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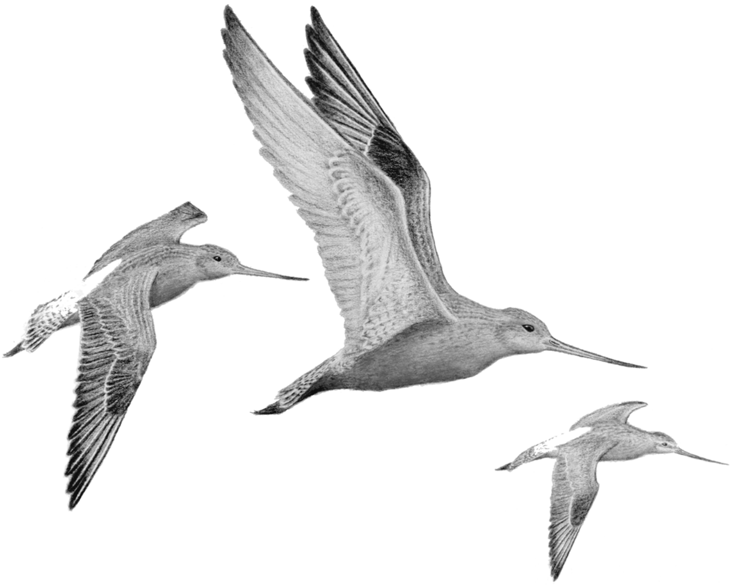
Born to fly – Migratory strategies and stopover ecology in the European Wadden Sea of a long-distance migrant, the Bar-tailed Godwit (*Limosa lapponica*)



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Born to fly – Migratory strategies and stopover ecology in the European Wadden Sea of a long-distance migrant, the Bar-tailed Godwit (*Limosa lapponica*)

Contents:

Detailed contents:

1. Synopsis: Stopover ecology, interactions with soft sediment coastal systems and their influence on life history decisions in the Bar-tailed Godwit (*Limosa lapponica*)

Migration is a general phenomenon in the animal kingdom, and therefore occurring in almost any vertebrate family (e. g. Dingle 1996). The ultimate cause for this behaviour is the optimal use of shifting or patchy resources in space and time often driven by seasonality in the habitats (Alerstam 1990, Dingle 1996). However, migration is a costly activity in terms of resource use like energy, survival, and lost opportunities in the areas that are left behind. Therefore, animals have to trade-off the benefits of heading for new opportunities with moving away from a known place. Since birds form one of the pronounced examples of migratory animals (Berthold 2000), they inspired a large amount of studies concerning migration (Berthold 2000, Bairlein 2001).

Being migratory or the disposition to be migratory is most probably older than the class *Aves* itself (Berthold 1999). With this disposition it can take only a few generations until a population may turn from a sedentary to a migratory one and new migratory routes become genetically fixed (Berthold 1998). For an evolutionary stable strategy (Parker 1984) this might be an essential prerequisite since a flexible reaction is needed for survival in changing environments. Recent migration systems in the Palearctic have developed after the last ice age within only 10,000 – 15,000 years (Moreau 1954, Berthold 2000). However, we have to keep in mind that the landscapes on earth have always been changing naturally, sometimes with large fluctuations within a few thousand years and the present state is not the final outcome of a development but transitional (Küster 1999).

Although some migration routes still inherit their historical development (Berthold 2000), today's migration systems are the outcome of evolutionary processes in the history of each individual species. Arctic breeders have taken the chance to utilise large food resources for reproduction during the arctic summer, as well as to escape competition and predation in more southerly areas they most probably originate from (Safriel 1995, Meltofte 1996). To which extend the two processes competition and optimisation have formed recent migration patterns has not yet been solved (Greenberg 1986, Meltofte 1996). The optimal bird migration theory (Alerstam & Lindström 1990), which gives the opportunity to test for different migration strategies and associated predictions for the migratory behaviour of the birds, is based on the optimisation criterion. An intriguing system to study the evolution of migration, as well as the constraints migratory birds have to cope with in their life histories is the leap-frog migration system (Salmonsen 1955). In this system with two or more populations, a more northerly breeding population passes the range of a more southerly breeding population to winter south of wintering range of the latter (e. g. Salmonsen 1955, Boland 1990). Although competition in breeding areas, as well as wintering areas, has been proposed as one of the driving processes in the evolution of this system (Pienkowski et al. 1985), strong evidence exists that the final outcome is the result of optimised resource use within the ranges of either population (Alerstam & Högstedt 1980, 1985, Bell 1996, 1997).

Within the annual cycle birds have to take several life history decisions concerning migration (Ens et al. 1994). Resources allocated to one trait cannot be allocated to another like current reproduction vs. future reproduction (Stearns 1992). Therefore, decisions taken at one stage can influence life at another stage. If e. g. energy expenditure is high in one part of the annual cycle, this can result in a high mortality during another part (Daan et al. 1996). Migratory birds therefore have to judge the costs of migration in comparison to its benefits. Even more decisive is to find a migratory strategy, as well as stopover and wintering sites, which allow maximising reproductive output of the entire life (lifetime reproductive success, LRS) which is often taken as a measure for fitness (Daan & Tinbergen 1997). In case of studies outside the breeding season, it is often impossible to measure the consequences of different decisions on fitness. Instead, energy expenditure is taken as a currency which allows comparing costs and benefits of different strategies and their ecological implications (Ricklefs 1996).

Depending on the migratory strategy (Piersma 1987a, Alerstam & Lindström 1990, Alerstam & Hedenström 1998), birds have different demands concerning a stopover site. In any case, it must offer the opportunity to build up sufficient fuel stores in time for a successful migration and settlement in the target area. In capital breeders like geese, conditions during spring stopover can influence breeding success (Drent & Daan 1980, Ebbinge & Spaans 1995). Even in arctic breeding waders, which might be income breeders and therefore seem to be independent from energy stores accumulated during stopover for egg laying (Klaassen et al. 2001), conditions in a stopover site might still be crucial for the initiation of breeding or the founding of a breeding territory (Székely 2002). In addition to the accumulation of body reserves, birds underlie a time constraint during spring migration, since individual timing of arrival in the breeding area in relation to food resources and competitors can decide whether a successful breeding is possible or not (Kokko 1999, Forstmeier 2002). Struggling for an optimal starting position for breeding is one of the possibilities animals have to increase their LRS. This race is important in the light of the fact that in some avian species only 3 – 9 % of the fledglings in one generation produce 50 % of the young of the next generation (Newton 1995).

From general to special: The case of the Bar-tailed Godwit

The Bar-tailed Godwit is a highly dimorphic wader species (Glutz et al. 1986, Cramp & Simmons 1983, Prokosch 1988, Engelmoer & Roselaar 1998, Scheiffarth 2001a) belonging to the family of the Scolopacidae. Outside the breeding season this species is restricted to coastal soft sediment habitats, where they feed mainly on polychaetes and small molluscs (Scheiffarth 2001b). The breeding area ranges form northern Norway eastwards to Alaska with five distinct, spatially separated populations. Engelmoer & Roselaar (1998) have proposed the subspecies status for each of these morphometrically differing populations which has, however, become a matter of debate and is not generally accepted for all populations (Tomkovich & Serra 1999). Birds breeding in eastern Siberia and Alaska belonging to the subspecies *L. l. baueri* and *L. l. menzbieri* winter from South-East Asia to Australasia and Western Polynesia (Cramp & Simmons 1983). Two subspecies occur regularly in the Western Palaearctic, namely *L. l. lapponica* and *L. l. taymyrensis* which form a leap-frog migration system (Drent & Piersma 1990). According to their ranges, if distinguished on a population level, birds breeding from Fennoscandia to the Kanin peninsula and wintering in Europe around the North and the Irish Sea are called the European population or the nominate form *L. l. lapponica*. Birds breeding from the Yamal peninsula to the delta of the Anabar river and wintering in West Africa with concentrations on the Banc d'Arguin, Mauretania and in Guinea Bissau are named the Afro-Siberian population or the subspecies *L. l. taymyrensis*. Both use the European Wadden Sea as a stopover site on their annual migrations (Fig. 1.1).

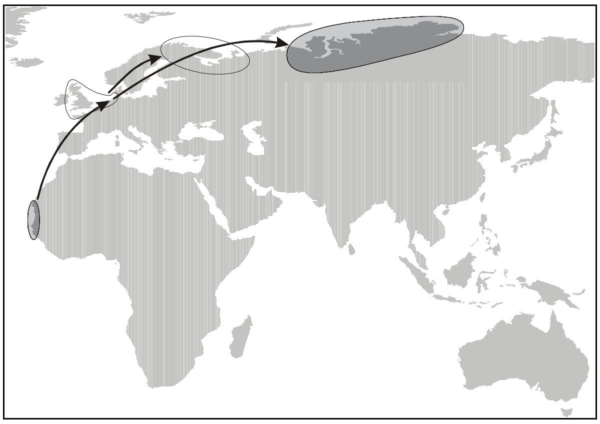


Fig. 1.1: Wintering and breeding areas of Bar-tailed Godwits migrating through the Wadden Sea. Areas used by the Afro-Siberian population are grey shaded, areas used by the European population are not filled.

The annual cycles of the two populations occurring regularly in the European Wadden Sea differ markedly, resulting in distinct constraints influencing the life history of the birds. Individuals belonging to the European population migrate 1,500 km between their breeding and wintering grounds which is a short distance as compared to birds of the Afro-Siberian population with travelling distances of 8,000 – 10,000 km each season. As European birds have a more southerly breeding distribution, they start breeding earlier than Afro-Siberian birds resulting in an earlier stopover in the Wadden Sea in spring (Prokosch 1988, Scheiffarth et al. 2002). Since these birds winter in Europe, they face a high energy turn-over due to high thermostatic costs together with low prey availability and the risk of sea ice, covering the feeding areas (Ch. 6, Scheiffarth & Nehls 1998). Additionally, when wintering in narrow British estuaries they might face a high risk of being predated, as was shown for other wader species (Cresswell & Whitfield 1994, Cresswell 1996, Hilton et al. 1999). On the total annual energy budget, energy expenditure during winter takes a portion 55 % whereas only 22 % are spent on migration (Drent & Piersma 1990). The high wintering costs are traded off against short migration distances and the advantage of wintering as close to the breeding areas as possible, with the opportunity to migrate in reaction to the onset of spring (Alerstam & Högstedt 1980). Even within the European population birds underlie this trade-off, as they have to choose between overwintering cold but close to the breeding areas in the northern Wadden Sea or wintering under comparatively mild conditions in Britain (Ch. 6). Wintering close to the breeding area might also give the advantage of being earlier at a spring stopover site with the opportunity to spend less energy to settle in this site and devote more energy already in preparations for breeding. In all, since these birds perform an energy minimised migration (Scheiffarth et al. 2002), there must exist vital costs connected with spending too much energy on migration. These costs reduce fitness either via elevating mortality or via reducing the reproductive output.

