Energetic constraints on the non-breeding distribution of coastal shorebirds

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The chain of coastal wetlands along the East Atlantic Flyway, spanning northern Europe to tropical Africa, harbours a 'wintering' population of approximately 7.5 million shorebirds, consisting of about 25 species. Notwithstanding the overall similarity in habitat (open mud- and sandflats containing shellfish, polychaete worms and crustaceans as food), individual shorebirds wintering at varying latitudes face very different environmental conditions. Latitudinal differences in day-length, temperature, wind, solar radiation and humidity define the variable climate space that they face during the non-breeding season. The distances to the breeding areas vary ten-fold between species and affect the required migratory performance in spring and fall. Latitudinal variations in the harvestable biomass of the benthic prey species affect foraging performance. I begin this paper by exploring the methodology used to measure environmental variability encountered by shorebirds along the East Atlantic Flyway. Emphasis is laid on variations in the thermostatic costs of shorebirds of different size. I follow this with an analysis of latitudinal trends in body mass of coastal shorebirds along the East Atlantic Flyway and along the coasts of South America. There were no relationships between body mass and migration distance when all species of the East Atlantic Flyway were combined. Along both flyways, small species 'wintered' closer to the equator than large species, suggesting that the smaller energetic scope for thermoregulation in small shorebirds limits their non-breeding distribution. Along the East Atlantic Flyway, plovers wintered closer to the equator than sandpipers, which in turn suggests that feeding opportunities are an important factor influencing non-breeding latitude. An energy-based conceptual framework as presented here allows energy intake and expenditure studies to be integrated quite easily. I have summarized possible research topics for shorebird ecologists based on the amount of time and technical support available. There is something for everyone to contribute in order to further the understanding of the (energetics of the) distribution and abundance of shorebirds.

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La cadena de humedales costeros a lo largo de la Ruta Migratoria del Atlántico Oriental, que se extiende del norte de Europa al África tropical, alberga una población 'invernal' de unos 7,5 millones de aves costeras, que incluyen unas 25 especies. A pesar de la similitud general del hábitat (tierras bajas inundadas con la marea alta y playas abiertas que contienen como alimento mariscos, poliquetos y crustáceos), las aves costeras que pasan el invierno en diferentes latitudes enfrentan condiciones ambientales muy diferentes. Las diferencias latitudinales relativas a duración del día, temperatura, viento, radiación solar y humedad definen el espacio climático variable que deben enfrentar durante el período en que no se reproducen. Las variaciones en la distancia a los criaderos observadas entre especies pueden llegar a un factor de 10, viéndose afectada la capacidad migratoria requerida en la primavera y el otoño. Las variaciones latitudinales en la biomasa cosechable de las especies de los organismos que viven en las profundidades de las aguas afectan la capacidad de búsqueda de alimento. En este artículo se explora primeramente la metodología empleada para medir la variabilidad ambiental que encuentran la aves costeras a lo largo de la Ruta Migratoria del Atlántico Oriental. Se hace hincapié en las variaciones en el costo termostático de las aves costeras de diferente talla. A continuación, se hace un análisis de las tendencias latitudinales en la masa corporal de las aves costeras a lo largo de esa ruta migratoria y a lo largo de las costas de Sudamérica. No se observaron relaciones entre masa corporal y distancia de migración cuando se combinaron todas las especies que emplean la Ruta Migratoria del Atlántico Oriental. A lo largo de ambas rutas migratorias, las especies pequeñas 'invernaron' más cerca del Ecuador que las especies de mayor tamaño, lo que parece indicar que los límites más reducidos de la termoregulación de las aves costeras de menor tamaño limita su distribución durante el período internupcial. A lo largo de la Ruta Migratoria del Atlántico Oriental, los chorlitos pasaron el invierno más cerca del Ecuador que los playeros lo que, a su vez, parece indicar que las oportunidades para encontrar alimento son un factor importante que influye sobre la latitud durante el período internupcial. Un marco conceptual basado en la energía, tal como el presentado en este artículo, permite integrar fácilmente los estudios sobre aporte y gasto de energía. Se sugieren posibles temas de investigación para los ecólogos especializados en aves costeras atendiendo al tiempo y al apoyo técnico disponible. Todos podemos hacer una contribución para llegar a comprender mejor los factores energéticos que inciden en la distribución y abundancia de las aves costeras.

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L'ensemble des milieux humides côtiers qui borde la voie migratoire de l'Atlantique-est, et qui s'étend de l'Europe septentrionale à l'Afrique tropicale, abrite une population «hivernante» d'environ 7,5 millions d'oiseaux de rivage répartis en quelque 25 espèces. Même si, globalement, l'habitat est semblable (estran sableux et vaseux exposé abritant des crustacés, des coquillages et des vers polychètes dont se nourrissent les oiseaux de rivage), les conditions environnementales sont très différentes selon les latitudes. Ainsi, l'espace climatique dans lequel les oiseaux de rivage vivent durant la saison internuptiale est caractérisé par les différences latitudinales de durée du jour, de température, de vent, de rayonnement solaire et d'humidité. Les distances que ces oiseaux ont à parcourir varient d'un ordre de grandeur; on comprend qu'elles aient un effet sur la performance migratoire au printemps et en automne. Les variations latitudinales de la biomasse récoltable des proies benthiques excercent un effet sur la performance alimentaire. L'auteur commence par examiner la méthodologie utilisée pour mesurer la variabilité de l'environnement que recontrent les oiseaux de rivage le long de la voir migratoire de l'Atlantique-est. L'accent est mis sur les coûts thermostatiques des oiseaux de rivage de diverses tailles. Suit une analyse des tendances latitudinales de masse corporelle des oiseaux de rivage que empruntent cette voie migratoire et de ceux qui se trouvent le long des côtes d'Amérique du Sud. On n'a pas observé de rapport entre la masse corporelle et la distance de migration pour toutes les espèces qui empruntent cette voie. Les espèces de petite taille «hivernent» plus près de l'équateur que les espèces de plus grande taille dans les deux cas, ce qui semble indiquer que la plus faible capacité de thermorégulation des premières limite leur répartition durant la période internuptiale. Ainsi, le long de la voie migratoire de l'Atlantique-est, les pluviers passent l'hiver plus près de l'équateur que les Scolopacidés, ce qui pourrait indiquer que les possibilités d'alimentation constituent un facteur important du choix des latitudes d'hivernage. Une structure conceptuelle fondée sur les échanges énergétiques, comme celle utilisée ici, permet d'intégrer facilement les études sur les apports et sur les dépenses d'énergie. Nous avons résumé les thèmes de recherche sur lesquels les écologistes spécialisés dans l'étude des oiseaux de rivage pourraient voulois se pencher, en fonction du temps et du soutien technique dont ils disposent. Tous peuvent contribuer à une meilleure compréhension de la dynamique énergétique de la répartition et de l'abondance des oiseaux de rivage.

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Introduction

On the basis of general habitat preferences, coastal shorebirds usually occur in open and exposed areas, whether during the breeding season or the non-breeding season. Their occurrence in two-dimensional habitats makes shorebirds amenable to observational study, and the availability of their prey can often be evaluated with relative ease as well. This makes the group of shorebirds, or waders (Charadrii), an excellent choice for detailed ecological and ethological research.

