting in Figure 19. Assuming an identical microhabitat usage as the islandicas (see above), TC is estimated to be 5.2×10^7 J/y, equal to a mean value of 1.66 W. Because the islandicas possibly have a lower 'Scholander curve' this value could be less (see below).

A Nearctic Knot living at the same spots as an Afrosiberian Knot would be living 34% cheaper on a yearly basis. Wintering would be much cheaper (1.54 versus 2.55 W), but the breeding season would be more expensive (2.13 versus 2.54 W). The data collected so far point to a possible specialization of the two subspecies. The islandica is a cold specialist and/or the canutus is a warmth one. Weathers (1979), Hails (1983) and Ellis (1984) showed tropical birds have lower BMRs than birds living in the temperate and polar regions. A study taking place at this moment also suggests a difference in (weight specific) BMR of the canutus and the islandica subspecies, the first having a lower BMR (N. Cadée, pers. comm.). Reduced BMR and an identical overall conductance would heighten T_{lc} , in that way possibly avoiding heat stress (Weathers 1979; Hail 1984; Klaassen 1990; Kersten & Piersma 1986). Also a lower TC results in less water evaporated, which on its turn may be very important avoiding dehydration and salt stress (Klaassen & Ens 1990). The consequences of a reduced BMR for T_{uc} are not known, although a decrease is expected on first sight. This however would probably be no real disadvantage, because the birds seem to live in areas not distressed by these extreme temperatures. But nevertheless the metabolism of the two subspecies seems adapted to the climate of their subspecific wintering areas. See Piersma et al. (in press) for a more extensive discussion about temperate versus tropical wintering in Knots.

By calculating the theoretical upper critical TC (TC_{uc}) of a Knot at T_{uc} (equation 39), the occurrence of exceeding this limit can be examined.

$$TC_{uc} = c_k(41 - T_{uc}) \quad (39)$$

When T_{uc} is assumed to be 38 °C, TC_{uc} would be 0.17 and 0.14 W for an adult and a second year bird respectively. This limit is also shown in figure 14a to c. This very low value of TC_{uc} implies that heat stress will be very uncommon even in the tropical wintering areas. Klaassen (1990) could not detect any behaviour indicating heat stress in waders wintering on the Banc d'Arguin. The tropical part in Figure 19 also shows heat stress would not occur frequently in Nearctic Knots. Even when global radiation is set to 1000 W/m² TC_{uc} would not be reached. Klaassen (1990) saw waders varying from Dunlins *Calidris alpina* to Bar-tailed Godwits *Limosa lapponica* with their bill tucked under the wing feathers, which is esteemed being an energy conserving behaviour, implying the environmental temperature was below TNZ.

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