In Afro-Siberian birds migration and all connected activities take 48 % of the annual energy budget whereas wintering in Africa demands only 21 % (Drent & Piersma 1990). In addition to the large share of migration in the energy budget, also in the annual time budget a high proportion is devoted to migration. Since these birds perform large movements over continents, have a short breeding season, and perform a time minimised migration (Scheiffarth et al. 2002), they have a rather fixed time schedule. This fixed schedule bears the risk of adverse weather and breeding conditions upon arrival in the arctic breeding areas. As these birds perform a time minimised migration, their body condition upon arrival in the breeding areas is dependent on the opportunities in the stopover areas (Lindström 1995, Ebbinge & Spaans 1995). On the other hand, in comparison to the European population, these birds encounter more stable and therefore predictable environmental conditions in the wintering quarters (Wolff 1991b), as well as at times when they stay in the Wadden Sea for stopover (Zwarts & Wanink 1993). Nevertheless, costs must exist for arriving late in the breeding areas, reducing fitness of the birds (Ens et al. 1994, Forstmeier 2002).

Aims of the study

Bar-tailed Godwits occur in large numbers and with large seasonal fluctuations in the European Wadden Sea (Meltofte et al. 1994). They use the area as a stopover and wintering site and form a good example of how arctic breeding waders use and depend on the Wadden Sea ecosystem. In a place visited by the European, as well as the Afro-Siberian population, interactions between Bar-tailed Godwits and the Wadden Sea ecosystem were investigated. Since long-distance migrants depending on a small number of stopover sites are the most vulnerable species to changes in their environment, detailed understanding of their biology is essential for the interpretation of fluctuations in numbers and to decide whether they are under human threat or not. This thesis concentrates on the most important stepping stone for most palearctic breeding waders on the migration between wintering and breeding areas (e.g. Exo 1994), taking the Bar-tailed Godwit as an example. By means of consumption estimates and a detailed diet analysis, the position of the species in the Wadden Sea ecosystem is analysed. Together with an estimate of maintenance metabolism, choices and constraints of Bar-tailed Godwits using the Wadden Sea as a stopover and wintering site are determined. This approach allows to judge the role the Wadden Sea plays in the annual, as well as life cycle of Bar-tailed Godwits. Specific questions and hypotheses addressed in this thesis are:

- If the Wadden Sea is an important site for migratory and overwintering birds with enormous numbers visiting the area, do they have a large impact on the benthic system? Which share do they take in the energy flow and which role do they play in the structure of the Wadden Sea ecosystem? What determines the level of consumption by birds in intertidal soft sediment systems?
- For a study on choices and constraints of migratory birds in a stopover site, their migratory routes, wintering areas, time of residency in the stopover area have to be known. For the Bar-tailed Godwit these parameters were obtained for the population in the study area.
- Sound knowledge of food composition is essential for the understanding of foraging ecology and energy flow in ecosystems. Since Bar-tailed Godwits are highly dimorphic, differences in their biology may also be reflected in their foraging ecology, resulting in differences in the diet. However, for birds feeding mainly on polychaetes, as Bar-tailed Godwits do, it is difficult to determine diet composition by visual observations or indirect methods alone. Therefore, a new approach had to be developed to combine faeces analysis with visual observations.
- The European Bar-tailed Godwit population uses the northern Wadden Sea as a stopover and a wintering site. For how long these birds stay in the northern Wadden Sea and whether they move on to another place for wintering depends to a large extent on the energetic balance they can achieve between prey intake and energy expenditure. In particular, energetic

costs for thermoregulation could determine winter distribution. The hypothesis is that these birds have to trade off a high energy expenditure in the northern Wadden Sea combined with a low energy intake against costs of moving away from a wintering site close to the breeding area.

- During spring migration two populations of Bar-tailed Godwits stopover in the northern Wadden Sea. Owing to different migration distances they show marked differences in body mass increase rates. Why do these two populations differ in their stopover ecology in the Wadden Sea? Do they follow different migratory strategies and which are the constraints acting on them during stopover?
- Migratory movements are a trade-off between wintering as close to the breeding area, energy expenditure and energy intake. Birds wintering closer to the breeding area have higher thermostatic costs and a higher energy turn-over. These birds should have a higher mortality than birds experiencing a lower energy turnover. If these birds have the same lifetime reproductive success as birds with a lower energy turn-over, they must produce more fertile young per season than the former birds.

Consumption of benthic fauna by carnivorous birds in the Wadden Sea

On average, birds are known to take only a small fraction of 10 – 25 % of the total benthic secondary production in temperate intertidal ecosystems (Hockey et al. 1992, Meire et al. 1994, Dittmann & Scheiffarth in press). For the Wadden Sea, mean consumption by carnivorous birds on intertidal flats was estimated to amount 8.7 g AFDM m^{-2} $year^{-1}$ (Scheiffarth & Nehls 1997). Despite different climatic conditions along the geographic area covered by the Wadden Sea (Eisma 1980), this average value should be similar all over the system due to differences in the birds communities. However, large differences exist between and within subareas since birds are not homogeneously distributed over tidal flats. Size of an intertidal area seems to play a strong role in determining the level of consumption by birds as the comparison of the Königshafen bay with the larger area of the Sylt-Rømø Wadden Sea has shown (Scheiffarth & Nehls 1997). Here, as well as on a larger scale, like Eastern England (Prater 1981) or the East Atlantic Seaboard (Hockey et al. 1992), it appears that smaller areas face higher bird densities than larger ones. This effect is not caused by a higher secondary biomass or production of these smaller areas but by the behaviour of birds to prefer foraging areas in the vicinity of roosts (Swennen 1984, Scheiffarth et al. 1996, Scheiffarth 1998) and to forage along the moving tideline for most time of the year (Evans 1979, Nehls & Tiedemann 1993) which is elongated in small and structured areas (Evans & Dugan 1984).

If we compare consumption estimates between marine ecosystems, it appears that seasonal and annual fluctuations in prey abundance probably have greater impacts on total consumption by birds than size of an area. The seasonal pattern of prey abundance is important as it leads to a desynchronization between production and consumption by birds on temperate mudflats north of the equator. However, seasonal changes although producing a distinct pattern, may be overruled by year-to-year variability. Winter mortality reduces the autumn biomass as a result from predation or from highly variable physical factors. In species as Cockles (*Cerastoderma edule*), Mussels (*Mytilus edulis*), and some polychaetes extreme annual fluctuations due to high mortality from stochastic events like storms or hard winters occur synchronized over large areas within the Wadden Sea (Beukema et al. 1993). In contrast to the Wadden Sea, a much higher proportion of the mean biomass (82.7%) as well as production (42.6%) are consumed by birds on the Banc d'Arguin, Mauritania (Wolff & Smit 1990). One major reason for this difference of temperate vs. tropical estuaries may be the stability with low annual variability and therefore long-term predictability of food resources on tropical mudflats (Wolff 1991b). Since shorebirds are long-living animals, populations seem to rely on the mean long-term minimum prey availability and population sizes cannot follow short-term changes as they occur in the Wadden Sea.

The seasonal patterns of consumption and production are not synchronized in the Wadden Sea. Furthermore, only a part of the biomass is harvestable for birds and underlies large year-to-year fluctuations (Beukema et al. 1993, Zwarts & Wanink 1993). Therefore, in most years neither total annual production, nor the actual standing stock can be fully exploited. Although the seasonal pattern of consumption as well as species composition differs between different parts of the Wadden Sea, total consumption is in the same order of magnitude.

Whether or not bird numbers are limited by food resources in the Wadden Sea must be investigated for every species individually, since they have a different sensitivity to fluctuating food resources (Beukema et al. 1993). Undoubtedly, such areas like the Königshafen are closer to the carrying capacity than the entire Wadden Sea, what makes them sensitive to changes in habitat structure.

Although birds consume only a small fraction of the annual secondary production in temperate soft sediment systems and, furthermore, due to behavioural and morphological constraints can exploit only a small fraction of the available biomass (Piersma 1987b, Zwarts & Wanink 1993), this may not lead to the conclusion that birds or top predators in general do not influence the structure of the ecosystem. In general, we look only at mean consumption or carbon flow, however results can differ if specific interactions between certain species are concerned with much higher predation rates than average (Petersen & Exo 1999). Furthermore, predation can structure prey populations in terms of distribution or age composition (Wilson 1991, Matthews et al. 1992), can influence behaviour of prey (e.g. Stibor & Lampert 2000), or influence life history of prey organisms and form evolutionary constraints (e.g. Zwarts & Wanink 1991, de Goeij 2001)

Numbers, distribution and migratory pathways of Bar-tailed Godwits in the Sylt-Rømø Wadden Sea

Bar-tailed Godwits from the Afro-Siberian, as well as the European population occurred in the Sylt-Rømø Wadden Sea but used different high-water roosting and consequently different feeding areas (Scheiffarth 2001a). Two groups of roosting areas emerged: the mainland coast, where mostly birds from the Afro-Siberian population stayed and the islands where mostly birds from the European population stopped over. The Königshafen, which was the main study site, was visited by birds from the European population, which was confirmed by morphometric, as well as ringing data. Whereas the time minimising Afro-Siberian birds (Scheiffarth et al. 2002) stayed only for one month each in spring and autumn in the northern Wadden Sea, birds from the energy minimising European population (Scheiffarth et al. 2002) stayed for 30 – 40 days in spring. Between years, adult birds turned out to be highly site-faithful in the choice of the spring stopover site. During that time they moulted from winter into breeding plumage. In autumn a much higher turnover of birds was observed. Additionally, fewer individuals visited their spring stopover site on their way to the wintering quarters than during their return migration.

The migration pattern of Afro-Siberian Bar-tailed Godwits is rather straight forward and principally well understood with mainly two large jumps from West-Africa to the European Wadden Sea and from there to the Siberian breeding areas (Piersma & Jukema 1990, Piersma & van de Sant 1992, Green et al. 2002). As the northern Wadden Sea functions as a stopover, as well as wintering site for European Bar-tailed Godwits, their migration pattern is more diverse. These birds winter around the North Sea and gather in the northern Wadden Sea before departure to their breeding areas. In autumn they either fly either directly to their wintering quarters (Atkinson 1996), stop over in the northern Wadden Sea for a short time before they move on to more westerly areas or they stay as long as possible in the northern Wadden Sea before they move to milder areas as a consequence of increasing thermostatic costs or decreasing prey availability (Scheiffarth & Nehls 1998).

In a sexual dimorphic species as the Bar-tailed Godwit (Prokosch 1988, Engelmoer & Roselaar 1998, Scheiffarth 2001a) it is obvious that different constraints act on the sexes. As a consequence, a differential migration pattern (Ketterson & Nolan 1983) emerged for male and female European Bar-tailed Godwits. Due to lower thermostatic costs for the larger females as compared to males (Ch. 6, Scheiffarth 1996), they can afford to winter in colder climates closer to the spring stopover sites or breeding areas than males. As in this population an equal sex ratio has been observed, in winter an excess of males in British estuaries and an excess of females in the northern Wadden Sea supports this picture of differential migration.