The same characteristics make shorebirds more exposed to the vagaries of weather than are most other groups of birds. A mudflat or open arctic tundra gives little protection to wind and cold, precipitation and solar heat. In addition, most coastal shorebird species are unwilling to hide from the elements even when they have the opportunity. Hiding behind a discarded beer can on a beach or sitting in a tight flock of conspecifics or in an open patch between the mangroves is usually as far as they want to go. Clearly, their adventure is not to seek the energetic rewards of crevices and thickets but to use the world at large, by flying great distances from their temperate-to-arctic breeding grounds to temperate-and-tropical wetlands and even to the southern shores beyond.

This contribution examines the energetics behind the non-breeding distribution of shorebirds. It builds on the same assumptions made by Evans (1976) in an earlier review, which stated that many of the behavioural decisions taken by animals are somehow (evolutionarily or ontogenetically) motivated by energetic considerations; within certain time frames, each animal simply has to balance its budget. The time within which the budget sheets are balanced depends on the size of the animal (almost a year in the great whales, but less than a day in shrews). Accounting in shorebirds is probably a matter of weeks or months.

Energetic considerations affect virtually all aspects of the biology of a species. As in any study, this one has its biases. I will concentrate on the repercussions of using different wintering latitudes on the day-to-day energy balance, especially as they pertain to the cost of living in different climatic environments. I will briefly examine the concomitant costs of travelling between the breeding and non-breeding areas. Allometric scaling of energetics-related phenomena on body size (provisionally approximated by mass) provides a means by which to examine the shorebird community as a whole. By comparing species across flyways, I hope to show which steps can be made towards understanding the wintering patterns of coastal shorebirds with the help of energetics (see Hockey *et al.* 1992 for a completely different attempt).

Application of the energetics approach

Budgeting over different lengths of time

Three basic ingredients make up a treasurer's balance sheet (see *Wader Study Group Bull.* 62: 5–6): the receipts, the expenses and the accumulated fund. These can be translated in biological terminology as energy intake, energy expenditure and bodily energy stores, respectively.

Two variants of energy budgeting studies will be distinguished here, based on whether or not the energy store enters the balance equation. For shorebirds, there is no need for energy intake and expenditure to be exactly in balance on a daily basis, as they have the possibility of storing energy-rich nutrients such as fat when in positive balance so as to keep them going for a couple of days or weeks when in negative balance. It is therefore possible to use the daily energy budget as a basic unit from which to build seasonal energy budgets. In the latter type of budget, not only intake and expenditure are accounted for, but also the build-up and use of energy stores, and here the resulting balance has to equal zero. The daily energy budget with its intake and expenditure sides is illustrated in Figure 1, whereas Figure 2 tries to visualize the seasonal (in this case annual) energy budget of a typical wader (and see Owen, Wells & Black 1992 for an empirical attempt to make a seasonal budget for geese).

The daily energy budget thus consists of an intake side (Figure 1 left) and an expenditure side (Figure 1 right), each of which can be dissected into several components. Only part of the gross energy intake (the energy equivalent of all the ingested food) can be retrieved during digestion. The remainder is voided as regurgitates or faeces. The metabolizable energy that remains can be used for productive purposes. Energy expenditure consists of four cost components: basal metabolic rate, cost of thermo-regulation, activity and the heat increment of feeding. The basal metabolic rate (commonly abbreviated as BMR) is the lowest possible rate of energy expenditure of a living bird; it is the amount of energy consumed when a bird is not digesting, not busy with any activities and not shivering because of the cold. When temperatures are not high enough to prevent shivering, birds additionally expend energy on thermoregulation. The sum of BMR and cost of thermoregulation (the energy expenditure of inactive and not-digesting warm-blooded animals under all environmental conditions) is called the thermostatic cost. The heat increment of feeding is the energy used in the digestive and assimilation processes. It is either lost as excess heat or used for thermoregulatory purposes (*e.g.* Masman, Daan & Dietz 1989; Meienberger & Dauberschmidt 1992; Sedinger,
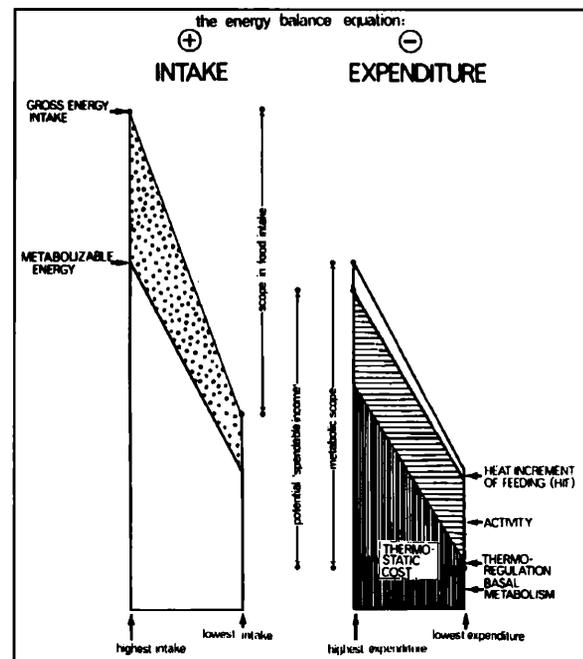

Figure 1. The energy balance equation illustrated. The left stacked bar represents the intake side of life, the right bar the expenditure side. The left and right sides of each bar are indicative of the highest and lowest weekly average intake or expenditure rates, respectively. Different kinds of shading indicate the breakdown in different yield and cost components, as explained in the text. The difference between energy intake and expenditure over a certain time interval will be expressed as storage (positive balance) or nutrient loss (negative balance).

White & Hauer 1992). Any surplus energy of intake over expenditure can be stored. A negative balance leads to a reduction in the energy content (and, thus, body mass) of a bird. For strategic reasons (*e.g.* before midwinter and migration), shorebirds have to store energy regularly.

The total variation in energy intake and energy expenditure in the medium term (*i.e.* weekly) is indicated by the difference between the left and right sides of the stacked bars in Figure 1. The variation in gross energy intake gives the scope in food intake rates (over a period of about a week). Not all 'income' is 'spendable' according to an animal's free choice, as, in order to stay alive, it has to keep up its core temperature and basic body functions (the obligatory cost factor called BMR). The range in total expenditure relative to BMR is called the metabolic scope (Bartholomew 1977; Peterson, Nagy & Diamond 1990).