Seasonality and differences in the diet of Bar-tailed Godwits in the Wadden Sea as a consequence of sexual dimorphism

Determining diet composition of birds foraging on tidal flats implies several uncertainties depending on the method applied (Goss-Custard 1973). A new approach combining direct (visual observation) and indirect (faeces analysis) methods in determining diet composition revealed seasonal, as well as sex related differences in the diet of the Bar-tailed Godwit (Scheiffarth 2001b). Some 94 % of the diet of Bar-tailed Godwits at the northern tip of the Wadden Sea island of Sylt consisted of polychaetes with some seasonal variation, but the proportion of polychaetes in the diet never dropped below 85 %. Furthermore, the apparent difference between males and females was based mainly on the choice of large polychaete species like *Arenicola marina* and *Lanice conchilega* by the larger sex, the female, and the bivalve *Macoma balthica* by males as the smaller sex in spring. The high proportion of polychaetes in the diet of Bar-tailed Godwits is in line with other studies (Scheiffarth 2001b).

Major determinants of prey choice are prey availability and harvestability (Zwarts & Wanink 1993). Therefore, seasonal changes in prey choice should reflect a seasonal pattern of prey availability. This parameter is in part related to surface activity of the invertebrate infauna which, in turn, is related to sediment temperature (Pienkowski 1983, Evans 1987). As the burrows of many polychaete species of the size classes chosen by Bar-tailed Godwits are deeper than bill length of the birds (Zwarts & Wanink 1993), they have to rely on visual cues or vertical upward migrations of the prey. Consequently, for females the seasonal pattern of *Arenicola marina* in the diet should reflect its availability (Zwarts & Wanink 1993). The low numbers of *Arenicola marina* eaten in winter is related to the fact that cast formation decreases rapidly below a temperature of 3°C (Smith 1975). Therefore, towards winter smaller prey species like *Scoloplos armiger*, *Nereis diversicolor*, and *Nephtys hombergii* are taken (s. a. Worrall 1984 for the same effect in Dunlins, *Calidris alpina*). In contrast to large polychaete species, *Macoma balthica* is always in the reach of the bill. However, this species is only preyed upon in considerable amounts by males in spring. At this time of the year profitable exploitation of this species is possible due to an upward movement in the sediment (Reading & McGrorty 1978, Zwarts & Wanink 1993) and a low proportion of shell mass in relation to biomass (Zwarts 1991, Scheiffarth unpubl.). A lower proportion of *Macoma balthica*, as well as higher proportion of large polychaete species in the diet of females as compared to males might be an effect of the longer bill of the females. For males, smaller prey is more profitable than for females, because for any prey item it takes less effort to move it up the shorter bill of a male. Therefore, male Bar-tailed Godwits should have a lower size acceptance threshold than females (Zwarts & Wanink 1993).

Males and females are not all year round equally separated in prey choice. Prey choice differs in late spring and summer but becomes similar towards winter. The differentiation in diet composition coincides with a separation in habitat choice. In late spring and summer females tend to feed at the waterline as all Bar-tailed Godwits do in winter, while males utilise exposed mudflats (own obs., C. Both, P. Edelaar & W. Renema pers. comm.). This effect can be caused either by a higher density of Bar-tailed Godwits at these times and the avoidance of competition between the sexes (C. Both, P. Edelaar & W. Renema pers. comm.). It may also be that when temperatures are high enough, another prey source may become available on the exposed mudflats, which can be exploited in a profitable way by the males. According to the diet composition of males this should be *Macoma balthica* and small polychaetes.

A further seasonal trend was the increase in size of *Nereis diversicolor* taken by Bar-tailed Godwits towards winter despite a deeper burrow depth of large individuals and a seasonal increase in burrow depth (Esselink & Zwarts 1989, Zwarts & Wanink 1993). This increase in prey size could be caused by several mechanisms. (a) In winter only the largest birds with longest bills stay in the northern Wadden Sea while smaller birds leave for milder wintering quarters. However, this hypothesis can not be confirmed as the results of a colour marking study show that birds resighted in winter are of the same size as the average of all birds caught and marked in spring (Scheiffarth 2001a). (b) If females take larger prey than males, the increase in the length of *Nereis diversicolor* found in faeces can be caused by a female bias in the population of overwintering Bar-tailed Godwits. Indeed, this female bias in winter was found (Scheiffarth 2001a) and may explain the observed pattern. (c) If Bar-tailed Godwits, and in particular females, switch from large, inaccessible prey species like *Arenicola marina* to smaller ones like *Nephtys diversicolor*, they compensate for the loss of the larger prey species with the choice of larger individuals of the smaller species. However, for the moment no final conclusion can be drawn and further investigations are necessary.

Energy minimised migration and expensive overwintering: the choice of the right wintering site

Choice of the right wintering site depends on the migratory strategy birds follow, as well as on several constraints acting on potential wintering sites. Major constraints are the food supply, energy demands for overwintering, and the predation risk. Wintering as far north as sustainable has for arctic breeding birds the advantage that they can stay as close to the breeding area as possible (Alerstam & Högstedt 1980). Yet, wintering densities of waders in the northern part of the Wadden Sea are lower than elsewhere in the wintering range for many wader species (Zwarts 1988, Meltofte et al. 1994). Zwarts & Wanink (1993) formulated several food related hypotheses why so few waders winter in the northern Wadden Sea. The most likely explanations were the low surface activity of many invertebrates at low temperatures (e.g. Smith 1975, Pienkowski 1983) resulting in a lower detection rate for visually hunting birds and an earlier seasonal decline in flesh content of some invertebrates as compared to other places for wintering waders in NW-Europe. However, suitability of a habitat is characterised by the energetic balance of intake and expenditure over a certain time frame. In particular for birds living in open landscapes, thermoregulatory costs can form a prominent part of the energy budget and can even force birds to leave an area since energetic demands cannot be sustained by the metabolic machinery (Ch. 6, Wiersma et al. 1993, Wiersma & Piersma 1994). From an energetic point of view, for Bar-tailed Godwits of the European population winter seems to be the most demanding time of the year where energy consumption peaks (Ch. 6). Their metabolic machinery is well adapted to these demands and under average winter conditions in the northern part of the Wadden Sea they are able to balance their energy budget. Energy intake and maintenance metabolism are closely correlated, indicating that thermostatic costs determine the energy budget. In contrast to the winter situation, during preparation for migration to the breeding grounds they do not utilise their potential for a high sustainable metabolic rate as the energy turn-over at this time of year stays well below their metabolic ceiling, resulting in a slow body mass increase. The high energy expenditure during winter might be compensated for by an energy minimised migration to the breeding grounds (Ch. 6, Scheiffarth et al. 2002).

Autumn migration away from the northern Wadden Sea is most probably driven by an increase in thermostatic costs. When deciding for a wintering site, Bar-tailed Godwits have to choose between different constraints acting at these sites (Fig. 1.2). Staying in the northern Wadden Sea gives the opportunity to winter as close to the breeding area as possible without any cost of movement, at low wader densities resulting in low competition, and a relatively low predation risk. Costs are a high maintenance metabolism and a low intake rate resulting in long foraging times. Furthermore, they might run into the danger of a cold spell, forcing them to move further south-west incurring extra costs they intended to avoid. When migrating to British estuaries, they can expect comparatively low thermostatic costs (Ch. 6) and a high intake rate (Smith 1975) at the expense of high wader densities and a high risk of predation (Cresswell & Whitfield 1994, Cresswell 1996, Hilton et al. 1999). Since males as the smaller sex have higher thermostatic costs than females, they leave to a greater extent the northern Wadden Sea than females (Scheiffarth 2001a).

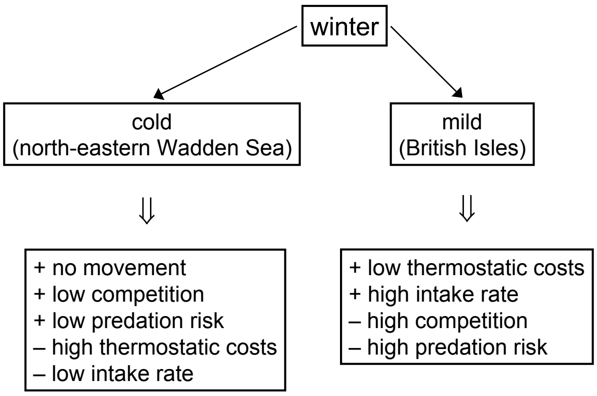


Fig. 1.2: Trade-offs for the choice of wintering sites.

In all, European Bar-tailed Godwits seem to trade-off thermostatic costs for wintering against cost of movement. The population as a whole has adapted the strategy of high wintering and low migration costs. Within the wintering range however, the birds have several choices with most birds moving to British estuaries for overwintering taking the advantage of low thermostatic costs and relatively high intake rates.

Energy minimised or time minimised spring migration?

Migration is a prominent part in the annual cycle of long distance migrants, since it can comprise up to 50 % of the annual energy budget (Drent & Piersma 1990). The majority of time and energy during the migration period is spend on the ground for the preparation of the flight (Hedenström & Alerstam 1997). Taking such a big share in the bird's life, migration and migratory strategies must be shaped by natural selection, since fitness costs can be connected with either arriving late or lean in the breeding area (Piersma 1987a, Ens et al. 1994, McNamara et al. 1998). The optimal migration theory (Alerstam & Lindström 1990) gives us the opportunity to formulate hypotheses on which traits are optimized for a maximization of LRS. Under the assumption that birds optimize their migration by minimizing either time of transport, energy expenditure for migration, or predation risk, constraints acting on the migratory decisions can be identified. For each of these optimization criteria different fattening and stopover strategies are predicted (e.g. Lindström 1995).

The leap-frog migration system of the Bar-tailed Godwit offers a good opportunity to look for differences in life history parameters between the two populations occurring in the Wadden Sea. Since the Euro-

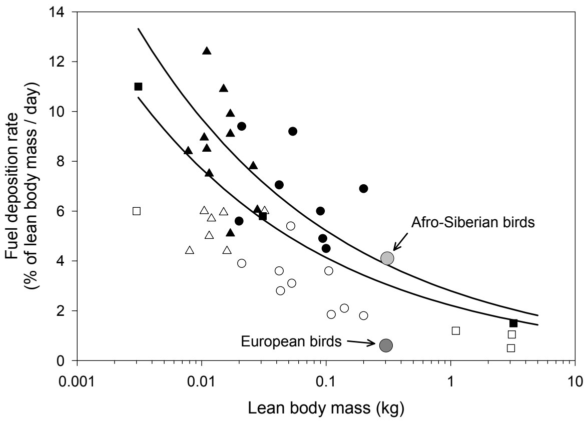


Fig. 1.3: Maximum fuel deposition rate (FDR) per day in relation to lean body mass for migrating birds. The upper line shows predicted FDR for non-passerines, the lower line for passerines. Realized FDR in the field are shown for passerines (triangles), non-passerines (squares), and waders (circles). Open symbols denote the highest population average found for a species and filled symbols show FDR for single individuals. FDR of the two Bar-tailed Godwit populations are marked separately. Modified after Lindström 1991.

pean population migrates much shorter distances than the Afro-Siberian population and further on devotes less time to migration (Drent & Piersma 1990), optimization criteria for birds of either population must differ. The most obvious indicator for different migration strategies are the large differences in body mass increase rate with European birds increasing in mass much below their theoretically achievable rate. In contrast, Afro-Siberian Bar-tailed Godwits increase in body mass close to the maximal predicted rate (Lindström 1991, Fig. 1.3). Energy intake rates in April/May did not differ between the two populations (1.5 kJ min^{-1} and 1.8 kJ min^{-1} for Siberian and European migrants, respectively) but total energy intake was higher for the Siberian migrants, since they spend 50 % of the day foraging vs. 30 % in the European birds. In contrast to European migrants, Afro-Siberian birds start to moult into breeding plumage already in their winter quarters. During their stopover in the Wadden Sea thermostatic costs are lower than at times when European birds are present. Thus, the higher energy demands of the Afro-Siberian birds seem to be fulfilled by a combination of physiological adaptations and a high working level. The low body mass increase in European Bar-tailed Godwits during spring migration is not a consequence of an insufficient access to food resources but an choice of an energy minimizing migratory strategy whereas Afro-Siberian birds choose for a time minimized strategy (Scheiffarth et al. 2002). As for these birds the cost of arriving late, or better at the wrong time (Forstmeier 2002), in the breeding area seems to form an evolutionary constraint, for European Bar-tailed Godwits a high energy expenditure during migration seems to result in a high fitness cost. Their annual energy turn-over is already higher than for Afro-Siberian birds due to high overwintering costs (Drent & Piersma 1990, Ch. 6).

Higher mortality in short distance migrants?

All living organisms have to compromise on how much energy is allocated to survival and how much to reproduction. Thus, by increasing current reproductive effort an individual decreases its survival and therefore its future reproductive chances (Begon & Mortimer 1986). If lifetime energy expenditure is limited to a certain level (Prinziger 1996), organisms have to decide when and how much energy should be devoted to which activities so that, within the limits the organism has, lifetime reproductive success is maximised. Under this assumption European Bar-tailed Godwits with a higher annual energy turn-over than Afro-Siberian Bar-tailed Godwits (Drent & Piersma 1990) should have a higher mortality. Although these birds try to balance high wintering costs by an energy minimized migration (Ch. 6), compensation seems not to be perfect. A similar case was indicated for two populations of Red Knot (*Calidris canutus*) where the temperate wintering population had a higher mortality than the tropical wintering population (Piersma 1994). Subsequently, if population sizes are stable, European Bar-tailed Godwits must have either a higher reproductive output or recruitment than Afro-Siberian birds to counterbalance the elevated mortality due to the high energetic expenses. Since a higher reproductive output is expected to put an extra cost on survival, the most likely process should be a higher recruitment of juveniles to the population (s. Boyd & Piersma 2001 for the importance of recruitment in a Red Knot population). A comparison of the breeding conditions and performance between these two populations should be an excellent test of the ideas on how migration strategies are connected to life history parameters.

Concluding remarks

Within one species two different migratory or even life history strategies could be observed. Even within these different strategies further subgroups like males and females appeared with differing constraints acting on them. Not only the differing physiological constraints between Afro-Siberian and European Bar-tailed Godwits interacted with the migratory strategy, but also within the populations these limits seem to influence the choice of the wintering site.

The role of the European Wadden Sea in the life cycle of Bar-tailed Godwits directly goes to the question of bottlenecks in the annual cycle of long-distance migrants. However, since organisms have to compromise on the differing environmental conditions they encounter during the annual cycle, they form a balanced construction which makes the search for a single bottleneck untraceable (Piersma 2002). Certainly, whether a stopover site or conditions encountered therein form a bottleneck or not depends on the migratory strategy followed. For time minimizing migrants like Afro-Siberian Bar-tailed Godwits which have to gain energy as efficiently as possible in the Wadden Sea, an undisturbed refuelling during spring migration is a prerequisite for a successful settlement in the breeding area several thousand kilometers away. For an energy minimizing migrant like European Bar-tailed Godwits refuelling rate or investment in refuelling might not influence breeding success in the next breeding season but can have a survival cost. Migrants might not go through a bottleneck in a stopover site but conditions encountered there might influence the ability to go through bottlenecks at other stages in the annual cycle.

2. Das Ökosystem Wattenmeer

Gregor Scheiffarth

Das Gebiet

Allgemeine Beschreibung

Das europäische Wattenmeer ist eine flache, durch die Gezeiten geprägte Küstenregion mit großen eulitoralen Wattflächen. Regelmäßig trocken fallende Watten sind weltweit verbreitet, jedoch ist das europäische Wattenmeer die größte zusammenhängende Wattenregion und repräsentiert 60 % aller Watten in Europa und Nordafrika (CWSS ohne Datum). Watten bilden sich als Übergangsbereich zwischen offener See und hochgelegenem Festlandsockel aus. Voraussetzungen sind ein allmählich abfallender Meeresboden, eine Zufuhr von Feinmaterial aus dem Meer und aus Flüssen, eine Barriere in Form von Inseln, Strandwällen oder Sandbänken zur Sicherung ruhiger Sedimentationsräume und ein flaches Hinterland (Veenstra 1976). Zusätzlich muss der Gezeiteneinfluss mit einem Tidenhub > 1 m den Seegangeinfluss überwiegen (Hayes 1979).

Geologisch ist das europäische Wattenmeer ein junges, nacheiszeitliches Gebiet mit einem Alter von 5.000 – 7.000 Jahren (Köster 1991). Größere Verlandungen sowie die Bildung der heutigen Marschen und Dünen fanden z.T. erst im Mittelalter statt (Ehlers 1994). Das Wattenmeer unterliegt seit mehreren Jahrhunderten menschlichen Einflüssen (Meier 1994, Wolff 1992). So ist die heutige Küstenlinie das Ergebnis des nacheiszeitlichen Meerespiegelanstieges, der Folge von Sturmfluten mit landseitigen Einbrüchen, Eindeichungen, Befestigungsmaßnahmen und Sandaufspülungen. Seit dem Mittelalter wurden ca. 10.000 km^2 der zum Wattenmeer gehörigen Habitate eingedeicht (Wolff 1991a).

Das europäische Wattenmeer erstreckt sich heute über eine Länge von 450 km entlang der Nordseeküste von Den Helder in den Niederlanden bis zur Halbinsel Skallingen in Dänemark (Abb. 2.1). Es weist im Mittel eine Breite von 10 km auf, kann an einigen Stellen aber bis zu 40 km breit sein. Begrenzt wird das Gebiet heute landseitig durch den Deich. Die seeseitige Begrenzung ist nicht eindeutig festgelegt; i.d.R. wird entweder die 10 m Tiefenlinie vor den Inseln oder - für das Wattenmeer im engeren Sinne - die Verbindungslinie zwischen den Inseln bzw. den äußeren Enden der Sandplaten genommen (Veenstra 1983). Insgesamt beträgt die Fläche des Wattenmeeres incl. der Inseln ca. 9.000 km^2.

Im Wattenmeer lassen sich mehrere Lebensräume unterscheiden. Hierzu gehören, neben den Inseln, das Supralitoral, das nur sporadisch bei hohen Wasserständen überflutet wird, das Eulitoral, als Bereich zwischen der mittleren Hoch- und Niedrigwasserlinie mit täglich zweimaliger Überflutung und das Sublitoral als der Bereich, der ständig mit Wasser bedeckt ist. Das Eulitoral, das mit einer Fläche von 4294 km^2 den größten Bereich einnimmt, besteht zu 75 % aus Sandwatt, 18 % aus Mischwatt und zu 7 % aus Schlickwatt, wobei regional starke Unterschiede auftreten (de Jong et al. 1993). Von der eulitoralen Wattfläche fallen 70 % für weniger als die Hälfte der Zeit trocken, während nur 5 % der Fläche für mehr als 2/3 der Zeit trocken fallen (de Jong et al. 1993). Mit jeder Tide strömen 15 km^3 Wasser aus der Nordsee in das Wattenmeer und verdoppeln damit das Wasservolumen in diesem Bereich (de Jong et al. 1993).

Entlang der Wattenmeerküste formen 23 Inseln mit Dünen und 14 hohe Sände ohne Dünen eine Barriere gegen die Nordsee (de Jong et al. 1993). Entsprechend ihrer Genese unterscheidet man 4 Inseltypen: Festlandreste, Barriereinseln, hochmobile Sandbänke (Ehlers 1994) und aufgrund von Sedimentationsprozessen in geschützten Bereichen aufgewachsene Halligen (Stock et al. 1996). Insbesondere das Nordfriesische Wattenmeer entwickelte sich, im Gegensatz zu anderen Wattenmeerbereichen, auf untergegangenen Marschen und Mooren im Wechselspiel zwischen Nutzung (Drainage, Salztorfabbau) und steigendem Meeresspiegel (Stock et al. 1996). Daher existieren dort die meisten Inseln mit Festlandresten.

Entsprechend dem ansteigenden Tidenhub Richtung innere Deutsche Bucht verändert sich die Morphologie der Watten. Im mesotidalen Bereich zwischen Den Helder und der Jade sowie zwischen Amrum und Skallingen findet sich ein Band von Barriereinseln mit dazugehörigen Rückseitenwatten, während der zentrale Bereich durch offene Wattflächen charakterisiert ist. Als dritter morphologischer Watttyp haben sich als Folge von Sturmflutereignissen große, geschützte Buchtenwatten entwickelt. Aufgrund von Eindeichun-