The daily energy balance figures can be summed or averaged over a monthly period. The differences between total intake and expenditure have to be balanced by energetically equivalent changes in the energy content of a shorebird. During episodes of pre-migratory fattening, the balance will be (must be) positive; during the long-distance flights, the
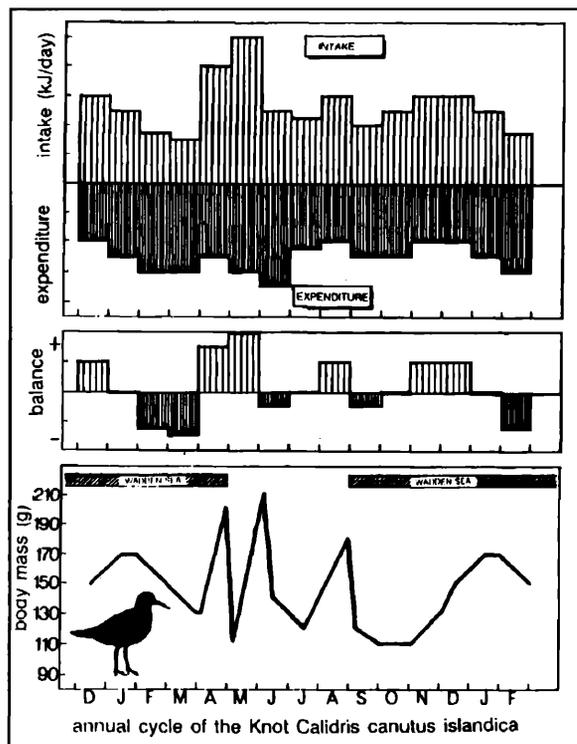
Figure 2. Seasonal changes in the relative intake and expenditure rates (top panel) and the resulting energy balance figure (middle panel) in relation to changes in the amount of stored energy in the birds' bodies as indicated by body mass (lower panel). The annual cycle characteristics of *islandica* knots (see Piersma & Davidson 1992) were used as an example.

Figure 3. Relationship between energy expenditure of Red Knots sleeping in a darkened metabolic chamber (depicted at right) in relation to the air temperature in the box. The heavy line (giving the total thermostatic costs) is fitted according to the Scholander model (Scholander *et al.* 1950; McNab 1980) for a core temperature of 41 °C. The shaded part of the diagram indicates the BMR of 0.95 W; the open area between this level and the heavy line indicates the cost of thermoregulation. The lower critical temperature above which energy is constant and equal to BMR is also indicated. This figure is adapted from Piersma, Drent & Wiersma (1991).

balances are strongly negative for a few days (high activity costs and no intake at all) (*e.g.* Piersma & Jukema 1990). After a midwinter mass peak, the intake rate does not (have to) equal the expenditure rate, and body mass (stored energy) is lost (Pienkowski, Lloyd & Minton 1979; Davidson 1981; Johnson 1985).

Estimating the various cost factors

How does one go about measuring or estimating the various cost factors listed in Figure 1? The complete story is, of course, a long one, but what follows is a brief listing of the most common approaches (see Gessaman 1987 for a more comprehensive review).

BMR is measured by placing a shorebird in a 'metabolic chamber', usually an airtight dark-walled Plexiglas box through which air is sucked or blown at a specified rate (Figure 3 at right). By measuring the differences in oxygen concentration between the incoming and outgoing air, the oxygen consumption of the bird in the box can be calculated. Usually the birds are measured in a noise-free, dark and temperature-controlled room, and most shorebirds tend to go to sleep readily. As was pointed out, the energy equivalent of the oxygen consumption per unit time of a sleeping
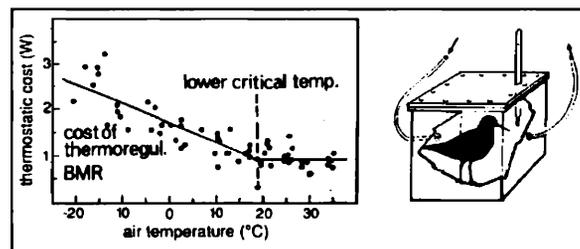
bird not digesting food at a congenial temperature (above the lower critical temperature; see McNab 1980; Wiersma, Bruinzeel & Piersma in press) is called BMR (see Castro 1987; Kersten & Piersma 1987; Mathiu *et al.* 1989; Piersma, Drent & Wiersma 1991; and Figure 3 for measurements of a shorebird species).

BMR, cost of thermoregulation and, thus, thermostatic cost are easy to measure in the set-up described above (*i.e.* just vary the air temperature; see the pioneering studies by Scholander *et al.* 1950 and Figure 3). The slope of the sum of BMR and the cost of thermoregulation on air temperature below the temperature interval at which thermostatic costs are constant and equal to BMR (below the lower critical temperature; Figure 3) is called conductance. Conductance of birds (of the same size) is a measure of the insulative properties of a bird's plumage: the higher the conductance, the lower the insulation and the larger the heat loss.

The oxygen measurements of birds in boxes do not necessarily describe the thermostatic cost levels of free-living birds adequately, as a sleeping bird in a box feels no wind and no radiation. Both are important factors that interact with temperature in the real world (Figure 4). Instead of trying to quantify all the avenues of physical heat losses and gains in different environments (Figure 4), we can take a short cut by using bird models to give us an integrated value for thermostatic costs in different habitats (Bakken *et al.* 1981; Bakken, Erskine & Santze 1983). Taxidermic mounts (hollow copper models covered by a real skin) are kept heated to a bird's normal internal temperature (approx. 41 °C in Red Knots *Calidris canutus*; T. Piersma, unpubl. data) by a subcutaneous heating wire. A data-logger registers the electric power required to do so (see Figure 5 right). Measurements with copper
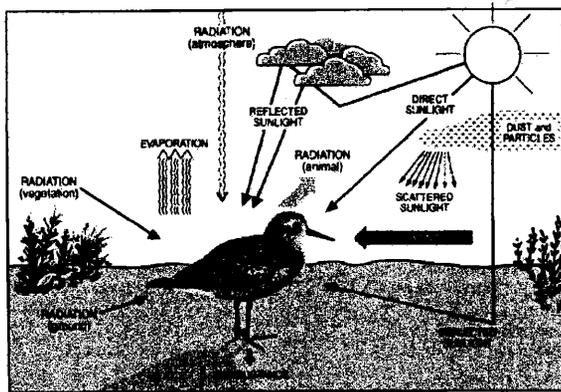
Figure 4. Summary diagram giving all the physical avenues of energy losses and gains affecting shorebirds owing to variations in climatic circumstances. This figure is adapted from the 'horse figure' in Porter & Gates (1969).

Figure 5. The thermostatic costs incurred by Red Knots with a BMR of 0.95 W (see Figure 3) under the average meteorological conditions in the breeding season in the Canadian Arctic, in the temperate winter in the Dutch Wadden Sea and in the tropical winter on the Banc d'Arguin, Mauritania (from Piersma, Drent & Wiersma 1991). Latitudes of the three areas are indicated in °N. The figure at the right gives an impression of the 'copper knot' set-up used to derive the predictive equation to relate thermostatic costs to the three climatic variables — temperature, wind speed and global solar radiation.

models in different habitats under a variety of weather conditions and calibrations under laboratory conditions to living birds yield habitat-specific equations relating thermostatic costs to climatic variables such as air temperature, wind speed and solar radiation (Piersma, Drent & Wiersma 1991; P. Wiersma & T. Piersma, unpubl. data). By subtracting BMR (independent of climatic variables by definition) from the thermostatic cost, the cost of thermoregulation is obtained.