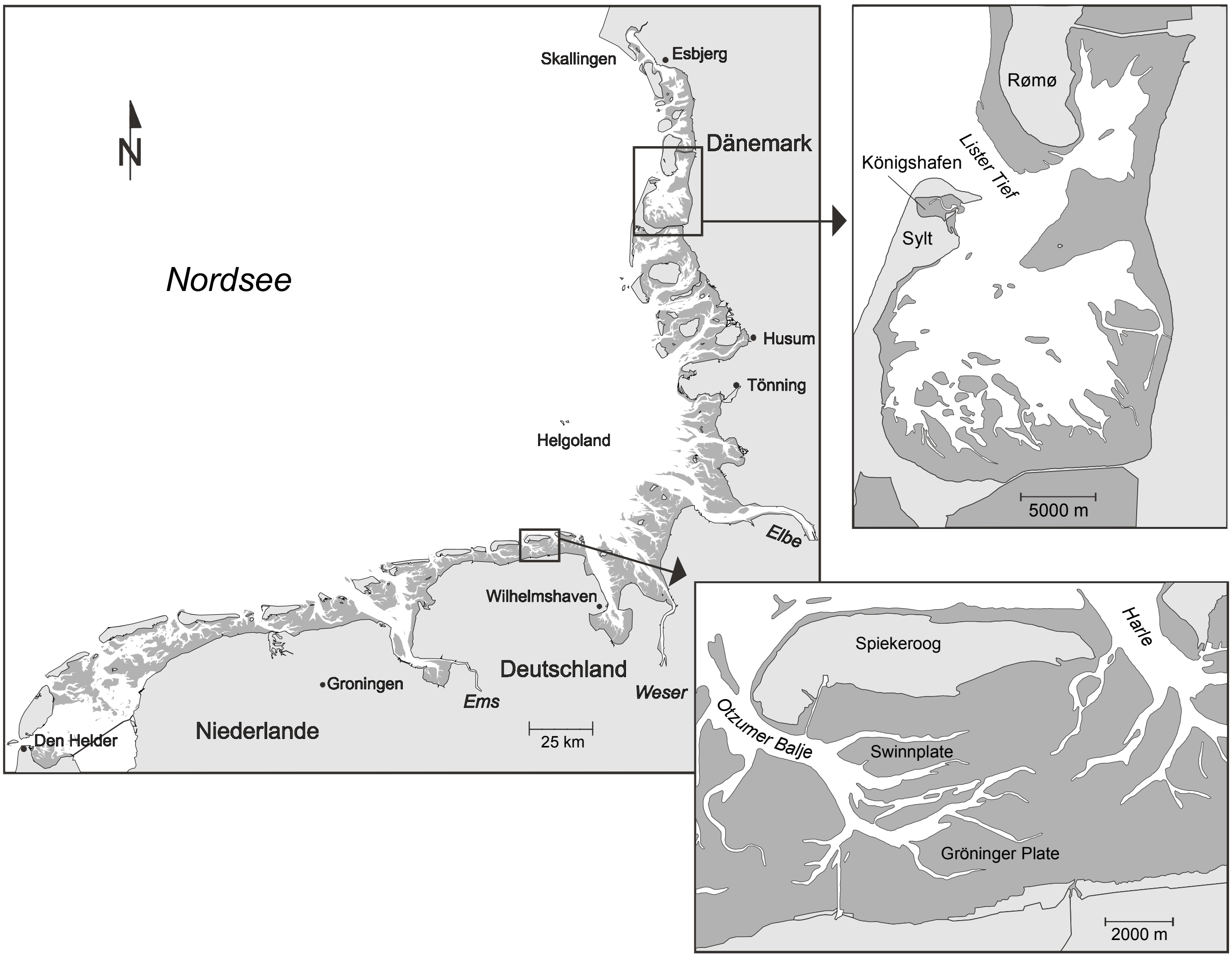


Abb. 2.1: Europäisches Wattenmmeer mit den Hauptuntersuchungsgebieten der Ökosystemforschung

gen seit dem 11. Jh. sind heute nur noch 4 große Buchten vorhanden: die Ho-Bucht, der Jadebusen, die Leybucht und der Dollard.

Die Wattenmeerregion ist durch ein atlantisches Klima geprägt, mit feuchten Sommern und relativ milden Wintern, in denen kurze Frostperioden auftreten können. Im Mittel schwanken die Temperaturen zwischen 17,1 °C im August und 1,8 °C im Februar (de Jong et al. 1993). Innerhalb des Gebietes gibt es einen West-Ost Gradienten, wobei die westlichen Teile ein ozeanisches Klima, die östlichen eher ein kontinentales Klima mit kälteren Wintern und stärkeren täglichen Temperaturschwankungen aufweisen (Eisma 1980). Die Wassertemperaturen im Wattenmeer unterliegen jahreszeitlichen Schwankungen zwischen 20 °C im Sommer und –1,5 °C im Winter. Die Temperaturschwankungen sind stärker ausgeprägt als in der offenen Nordsee. Während im Sommer die Wassertemperatur 3 °C über dem Nordseewasser liegt, ist die Wassertemperatur im Winter um 2 °C erniedrigt (Ehlers 1994). Daher beginnt die winterliche Eisbildung der Nordsee auch stets im Wattenmeer, wobei innerhalb des Gebietes die Eisbildung zuerst im nordöstlichen Teil beginnt. Leichte Vereisung der Wattflächen findet sich an einigen Stellen in jedem Winter, eine starke, lang anhaltende Vereisung kommt alle 8 - 10 Jahre vor (Strübing 1996).

Über die Flüsse fließen jährlich 60 km^3 Süßwasser in das Wattenmeer, wobei das Wassereinzugsgebiet mit einer Fläche von 230.859 km^2 bis in das österreichisch-tschechische Grenzgebiet hineinreicht (de Jong et al. 1993). Aufgrund des Süßwassereinstroms ist die Salinität des Wassers im Wattenmeer gegenüber der Nordsee (35 ‰) erniedrigt und unterliegt großen Schwankungen mit höchsten Werten im Oktober und niedrigsten Werten im März/April (Postma 1983). Die geringste Salinität wird im Bereich der Flussmündungen gemessen, wobei in der inneren Deutschen Bucht besonders niedrige Werte durch den Zufluss von Elbe und Weser erreicht werden. Auf den eulitoralen Wattflächen liegt die mittlere Salinität bei 30,7 – 32,5 ‰, die neben jahreszeitlichen auch große diurnale/tidale Schwankungen durch Verdunstung und Niederschlag aufweist (Postma 1983).

Naturräumliche Strukturen und Prozesse

Die naturräumliche Gliederung des Wattenmeeres hat sich im Laufe der Jahrhunderte aufgrund von menschlichen Eingriffen in den Verlauf der Küstenlinie verändert. Vor dem Beginn der systematischen Eindeichungen gab es eine große Vielfalt an Lebensräumen, von denen heute, insbesondere im landnahen Bereich, nur noch ein Ausschnitt vorhanden ist (z.B. Wolff 1992). Seeseits, vor den eigentlichen Watten, lag eine Reihe von Barriereinseln und hohen Sandplaten, auf denen z.T. Dünen aufgewachsen waren. Diese Inseln waren aufgrund größerer Tideprismen kleiner als heute (Flemming & Davis 1994). Es folgte der eigentliche Wattbereich mit eulitoralen Wattflächen, Prielen und tiefen Rinnen. In hoch gelegenen, strömungsberuhigten Bereichen muss es große Schlickwatten gegeben haben (Flemming & Nyandwi 1994). Beim allmählichen Übergang zum Land folgten im Supralitoral zunächst ausgedehnte Salzwiesen und -marschen, gefolgt von Brackwasser- und Süßwassermarschen sowie Mooren (Wolff 1993).

Seine Funktion als Übergangsbereich zwischen Land und Meer erfüllt das Wattenmeer auch heute noch. Jedoch ist durch den massiven Deichbau kein allmählicher Übergang mehr von Salzwasser- zu Süßwasserhabitaten vorhanden. Zwar beeinflusst das Hinterland nach wie vor durch Süßwasserzufuhr das Watt, Salzwasser kann aber nicht mehr in das Hinterland eindringen (Wolff 1991a).

Aufgrund der Eindeichungen gingen vor allem Salzwiesen und Brackwassermarschen verloren (Wolff 1991a). Heute umfasst das Wattenmeer nur noch die folgenden Lebensräume: unterhalb der Niedrigwasserlinie das Sublitoral, zwischen Niedrig- und Hochwasserlinie das Eulitoral und oberhalb der Hochwasserlinie die Salzwiesen, Strände, und Dünen. Während das tiefe Sublitoral noch durch die angrenzende Nordsee geprägt ist, beginnt sich der Charakter des Wattenmeeres als Übergangsbereich zwischen See und Land im flachen Sublitoral stärker auszuprägen. Hier unterliegen die Lebensbedingungen durch sporadisches Trockenfallen bei niedrigen Wasserständen (Springtiden und starke Ostwindlagen) stärkeren Schwankungen als im tiefen Sublitoral. Im Eulitoral herrschen die variabelsten Lebensbedingungen für die Organismen. Durch das zweimal tägliche Überfluten bzw. Trockenfallen sind die Organismen abwechselnd terrestrischen und marinen Bedingungen ausgesetzt. Zusätzlich sind in diesem Bereich die Schwankungen der abiotischen Parameter während der Niedrigwasserperiode sehr stark ausgeprägt. So können z.B. an einem heißen Sommertag um Niedrigwasser die Salinität und die Temperatur an der Sedimentoberfläche stark ansteigen. Bei auflaufendem Wasser finden dann eine rapide Abkühlung und eine Erniedrigung der Salinität auf das Niveau des Seewassers statt. Die meisten Organismen des Eulitorals, die sich an diese variablen Bedingungen angepasst haben, kommen auch im Sublitoral vor, jedoch haben einige Arten ihren Verbreitungsschwerpunkt im Eulitoral. Hierzu gehören *Arenicola marina*, benthische Diatomeen und viele Arten der Meiofauna.

Im Gegensatz zur offenen Nordsee wird durch die geringen Wasserstände im Wattenmeer ungefähr die Hälfte der Primärproduktion durch benthische Diatomeen geliefert (Asmus et al. 1998). Da sich im Wattenmeer aufgrund der starken Turbulenz keine stabile Schichtung ausprägt, besteht eine enge Kopplung zwischen Sediment und Wassersäule. Daher steht sowohl ein Teil der benthischen Primäproduktion durch Resuspension in der Wassersäule zur Verfügung, als auch ein Eintrag von Detritus und pelagischer Primärproduktion für das Benthos. Insgesamt ist das Wattenmeer durch den Eintrag von Feinmaterial aus den Flüssen und aus der Nordsee ein Depositions- und Remineralisationsraum.

So wie der Übergang vom Sub- zum Eulitoral gestaltet sich auch der Übergang vom Eu- zum Supralitoral fließend. Im Übergangsbereich zur Salzwiese finden sich erstmals Pflanzen- und Tierarten terrestrischen Ursprungs, wie der Queller (*Salicornia sp.*) und Käfer der Gattung *Bledius*, die noch kurze, regelmäßige Überflutungen mit Salzwasser vertragen, bzw. im Fall des Quellers zur Ausbreitung benötigen. Mit ansteigendem Höhenniveau bis zum Deichfuß findet man entsprechend der unterschiedlichen Überflutungshäufigkeit verschiedene Salzwiesenzonen. Gerade im Winter bei Sturmfluten zeigt sich die Funktion der Salzwiese als Sedimentationsraum für Feinmaterial.

Ohne die Salzwiesen besiedeln über 2.100 Tier- und Pflanzenarten das Wattenmeer (Reise et al. 1998). Für viele, insbesondere wandernde Tierarten ist das Wattenmeer von zentraler Bedeutung. So fungiert das Wattenmeer als ‚Kinderstube‘ für viele Fischarten der Nordsee. Für viele Zugvogelarten ist das Wattenmeer ein essentieller Trittstein auf ihren mehrere tausend Kilometer langen Wanderungen zwischen arktischen Brutgebieten und tropischen Überwinterungsgebieten.

Schutzstatus des Wattenmeeres

Der Schutz einzelner Teilbereiche des Wattenmeeres im Rahmen von Vogel- und Naturschutzgebieten hat eine bis an die Anfänge des 20. Jh. zurückreichende

Tradition. Heute ist das Wattenmeer durch nationale Gesetze und internationale Abkommen großflächig geschützt (CWSS ohne Datum). In den Niederlanden trat 1980 das nationale Planungsdokument Wattenmeer (Planologische Kernbelissing Waddenzee, Pkb) in Kraft, das als Planungsgrundlage für alle Aktivitäten im Wattenmeer gilt. Der in diesem Plan ausgewiesene Bereich ist zu 90 % auch gleichzeitig Naturschutzgebiet. In Dänemark wurde das Wattenmeer 1982 als Natur- und Wildreservat ausgewiesen, in dem alle Aktivitäten, die die natürliche Umgebung zerstören oder permanent verändern verboten sind. Der deutsche Teil des Wattenmeeres wurde 1985, 1986 und 1990 durch die für den jeweiligen Bereich zuständigen Bundesländer (Schleswig-Holstein, Niedersachsen, Hamburg) als Nationalpark ausgewiesen. In den Nationalparks sollen die natürlichen Prozesse soweit wie möglich ohne menschlichen Einfluss ablaufen können.

Als internationale Abkommen gelten für das Wattenmeer die Ramsar Konvention zum Schutz von Feuchtgebieten, die EU-Vogelschutzrichtlinie und die EU Flora-Fauna-Habitat Richtlinie. Darüber hinaus wird zwischen den drei Anrainerstaaten ein Schutz des Wattenmeeres auf trilateraler Ebene angestrebt. Seit 1978 werden dazu auf regelmäßig stattfindenden Regierungskonferenzen gemeinsame Maßnahmen zum Schutz des Wattenmeeres beschlossen. Über das 1987 gegründete „Gemeinsame Wattenmeersekretariat“ (CWSS) werden die trilateral beschlossenen Maßnahmen koordiniert.

Untersuchungsgebiete der Ökosystemforschung Wattenmeer

Während in Schleswig-Holstein der angewandte Teil der Ökosystemforschung Wattenmeer (Oeschger 1999) das gesamte schleswig-holsteinische Wattenmeer großflächig bearbeitete, konzentrierte sich der grundlagenorientierte Teil (SWAP) auf das Sylt-Rømø Wattenmeer. In Niedersachsen wurde sowohl im angewandten, als auch im grundlagenorientierten Teil (ELAWAT) hauptsächlich im Rückseitenwatt der Insel Spiekeroog gearbeitet. Die beiden Teilgebiete, in denen sich die Forschung konzentrierte, werden im Weiteren vorgestellt (Tab. 2.1).

Das Sylt-Rømø Wattenmeer

Das Sylt-Rømø Wattenmeer (Lister Tidebecken) liegt im nördlichen Teil des Wattenmeeres im deutsch-dänischen Grenzgebiet. Als Besonderheit gilt seine Ausprägung als Lagune durch den Bau von Verbindungsdämmen auf den ehemaligen Wattwasserscheiden zwischen dem Festland und den Inseln Sylt bzw. Rømø. Daher findet ein Austausch mit der Nordsee ausschließlich über das Lister Tief statt. Mit 401 km^2 gehört es zu den größten Tidebecken des Wattenmeeres und gleicht den anderen großen Tidebecken (z.B. Vlie) im Anteil an eulitoraler Wattflächen an der Gesamtfläche von ca. 40 %. Dieser Anteil ist wesentlich geringer als in den benachbarten nordfriesischen und dänischen Tidebecken, wo er bei ca. 70 % liegt (Reise & Riethmüller 1998).

Tab. 2.1: Kenngrößen der Hauptforschungsräume der Ökosystemforschung Wattenmeer (Gätje & Reise 1998, Dittmann 1999).

	Sylt-Rømø Wattenmeer	Spiekerooger Rückseitenwatt (Tidebecken Otzumer Balje)
Tidenhub	2 m	2,8 m
Tideprisma	560 Mio m^3	131 Mio m^3
Seegatquerschnitt	44603 m^2	11400 m^2
Gesamtfläche (unterhalb MThwL)	401,4 km^2	74,3 km^2
Eulitoralfläche, davon	159 km^2 (40 %)	60,2 km^2 (81 %)
Sandwatt	114,7 km^2 (72 %)	[36,5 km^2 (60 %)]*
Mischwatt	39 km^2 (25 %)	[22 km^2 (36 %)]*
Schlickwatt	5,3 km^2 (3 %)	[2,5 km^2 (4 %)]*
Klima (Jahresmittel)		
Windgeschwindigkeit	7 m s^{-1}	6 m s^{-1}
Lufttemperatur	8,4 °C	9,3 °C
Wassertemperatur	9 °C	10,6 °C

* Die Flächenangaben der Wattsedimente beziehen sich nicht auf das Tidebecken der Otzumer Balje, sondern auf das Rückseitenwatt der Insel Spiekeroog zwischen Otzumer Balje und Harle (de Jong et al. 1993).

Das Spiekerooger Rückseitenwatt

Das Spiekerooger Rückseitenwatt liegt im östlichen Teil des Barriereinselsystems der südlichen Nordsee, annähernd zentral hinter der Reihe der ostfriesischen Inseln. Es wurde bei der Auswahl als Hauptforschungsgebiet als Idealtypus eines Rückseitenwattes angesehen (Dittmann et al. 1997). Über die Otzumer Balje zwischen den Inseln Langeoog und Spiekeroog steht es mit der offenen Nordsee in Verbindung. Begrenzt wird das Tideeinzugsgebiet der Otzumer Balje durch die Wattwasserscheiden ‚Langeooger Plate' im Westen und ‚Hohe Bank' im Osten. 70 % des Wassers im Einzugsgebiet gelangen über die Otzumer Balje, die restlichen Wassermassen über die Wattwasserscheiden in das Gebiet (Niesel 1999). Der Eulitoralanteil von 81 % liegt in der gleichen Größenordnung wie bei anderen ostfriesischen Tidebecken (Hild 1999).

3. Consumption of benthic fauna by carnivorous birds in the Wadden Sea

Gregor Scheiffarth & Georg Nehls

Abstract

Consumption by carnivorous birds was estimated for the Sylt-Rømø tidal inlet in the northern part of the Wadden Sea, as well as the subarea Königshafen, a small, tidal bay. The bird community of the Sylt-Rømø Wadden Sea was dominated by Dunlin (35 % of all birds counted), Eider (9 %), Oystercatcher (8 %), Knot (8 %), and Shelduck (7 %). The community in the Königshafen was dominated by Eider (20 %), Knot (17 %), Bar-tailed Godwit (17 %), Dunlin (13 %), and Oystercatcher (8 %). Annual consumption was estimated at 3.4 g AFDW * m^{-2} * $year^{-1}$ for the entire Sylt-Rømø Wadden Sea and 19.2 g AFDW m^{-2} * $year^{-1}$ for the Königshafen. Restricting the calculations to the intertidal area resulted in a consumption of 8.7 g AFDW * m^{-2} * $year^{-1}$ for the Sylt-Rømø Wadden Sea and 17.6 g AFDW m^{-2} * $year^{-1}$ for the Königshafen. In the two areas, consumption was dominated by the Eider with 37 % and 60 % of the total consumption, respectively. In comparison to the western parts of the Wadden Sea the seasonal pattern of consumption as well as species composition differed, most probably as an effect of different climatic conditions, whereas annual consumption on intertidal flats seems to be in the same order of magnitude. On average, 15 – 25 % of the mean annual macrozoobenthic biomass seems to be taken by carnivorous birds in the Wadden Sea, which is in the same order of magnitude as in other northern temperate estuarine areas.

Introduction

The Wadden Sea, a large intertidal area (8000 km^2) stretching along the south-eastern shore of the North Sea, is of particular importance for migratory birds, which use this area as a stop-over site on their annual migrations between southern wintering and northern breeding areas. About 10 - 12 million birds spend at least a part of their annual life cycle in this area (Meltofte et al. 1994). Birds are the most prominent members of intertidal ecosystems, often roaming around in spectacular flocks of many thousands. Although the efficiency of energy transfer to birds in intertidal systems is high in comparison to terrestrial ecosystems (Baird & Milne 1981, Baird et al. 1985, Krebs 1985), their role in intertidal ecosystems, if measured as their contribution to energy or carbon flow, is generally considered to be of minor importance, since their consumption only affects a small fraction of primary production and detritus import (Kuipers et al. 1981, Baird et al. 1991, Baird & Ulanowicz 1993, Meire et al. 1994). This reflects partly the high trophic level of birds and the low production efficiency of animals (Humphreys 1979, Banse 1995). However, large differences between areas in the densities of birds and the utilization of benthic communities (Zwarts 1988, Wolff 1991b, Hockey et al. 1992) indicate that structural differences in these areas affect avian predation pressure. Several mechanisms mitigating avian predation pressure have been proposed: (a) the degree of seasonal synchronisation between production and predation by birds: birds wintering in northern temperate areas use these places at times when annual production is lowest, whereas birds wintering south of the equator meet the annual production peak (Evans 1979, Hockey et al. 1992); (b) high interannual fluctuations of the benthic macrofauna biomass in northern areas lead to low average consumption (Nehls 1989, Wolff 1991b); (c) the harvestable fraction of benthic communities, as determined by the quality and the availability of benthic invertebrates to birds, differs seasonally and regionally with low availability and quality in temperate regions in winter (Beukema et al. 1993, Zwarts & Wanink 1993); (d) the size of tidal areas, with higher densities of birds in smaller areas (Prater 1981, Hockey et al. 1992). The first three of the four mechanisms mentioned are caused by the climatic conditions as determined by the geographical positions of the intertidal areas. The geographical position further influences the suitability for birds, as the climatic conditions influence their daily food requirements (Castro et al., 1992, Wiersma & Piersma 1994). The consequences of these climatic influences are, that the densities of most migratory shorebirds and the total consumption by birds are much higher in southern areas (Zwarts 1988, Hockey et al. 1992).