Recent studies have shown that the thermostatic cost weighs heavily in the energy budgets of medium-sized shorebirds (Piersma, Drent & Wiersma 1991). On the basis of the measurements by heated taxidermic mounts (the 'copper knots') and the relevant climatic data, Piersma, Drent & Wiersma (1991) estimated the thermostatic costs of Red Knots on their arctic breeding grounds and in the temperate and tropical non-breeding areas (Figure 5). Thermostatic costs amount to about 3 W during both the arctic summer and the temperate winter (as in the Dutch Wadden Sea), but only half this value in the tropical winter (as on the Banc d'Arguin in Mauritania). The high thermostatic costs in summer and the northern winter give them only little leeway (between the thermostatic cost level and the estimated maximum metabolizable energy level, ME_{max}) for other cost factors. The study on latitudinal variation in the energetics of non-breeding Sanderlings *Calidris alba* by Castro, Myers & Ricklefs (1992) has confirmed that coastal environments that are costly in thermostatic terms are indeed accompanied by high field metabolic rates.

Finally, we have to consider the costs of various activities. Walking, feeding and preening, roosting and flying are the most common activities of shorebirds in the non-breeding season, and very little published work is available to estimate the magnitude of their costs (Pienkowski *et al.* 1984).
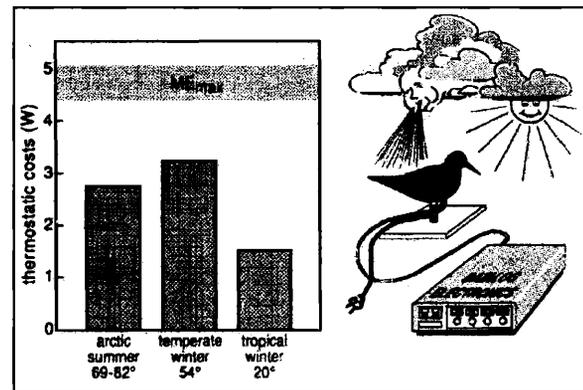
The cost of flight in birds has been repeatedly considered in very general terms (Masman & Klaassen 1987; Castro & Myers 1988; Pennycuick 1989; Rayner 1990), and the estimates obtained are reasonable on this basis (Piersma & Jukema 1990). Roosting and resting probably add little to the thermostatic cost as estimated by the heated taxidermic mount approach. The cost of activities such as walking and feeding can be studied by varying the work level of birds under controlled circumstances and measuring their total energy expenditure with the doubly labelled water technique and by having birds walking on treadmills while simultaneously measuring their oxygen consumption (see, *e.g.*, Fedak, Pinshow & Schmidt-Nielsen 1974; Paladino & King 1984; Zerba & Walsberg 1992). Both approaches are currently being employed on Red Knots at our laboratory (M. Poot, L. Bruinzeel & T. Piersma, unpubl. data).

Estimating the potential nutrient yields of feeding habitats

The rate at which animals can extract food from their environment obviously depends on the size and density of available food items. The generalized form of such relationships (the functional response equation) was first described by Holling (1959). In principle, it should be possible to derive the relationships between food abundance and intake rates for all types of prey and predators (Holling 1965); however, even when we are concerned with one type of predator, there are a couple of difficulties to be resolved. For example, not all prey of a species are equally suitable for a predatory shorebird (Figure 6). Some may be too
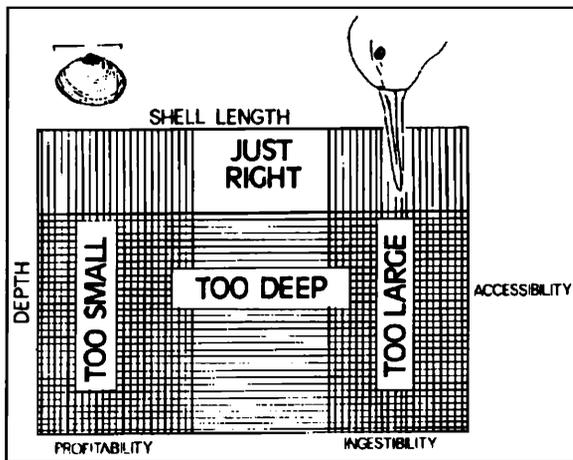
Figure 6. 'Ecological cage' of a mollusc-eating shorebird predator with the 'predation window' from which the examined can eat. Some molluscs are too small to be profitable or are too large to be ingestible, and all size categories can be too deeply buried to be within reach of the bill. The fraction that is 'just right' is called 'harvestable'.
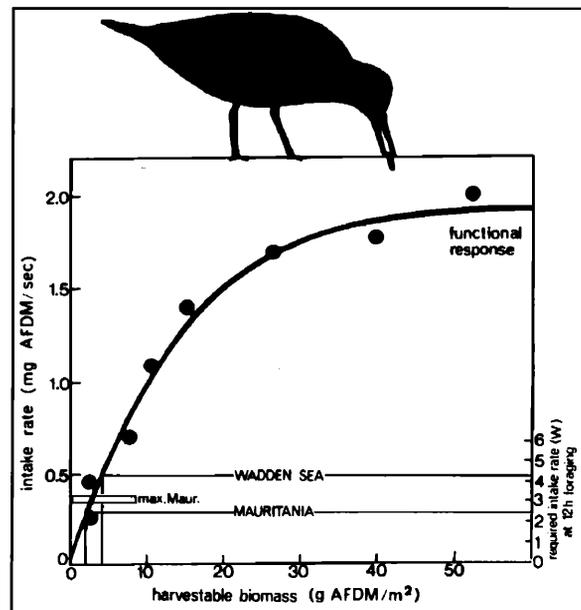

Figure 7. Generalizing the relationship between the harvestable biomass of a benthic prey species and the intake rate of a predator: the approximate functional response curve of Red Knots feeding on Macoma balthica. The data points are from small-scale laboratory experiments as well as from field observations (T. Piersma, unpubl. data); see Zwarts & Blomert (1992) for further information on this predator–prey relationship.

small to be worth the energy invested in searching, catching and ingesting them (i.e. they are not profitable), whereas others may be too large to be swallowed (i.e. they are not ingestible), and still others may occur too deep in the sediment (or the water column), beyond the reach of the bill (i.e. they are not accessible). Only prey that fall in the 'predatory window' of the particular shorebird species determine the potential food intake rate; we call this the harvestable fraction (Zwarts, Blomert & Wanink 1992). Studies by Myers, Williams & Pitelka (1980), Hulscher (1982), Wanink & Zwarts (1985), Zwarts & Blomert (1992) and Zwarts, Blomert & Wanink (1992) and our own work on Red Knots have shown that in probe-feeding waders, especially those feeding on slow-moving bivalve prey, it is possible to quantify the harvestable biomass and, in some cases, to relate it to intake rate by a type-2 functional response equation (Figure 7; see Holling 1959, 1965). Indeed, we have now been able to verify these results for Red Knots for a variety of prey types under standardized laboratory conditions simulating intertidal mudflats (T. Piersma, J. van Gils & P. de Goeij, unpubl. data).