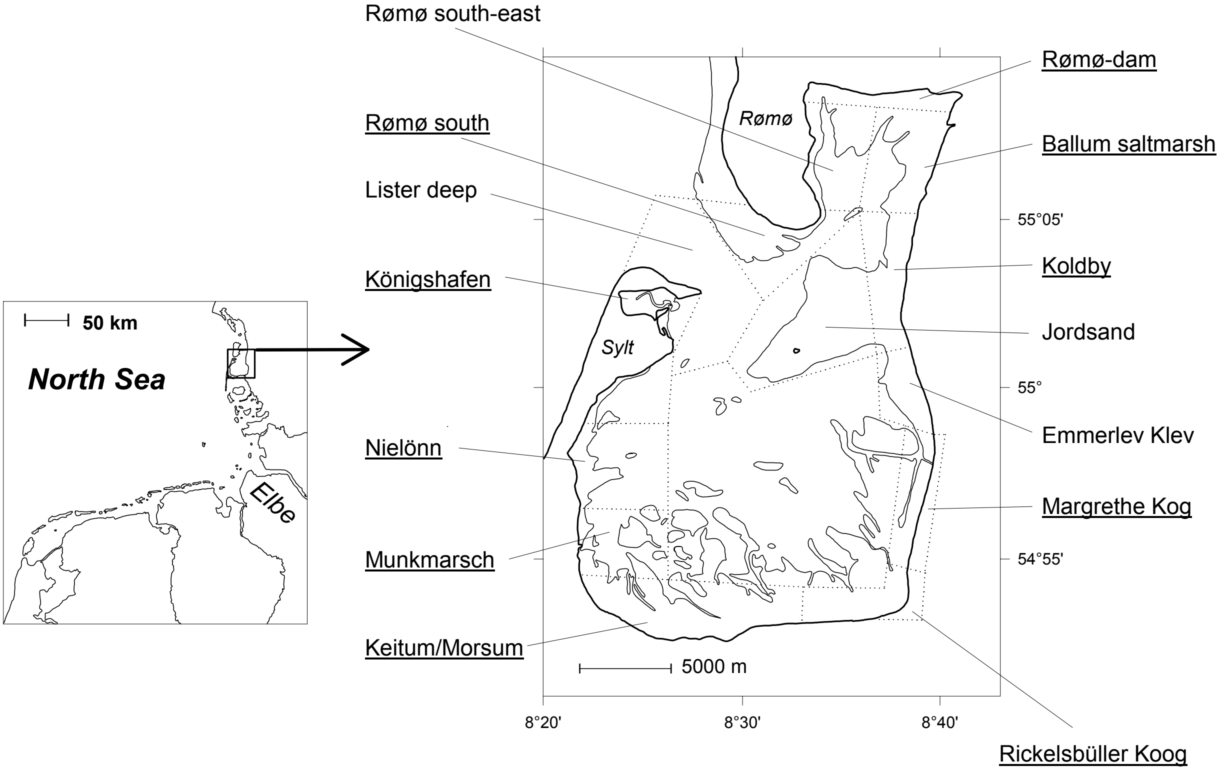


Fig. 3.1: Sylt-Rømø Wadden Sea with subareas used for counting birds. In sectors with underlined names, regular land-based spring-tide counts were conducted. Thin line delimits intertidal flats.

The consumption by birds in the Wadden Sea has been mainly investigated in the westernmost parts of the area, where birds consume 5 g AFDW * m^{-2} * $year^{-1}$, which are 10 - 20 % of the annual macrozoobenthic production (Smit 1981a, Wolff 1991b). Since the entire Wadden Sea spans a region of 2.5° latitude and 4° longitude, the climatic conditions at the western end are milder than at its northern end (Eisma 1980) and bird densities apparently respond to these differences. The densities of wintering waders and hence their consumption was estimated to be eight to ten times higher in the western Dutch Wadden Sea than in the northern Danish Wadden Sea (Zwarts 1988). We investigated bird populations in a tidal inlet in the northern part of the Wadden Sea and calculated their annual consumption. The aim of the study was to analyse whether consumption by birds is actually lower in this part of the Wadden Sea, or whether differences in species composition and seasonal pattern of consumption result in an equal amount of annual consumption. By comparing a relatively large intertidal area with a small bay we further investigated the impact of area size on bird densities and consumption.

Material and methods

Study area

This study was carried out in the Sylt-Rømø Wadden Sea, a tidal basin in the northern part of the Wadden Sea in the German-Danish borderland (Fig. 3.1). The islands of Sylt and Rømø, which protect the area from the North Sea, are connected with the main land by causeways. These borders enclose a clearly defined area, which comprises 137.7 km^2 of intertidal flats and 299.9 km^2 of subtidal area (Tab. 3.1). Sandflats are the most common type of tidal flats, whereas only a small proportion of the area is covered by mudflats, mainly near the two dams.

The results of the investigation on the whole Sylt-Rømø Wadden Sea are compared with those covering the subarea Königshafen. The latter is a shallow tidal bay at the northern end of Sylt with 4.32 km^2 of intertidal and 1.43 km^2 of subtidal area. Intertidal sediments consist predominantly of coarse sand, blown in by the wind from nearby dunes, which makes this bay different from other sheltered bays in the Wadden Sea (Austen 1994). Additionally, a relatively high proportion of the area is covered by mussel-beds (*Mytilus edulis*) (Reise et al. 1994), concentrated at the mouth of

Tab. 3.1: Biomass and area composition of the Sylt-Rømø Wadden Sea and the Königshafen

	Sylt-Rømø Wadden Sea	Königshafen	Source
Mean intertidal biomass [g AFDW*m^{-2}]	50	65	Reise et al. (1994); Lackschewitz (1995)
Mean intertidal biomass, without mollusc shells [g AFDW*m^{-2}]	40	56	Lackschewitz (1995)
Total area (sub- + intertidal) [10^6 m²]	437.6	5.75	Backhaus et al. (1995)
Intertidal area [10^6 m²]	137.7	4.32	Backhaus et al. (1995)
% mudflat	2.96	0.4	Bayerl (pers. comm.); Austen (1994)
% sandy mudflat	21.79	10.8	
% sandflat	75.25	88.8	
% intertidal covered by mussels	0.28	1	Reise et al. (1994); Lackschewitz (1995)

the bay near the low-water line (for a further description, see Reise 1985). The Königshafen is relatively isolated within the Sylt-Rømø Wadden Sea with the next high-tide roosts for birds 8 - 9 km away and the next feeding areas at a distance of 6 - 7 km.

Bird counts

Birds were counted in 10 subareas (Fig. 3.1, underlined areas) during high-tide at each spring-tide (approx. every 15 days) between 1989 and 1995 from dikes, dams or dunes, with the help of telescopes (for a description of the spring-tide counts, see Rösner & Prokosch 1992). Breeding and non-breeding birds were not differentiated. On average, in 3.4 years (SD: 1.3, range: 0 - 6) 5.2 counts (SD: 2.7, range: 0 - 14) per month and subarea were conducted. Additionally, aerial surveys were conducted by the Danish National Environmental Research Institute with 37 counts in the northern and eastern parts of the investigation area (Lister Deep - Rickelsbüller Koog) and 8 counts in the western part of the area (Königshafen - Keitum/Morsum; for method, see Pihl & Frikke 1992). In the analysis of the aerial counts the results from the subareas Margrethe Kog and Rickelsbüller Koog were excluded, since there were major differences between the latter and simultaneous ground surveys. Usually, the aerial estimates in these areas, which were difficult to scan, were below the estimates of the ground surveys. Redshank, Curlew, Ringed Plover, and Turnstone were excluded from the analysis of all aerial surveys because of major disagreements with ground surveys, which were thought to be more accurate in these species.

For Eiders, special aerial surveys were conducted. Since 1988, 65 surveys were analysed (for a description of the methods, see Nehls 1991). Ground surveys were only used for the Königshafen, which is the only subarea where Eider numbers can be realistically obtained by land-based counts.

As birds are highly mobile animals, the two dams north and south of the investigation area are no real borders restricting the movements of the birds. This can be a problem when relating bird numbers to a distinct area. Certainly, there is an exchange in birds with adjacent areas, but it was neglected here, as immigration and emigration were supposed to cancel each other out. The problem may become more difficult when relating high-tide counts from the Königshafen to its intertidal area. At least for gulls (Dernedde 1993), Bar-tailed Godwit and Eider, low-tide counts gave equal numbers for most of the counts. Nevertheless, there may be a slight overestimation of the density estimates for some species based on high-tide counts.

Analysis of the counts

Despite the integration of the bird counts in an international monitoring project (see Rösner et al. 1994), there were only very few simultaneous counts covering all subareas. To calculate the mean bird numbers for the whole Sylt-Rømø Wadden Sea, each subarea and species had to be treated separately. For each month in each year an average was calculated. Thereafter, the mean for each month across all years was calculated. This method of calculation stresses more the variation between years as if only the mean of all counts per month had been calculated. For June, the missing values for five subareas were interpolated. To obtain the

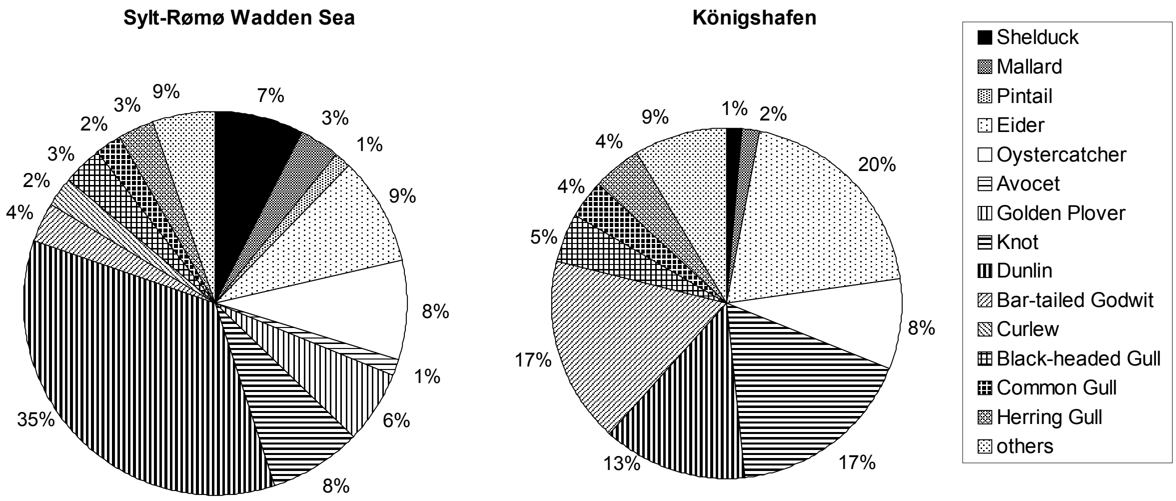


Fig. 3.2: Species composition of bird communities (carnivores) in the Sylt-Rømø Wadden Sea (left, 107656 birds * month^{-1}) and the Königshafen (right, 5652 birds * month^{-1}).

bird numbers for the whole Sylt-Rømø Wadden Sea, the monthly means of each subarea were added up.

Calculation of consumption

To convert bird numbers into consumption, several assumptions have to be made. We followed the approach of Meire et al. (1994), with few alterations.

The basic formula for conversion is as follows:

$$C = D * 3 * BMR * (1/Q)/E$$

where: C = monthly consumption for each species [g AFDW] (ash free dry weight per month)

D = number of bird-days per month

BMR = basal metabolic rate, estimated by using weight dependent equations:

BMR [W] = 5.06 * $W^{0.729}$ for waders (Kersten & Piersma 1987)

BMR [W] = 4.8 * $W^{0.672}$ for Anseriformes (Brunckhorst & Hüppop pers. comm.)