Obviously, differences in the types of prey (in relation to their mass, size, behaviour and depth of extraction from the sediment) will influence the form of the functional response equation. For this reason, comparisons between equations for different prey types can be used to explain diet selection in shorebirds (Wanink & Zwarts 1985). In order to compare feeding areas on the basis of their potential nutrient yields, we would require the functional response equations for all kinds of prey encountered as well as accurate data on the size and depth distributions of these prey at the sites to be

compared. This is an ambitious programme, which has yet to be carried out.

A very rough attempt to illustrate this approach can, however, be made on the basis of the generalized functional response curve relating measured intake rates of Red Knots to the harvestable biomass of Balthic Tellins Macoma balthica in the Dutch Wadden Sea (Figure 7). To achieve energy balance in the cold and windy Dutch Wadden Sea in winter, given that they forage for the entire low-water periods throughout day and night (about 12 hours), Red Knots would require an intake rate of about 0.5 mg ash-free dry mass (AFDM) per second. This would require a harvestable biomass of 3–5 g AFDM/m² (Zwarts, Blomert & Wanink 1992: Figure 11). Harvestable biomasses of bivalves on the Banc d'Arguin in Mauritania, the stronghold of Red Knots and many other shorebirds wintering in West Africa (see below and Ens et al. 1990), are much lower (Figure 7). Indeed, the data in Zwarts, Blomert & Hupkes (1990) suggest that during migratory fattening on the Banc d'Arguin, a period of peak demand when Red Knots feed for all available time, day and night, intake rates are limited to 0.37 mg AFDM/s. If this situation is typical for the entire winter period spent on the Banc d'Arguin, Red Knots would not be able to balance their budget there if the climate were as demanding as in the Dutch Wadden Sea (cf. Figure 5). It is likely that
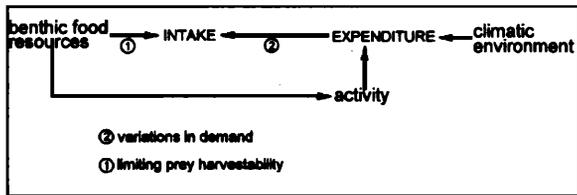
Figure 8. A crude interactive model to outline how the expenditure and intake sides of the energy balance equation (Figure 1) are causally interconnected. Variations in demand as well as prey availability can delimit the occurrence of a specified shorebird predator. See Piersma (1987) for a much more comprehensive scheme of relationships between benthic biomass production and shorebird foraging.

Red Knots are able to use the Banc d'Arguin only as a wintering area (one that is relatively poor in food), in view of the low local thermostatic costs (Piersma, Drent & Wiersma 1991).

Interactions between the intake and expenditure sides of individual energy budgets

The interactions between intake and expenditure can be summarized in the simplified scheme of Figure 8. For a shorebird in energy balance, higher levels of energy expenditure require a higher daily food intake. This is achieved by higher intake rates per unit feeding time or longer feeding periods, or both. Longer feeding periods are necessary if the benthic food resources on the foraging grounds limit intake rate. If this is indeed the case, then the period during which a relatively costly activity like feeding increases may in turn result in increased expenditures (Figure 8).

Generalizing the energetics approach: scaling on size

To enable a comparison of shorebird 'communities' along the gradients provided by the major flyways, it is necessary to extract from nature some generalities about the levels of intake and expenditure and their components. The allometric scaling of energy-related phenomena on body size has provided a powerful tool to extrapolate detailed knowledge, based on studies of a limited array of species, to the remaining unstudied species or to communities (Calder 1974, 1984; Kendeigh, Dolnik & Gavrilov 1977; Schmidt-Nielsen 1984). Although size and mass are distinct variables (see Piersma & Davidson 1991), body mass (which may include a size-independent storage component) is commonly used as an approximation of body size, and I will continue this practice here. Important examples of allometric scaling are the log–log regressions of BMR on body mass (Lasiewski & Dawson 1967; Aschoff & Pohl 1970) and of field metabolic rates on body mass (Nagy 1987). By allometrically scaling BMR on body mass, Kersten & Piersma (1987) were

able to show that shorebirds in general have high metabolic rates compared with other non-passerine birds, which implies that a common explanation has to be sought for the group as a whole. Zwarts *et al.* (1990a: Figure 7) give an example of the allometric scaling of food intake rate and individual prey mass on body mass of shorebirds on the Banc d'Arguin, Mauritania.

As much more is known about the scaling of expenditure-related processes on body mass than of intake-related phenomena, and as the components of energy expenditure and the external factors (*e.g.* climate) influencing them are relatively well understood, I will limit further discussion of the energetics of shorebirds in relation to their distribution along the flyways to the expenditure side of the balance sheet. This is like telling only half the story, but, in the absence of relevant information on latitudinal trends in food and feeding opportunities in relation to the size and mass of shorebirds, there is no other way. Let us concentrate on two aspects of energy expenditure that may vary with shorebird size and with latitude: the costs to cover the distances between breeding and non-breeding areas in flight and the thermostatic costs.

Little is clear about the dependence of migratory flight performance on body size. If it would be more costly or take longer for shorebirds of a certain size to migrate, then we would predict them to cover shorter migratory distances than heavier or lighter birds, everything else being equal. For such an analysis, we would need to know the relative energy requirements to cover the same distance in migratory flight in shorebirds of different body sizes. The empirical models that are available today disagree about the size/mass effects on flight range in shorebirds (McNeil & Cadieux 1972; Summers & Waltner 1978; Davidson 1984; Castro & Myers 1989), for reasons that are unclear.

We also need to know how long it would take shorebirds of different body size/mass to deposit the required energy stores to cover a certain distance (Zwarts *et al.* 1990b). Lindström (1991) showed that larger bird species have relatively lower rates of fat deposition and suggested that larger species may have lower speeds of migration. As all species, whether large or small, have the same time limitations, we would predict that those with the lower speeds of migration would migrate the shortest distances. However, in view of all these uncertainties, it may be more insightful to look at the empirical patterns of flight distances shown by shorebirds of different body mass along the East Atlantic Flyway (Figure 9). Although migration distances vary ten-fold between shorebird species (Figure 9), there are no clear trends in migration distances (or in the average breeding latitude) in relation to body mass, except
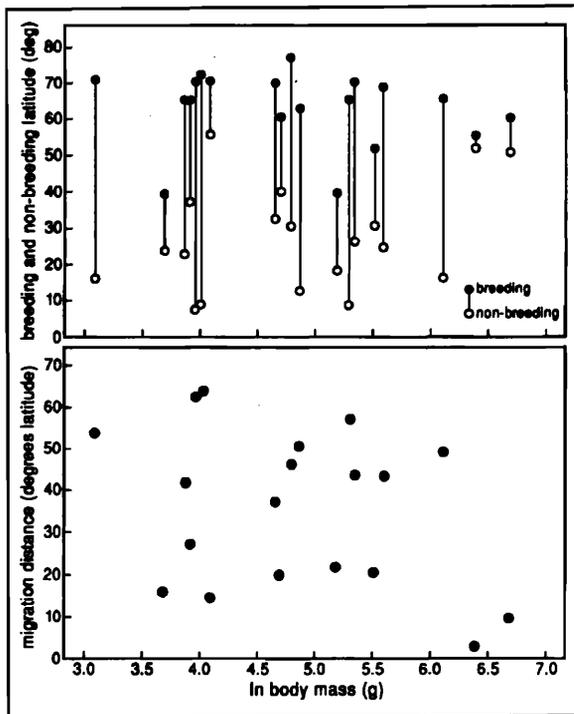
Figure 9. Allometry of breeding and wintering latitude and migration distance in the shorebird species of the East Atlantic Flyway. The average breeding latitude is from Piersma *et al.* (1990: Table 1), and the average non-breeding latitude is computed from Smit & Piersma (1989: Tables 3 & 5).
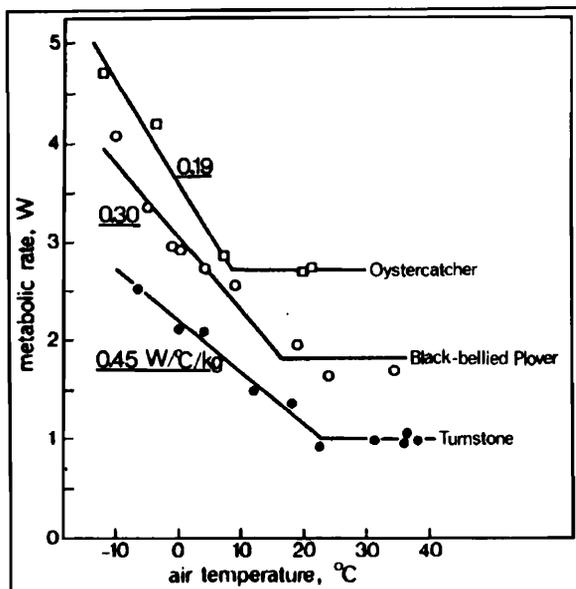

Figure 11. Scope for expending energy on thermoregulation and activity by shorebirds of increasing body mass (adapted from Visser 1991, p. 159). The scope is constrained by the absolute minimum expenditure (BMR, according to the equation of Kersten & Piersma 1987) and the maximum metabolizable energy (ME_{max}, according to the equation of Kirkwood 1983, on the basis of daily energy intake rates of maximally performing individuals such as lactating mammalian mothers and brood-provisioning avian parents).

Figure 10. The metabolic rates of Eurasian Oystercatcher *Haematopus ostralegus*, Black-bellied Plover *Pluvialis squatarola* and Ruddy Turnstone *Arenaria interpres* measured by conductance. Heavier shorebirds have higher absolute conductance values but lower relative conductance values. In combination with their lower critical temperatures, the relative thermostatic costs decrease with increasing body mass. The values for Eurasian Oystercatcher, Black-bellied Plover and Ruddy Turnstone presented here are from Kersten & Piersma (1987).
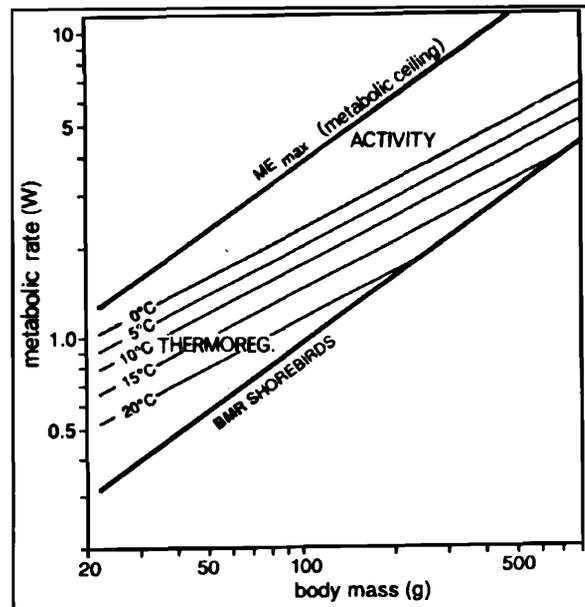
that the two largest species (Eurasian Oystercatcher *Haematopus ostralegus* and Eurasian Curlew *Numenius arquata*) show the shortest migration distances. This is not due to these species being unable to cover long migration distances, as some Eurasian Oystercatchers and Eurasian Curlews winter as far south as Guinea-Bissau (9°N) and represent the northernmost breeders and farthest migrants amongst their species (Zwarts 1988).

An important variable that influences the level of thermostatic costs in shorebirds of different size is their conductance. Although larger birds have higher conductances (Figure 10), this is not so on a mass-specific basis (Aschoff 1981). Larger and heavier shorebirds devote relatively less energy to thermoregulation and have therefore, within the constraints of their metabolic physiology, more energy available to cover the remaining expenditure — that is, mainly the cost of activity (Figure 11). Figure 11 also shows that the range of air temperatures over which shorebirds do not have to expend energy on thermoregulation is much smaller in small than in large species. An 800-g Eurasian Curlew can spend all its energy on BMR and activity even if air temperatures are as low as 10 °C, but a 20-g Little Stint *Calidris minuta* has to spend quite a bit of its energy on thermoregulation even if it is 20 °C. On the basis of Figure 11, we predict that the smaller species occur in relatively
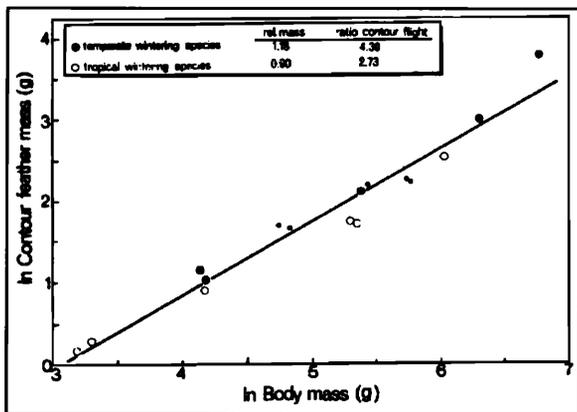
Figure 12. The dry mass of contour feathers (a parameter of the quality of the main insulative layer) in relation to body mass in a series of wader species that are assignable (or not: small symbols) to different wintering latitudes. Species averages (based on 1–85 individuals) are given. The linear regression line across the species averages is indicated and given by the equation: $Y = 0.0657X^{0.892}$ ($n = 16$, $r^2 = 0.96$).

benign climates (high temperatures, low wind speeds) and that only the large species spend the non-breeding season in the cold and windy north.

Before examining the mass-related distribution of shorebirds along the East Atlantic Flyway, I wish to point out a further interesting complication. Tropical- and temperate-wintering shorebirds of the same species and/or mass may differ with respect to their conductance or with respect to their rate of energy expenditure under warm climatic conditions. Piersma, Drent & Wiersma (1991) suggest that tropical-wintering Red Knots have a lower mass-specific BMR than conspecifics wintering in north-western Europe, which implies subspecific differences in physiology. An allometric analysis of the dry mass of contour feathers of shorebirds from different wintering areas (Figure 12) suggests that temperate-wintering species have a relatively heavy plumage and that tropical-wintering species have a relatively light plumage, whether expressed relative to the predicted average for all species or relative to the mass of the flight feathers (the latter serving only a minor role in the insulation of the body). If the dry mass of contour feathers is a good (inverse) measure of conductance, tropical-wintering shorebird species may have relatively higher conductances than temperate-wintering ones. The fact that the two smallest shorebird species, both of which are wintering in the tropics, nevertheless have higher than average contour feather masses (Figure 12) may indicate that what we consider as tropical (and hotter than average) conditions still requires a larger than average investment in an insulative layer for the smallest birds. This provides an added argument for predicting that small species should winter in the warmest climates.

Size-dependent shorebird distribution along the East Atlantic Flyway

The chain of coastal wetlands along the East Atlantic Flyway, spanning northern Europe to tropical Africa, harbours a 'wintering' population of approximately 7.5 million shorebirds, consisting of about 25 species (Smit & Piersma 1989). An analysis of body size and taxon/feeding style in relation to the average numbers and distribution of coastal waders along the East Atlantic Flyway (Smit & Piersma 1989) is presented in Figure 13. I have differentiated between plovers and sandpipers in view of their distinct phylogenies and feeding methods: plovers usually feed by sight, sandpipers usually by touch (Pienkowski 1981a). The sandpipers were split into a group of small species (weighing less than 148 g) and a group of large species (heavier than 148 g). Plovers and small sandpipers winter predominantly in the tropics, with the average plover being encountered at even more southerly latitudes (25°N) than the average small sandpiper (30°N). Most of the large sandpipers and Eurasian Oystercatchers winter at temperate latitudes around 38°N. Although this type of data does not allow statistical testing, the hypothesis still maintains that smaller shorebirds winter at more southerly latitudes (which, along the East Atlantic Flyway, correlates with lower thermostatic requirements; Drent & Piersma 1990; Piersma, Drent & Wiersma 1991) in view of their relatively high energetic requirements for thermoregulation (Figure 11). The fact that plovers show an even more southerly distribution than the small sandpipers is in line with the arguments put forward by Pienkowski (1981a, 1981b, 1983). As the visual prey detection by plovers is particularly susceptible to the adverse effects of wind and low temperature (interfering either with the detection itself or with prey activity), plovers in general should select warmer climates than shorebirds with a probing, and less easily affected, style of feeding.

Testing the trends: latitudinal distribution patterns on the South American continent

Morrison & Ross (1989) counted coastal shorebirds along the entire shoreline of the South American continent from the air. This provides a particularly nice and uniform data set to test if the trends in body size of shorebirds in relation to latitude found along the East Atlantic Flyway are true for other areas as well. This is because the climatic gradient along the South American shores is exactly the opposite of the one found along the shores of Europe and West Africa. The more southerly and farther from the breeding areas one goes, the colder and windier the environment. A comparison
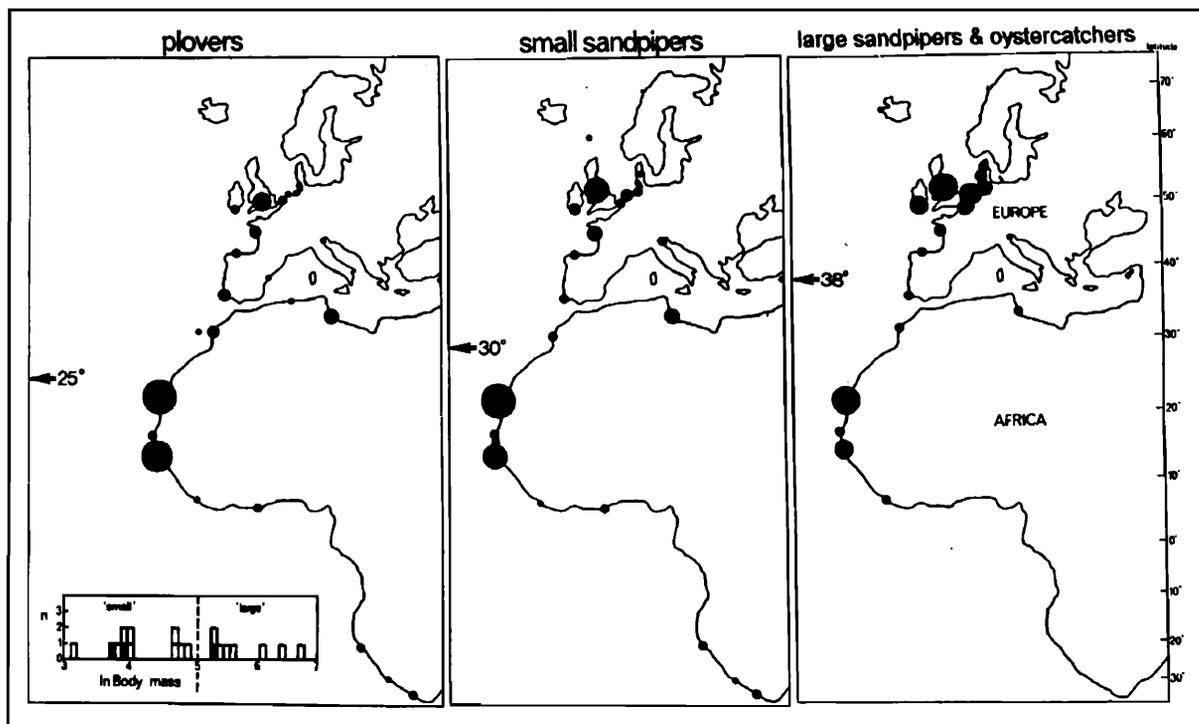
Figure 13. Relative distribution pattern of plovers (Charadriidae) and small and large sandpipers and oystercatchers (Scolopacidae and Haematopodidae) along the East Atlantic Flyway (based on Tables 3 & 5 in Smit & Piersma 1989). The inset gives the boundary mass between 'small' and 'large' sandpipers/oystercatchers at ln(mass) = 5 (*i.e.* body mass = 148 g); open histograms are sandpipers/oystercatchers, and the three closed squares represent the three plovers. The 'small sandpiper' group is composed of *Calidris minuta, C. alpina, C. alba, C. ferruginea, C. maritima, C. canutus, Actitis hypoleucos, Arenaria interpres, Tringa totanus* and *T. erythropus.* The 'large sandpiper' group is composed of *Himantopus himantopus, T. nebularia, Recurvirostra avosetta, Limosa lapponica, L. limosa, Numenius phaeopus, N. arquata* and *Haematopus ostralegus.*

between size-related shorebird distribution along the South American and European/West Africa coasts would thus control for migration distance, as the climatic trends in relation to distance are reversed. The distribution of coastal shorebirds of different sizes over the entire South American continent is presented in Figure 14. The data are summarized and compared with the pattern of the East Atlantic Flyway in Figure 15. Clearly, the trends are the same. Along both the European/ African coastline and the South American coasts, the average body mass of shorebirds is smallest close to the equator (although species of all sizes occur at all latitudes). This suggests that, with respect to body size and mass, climate (and therefore thermostatic costs) is likely to be a more important factor determining non-breeding area than the distance that has to be covered to get there from the breeding grounds and to get back.

Scope for future work

The present analysis of the distribution of coastal shorebirds in relation to latitude and likely thermostatic costs is just one example of the use of energetics in the analysis of distribution and abundance. Thermostatic costs, as incurred by shorebirds of varying body size and mass, could be

an important selective factor in the determination of non-breeding latitude. The differences between plovers and sandpipers at non-breeding latitudes along the East Atlantic Flyway further suggest that it is the thermostatic requirements, relative to the quality of the feeding grounds (the potential nutrient yields in different areas), that count most. I was surprised that such a coarse-grained analysis (with so many interfering variables not taken into account) yielded such clear patterns. At the same time, the described latitudinal trends, although giving good hints, have little predictive power and do not really show the energetic constraints faced by individual shorebirds of different species. Perhaps intraspecific comparisons would turn out to be even more insightful than the present comparison between species.

In order to obtain such information, we need much more work on (1) the definition of microclimatic conditions for different types of shorebirds, (2) metabolic adaptations to climate within and between species, (3) the energetics of migratory flights and the use of migratory corridors with favourable winds (cf. Piersma & de Sant 1992) and (4) the use of stop-over sites in relation to the distances between them, their quality and the time constraints of the birds, building on the theoretical work of Alerstam & Lindström (1990). We also
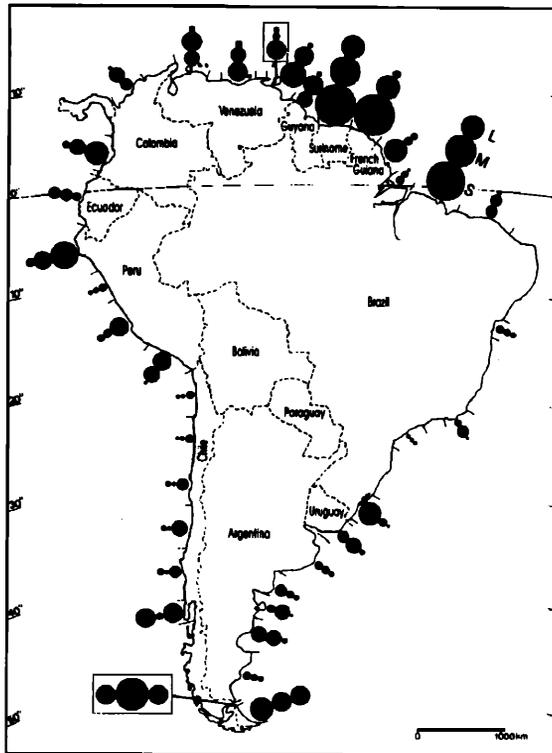
Figure 14. Distribution patterns of variously sized shorebird species around the South American continent according to the results of aerial counts presented by Morrison & Ross (1989) and summarized by Morrison & Myers (1989) in their Figure 2 (on which this figure is based). S = small shorebirds (from Least Sandpiper *Calidris minutilla* to Buff-breasted Sandpiper *Tryngites subruficollis*), M = medium-sized shorebirds (from Stilt Sandpiper *Calidris himantopus* to Greater Yellowlegs *Tringa melanoleuca*) and L = large shorebirds (comprising Willet *Catoptrophorus semipalmatus*, Whimbrel *Numenius phaeopus* and Hudsonian Godwit *Limosa haemastica*) (see Table 2.2 in Morrison & Ross 1989). The surface of the dots is proportional to the numbers found along the indicated stretch of coastline, the biggest dot representing 100,000–300,000 birds.

Figure 15. Latitudinal trends in the average mass of shorebirds spending the non-breeding season along the coasts of the East Atlantic Flyway (computed from Tables 3 & 5 in Smit & Piersma 1989) or along the shores of South America (computed from Table 3.2 in Morrison & Ross 1989).

badly need (5) more comparative descriptive work on the quality of feeding habitats by careful empirical studies on food selection and prey harvestability. Along the shores of South America, preciously little work has hitherto been carried out, although important studies are now in progress at several locations.

If this paper is read as a guide to the technically advanced and suggests near-impossible field and laboratory studies, I have failed. I hope that everyone sees that the framework of energetics offers the possibility of integrating the results of research efforts of very different intensity and character. Table 1 lists possible research activities for people with different means to carry out their studies. Only by combining the results of the research efforts of workers from a wide geographical range, studying a wide range of topics
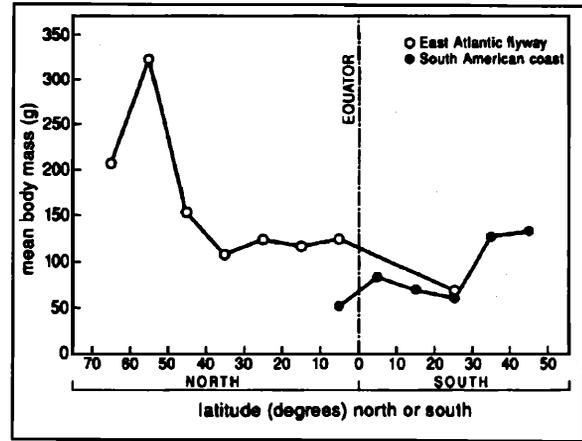
and a large number of species, can the conceptual richness of shorebird biology be harvested.

If, as shorebird ecologists, we are to advise governments and conservation bodies about the function and critical importance of the wetlands under their responsibility, we need to know much more than the numbers and species composition of shorebirds frequenting these areas. We need to know how and why a species uses a site and whether there are alternatives. Studies on the energetics of shorebirds, whether focusing on the intake, the expenditure or the storage part of the balance sheet, are (because of their relative conceptual simplicity) likely to contribute importantly to our understanding of the limitations on the distribution and sizes of shorebird populations. Many more empirical studies, whether on a small or a large scale, and the appropriate integration of their results (*e.g.* in thematic workshops) are urgently called for.

Acknowledgements

Table 1. Summary of the possible research activities for students of shorebird biology with different levels of research time and technical support.

Time	Technical facilities	Distribution of shorebirds	Energy intake	Energy expenditure
Short	Limited	- Point counts - Catching (weights, measurements, moult)	- Diet study (visual observations, pellets, droppings) - Use of feeding habitats - Harvestable biomass (benthic sampling of selected species)	- Activity budgets - Microhabitat selection during feeding and roosting
Long	Limited	- Counts (seasonal occurrence) - Catching (seasonal mass changes, biometry, moult)	- Food choice re season and weather - Harvestable biomass re season in a range of species - Measurement of intake rates	- Activity budgets re season and weather - Seasonal changes in the use of microhabitats
Long	Large	- Radio-tracking (tidal and seasonal movements of individual shorebirds)	- Experiments to measure functional response curves of different prey - Field experiments on causation of variation in prey abundance and harvestability	- Respirometry to measure BMR, cost thermo-regulation and cost of activity - Effects of weather and microhabitat on thermo-static costs

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