BMR [W] = 3.56 * $W^{0.734}$ for all other species (Aschoff & Pohl 1970b)

W [kg] = weight of the target species; for each month the actual weight was used. Weights were obtained from literature with data which were recorded as close to the investigation area as possible. This resulted in the following ranking of sources: 1. Prokosch (1988), 2. Smit & Wolff (1981a), 3. Cramp & Simmons (1983)

BMR values were transformed into KJ/day

Q = assimilation efficiency (80 %; mean value of different sources; Kersten & Piersma 1987, Castro et al. 1989, Zwarts & Blomert 1990)

E = 22 KJ/g AFDW; mean energy content of marine benthic animals in the Wadden Sea (Zwarts & Wanink 1993)

Daily energy expenditure (DEE) was assumed to be 3 * BMR (Kersten & Piersma 1987). For Eiders, monthly consumption estimates from a feeding study in the Königshafen were used (Nehls 1995).

Further assumptions were:

- divers, terns, Cormorant, and Greater Black-backed Gull feed exclusively in the pelagic zone
- Teal, Mallard, Pintail and Golden Plover fulfil 50 % of their energy demands on the zoobenthos of intertidal flats
- diving ducks feed 50 % in the subtidal zone and 50 % in the intertidal zone
- gulls, other than Greater Black-backed Gull, were supposed to rely on food resources from the Wadden Sea. Although these species may also feed on anthropogenic food sources (e.g.: discards, waste), these play only a minor role in the diet in this area (Dernedde 1993)

Reliability of consumption estimates

Calculation of consumption is based on allometric equations as well as on many assumptions. However, biomass intake of the main predator, the Eider, is based on observations in the Königshafen. A principal assumption for all other birds was a constant DEE of 3 * BMR throughout the year. Observations of feeding Bar-tailed Godwits in the Königshafen during the migration periods confirmed this value (Ch. 6). The smaller the birds are, the more pronounced a seasonal pattern of DEE becomes (Wiersma et al. 1993), which was not considered in the calculations. We do not think that this has a large effect on the results, since most of the smaller birds leave the area in winter, when DEE is highest. At this time of year, the dominance of the

Tab. 3.2: Mean numbers of birds and consumption in the Sylt-Rømø Wadden Sea and the Königshafen. For the calculation of consumption, monthly weight changes were considered; thus, annual consumption values cannot be calculated directly from mean daily biomass intake and mean number * month^{-1}; for method of calculation, see text. For Eider, food intake was estimated on the results of a feeding study (Nehls 1995), and not on the allometric relationship based on body weight

		Sylt Rømø Wadden Sea		Königshafen	
	Mean weight [kg]	Mean number of birds *month^{-1}	Consumption *year^{-1} [g AFDW*10^{6}]	Mean number of birds *month^{-1}	Consumption *year^{-1} [g AFDW*10^{6}]
Shelduck *Tadorna tadorna*	1.038	8067	209.12	71	1.83
Mallard *Anas platyrhynchos*	1.080	3671	49.72	107	1.44
Pintail *Anas acuta*	0.810	1451	16.30		
Eider *Somateria mollissima*	(2.200)	9815	553.90	1112	66.35
Oystercatcher *Haematopus ostralegus*	0.546	8997	158.66	467	8.23
Avocet *Recurvirostra avosetta*	0.300	1414	16.17	4	
Golden Plover *Pluvialis apricaria*	0.216	6708	30.32	109	
Knot *Calidris canutus*	0.148	8226	57.67	980	6.61
Dunlin *Calidris alpina*	0.054	37940	123.01	742	2.42
Bar-tailed Godwit *Limosa lapponica*	0.324	3774	46.38	979	11.99
Curlew *Numenius arquata*	0.833	2623	63.49	12	
Black-headed Gull *Larus ridibundus*	0.271	3486	25.16	255	1.85
Common Gull *Larus canus*	0.394	2466	23.84	205	1.99
Herring Gull *Larus argentatus*	1.005	3458	66.58	242	4.67
Others		5557	49.71	365	3.47
Total			**1490.03**		**110.85**

Eider is even more pronounced, so that consumption values appear to be reliable (for further discussion of calculation of consumption, see Meire et al. 1994).

Results

Species composition

Regarding carnivorous species only, Dunlin is the most abundant species (35 %) in the Sylt-Rømø Wadden Sea followed by Eider (9 %), Oystercatcher (8 %), Knot (8 %), and Shelduck (7 %). These five species comprise 67 % of all carnivorous birds (Fig. 3.2). Similarly, again five species make up 75 % of all individuals in the Königshafen subarea. However, in this subarea the Eider is the most abundant species (20 %) followed by Knot (17 %), Bar-tailed Godwit (17 %), Dunlin (13 %), and Oystercatcher (8 %). The major difference between both areas is the greater dominance of the Eider in the Königshafen, which is an effect of the higher coverage with mussel beds. Furthermore, in the Königshafen the bird community consists of a higher proportion of Bar-tailed Godwits, as well as a reduced proportion of Dunlin and Shelduck, both of which are supposed to be related to the difference in sediment composition between the two areas.

Consumption by birds

Converting bird numbers into biomass-consumption results in an annual consumption of 1490 t AFDW for the whole Sylt-Rømø Wadden Sea and 111 t AFDW for the Königshafen (Tab. 3.2). In the Sylt-Rømø Wadden Sea, the most important predator is the Eider, accounting for 37 % of biomass consumption. Together with Shelduck, Oystercatcher, and Dunlin these four species take 70 % of all biomass consumed by birds in this area. All other bird species play only a minor role (Fig. 3.3). Consumption is clearly dominated by large birds. Despite the fact that 4 times as many Dunlins as Eiders use the area, the former, small, species consumes only 22 % of the biomass consumed by the Eider. In the Königshafen, the dominance of the Eider in terms of consumption is even more pronounced: almost 2/3 of all biomass consumed by birds

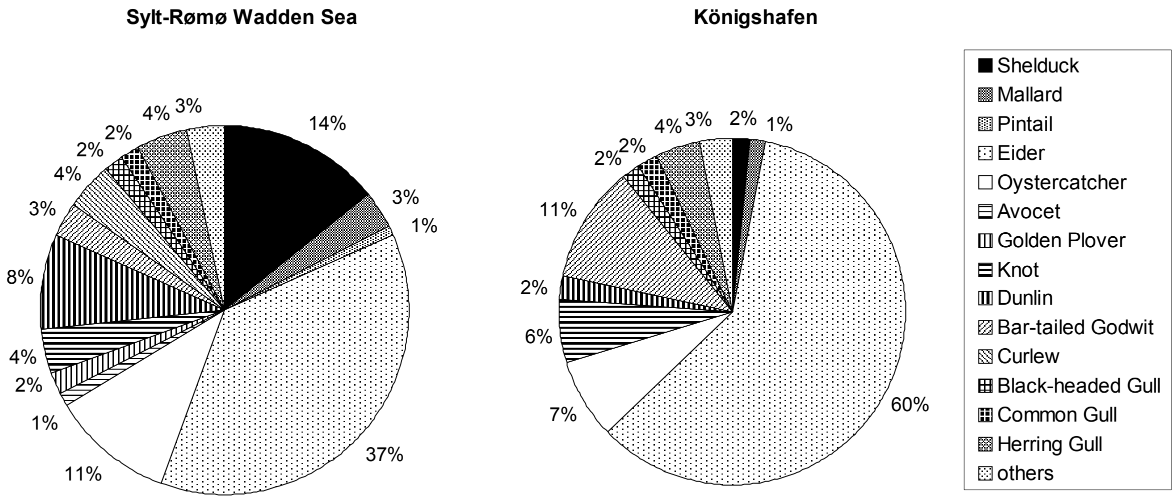


Fig. 3.3: Distribution of consumption by carnivorous birds over species in the Sylt-Rømø Wadden Sea (left, 1490 * 10^6 g AFDW * $year^{-1}$) and Königshafen (right, 111 * 10^6 g AFDW * $year^{-1}$)

is taken by this species. Together with Bar-tailed Godwit, Oystercatcher, and Knot these four species account for 84 % of the consumption by birds.

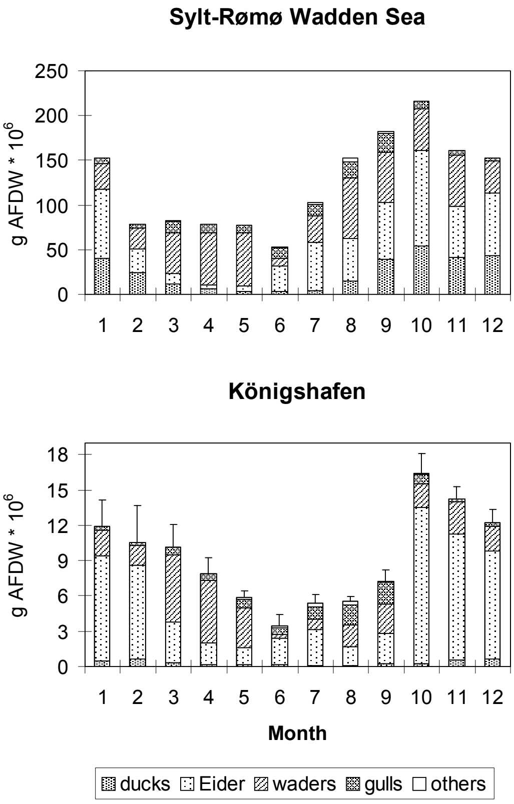
In relation to the total area, consumption by birds amounts to 3.4 g AFDM * m^{-2} * $year^{-1}$ in the Sylt-Rømø Wadden Sea and 19.2 g AFDM * m^{-2} * $year^{-1}$ in the Königshafen (Tab. 3.3). Restricting these calculations to the intertidal area, where most of the species feed, consumption totals 8.7 g AFDM * m^{-2} * $year^{-1}$ for the Sylt-Rømø Wadden Sea and 17.6 g AFDM * m^{-2} $year^{-1}$ for the Königshafen. Even when excluding from these calculations the most dominant predator, the Eider, 80 % of whose food consist of Mussels (Nehls 1995), the difference between the two areas is still obvious. The subtidal compartment is heavily utilized in the Königshafen and remains almost unused in the Sylt-Rømø Wadden Sea. This difference is related to the much higher share of subtidal area in the Sylt-Rømø Wadden Sea than in the Königshafen, which results in a lower average density of predators in this compartment. Predation in the subtidal compartment is concentrated on Mussel or Cockle beds (*Cerastoderma edule*), whereas other food resources remain almost unexploited by birds. In both areas, biomass taken from the pelagial is negligible due to the low abundance of birds feeding on fish (ca 1 % of total consumption). Furthermore, consumption in this compartment is almost exclusively restricted to summer and early autumn.

Due to migratory movements of birds, consumption is not equally distributed throughout the year. In the Sylt-Rømø Wadden Sea, consumption reaches a peak in autumn and remains on a high level until January (Fig. 3.4). This pattern is mostly influenced by the presence of Eiders and other ducks, especially Shelduck. In contrast, waders have the biggest share in consumption during spring.

The same seasonal pattern appears for the Königshafen. Again, this pattern is mostly influenced by the Eider, with an increasing importance of waders in spring. In all, high levels of consumption are reached, when benthic biomass is already decreasing or on a

Tab. 3.3: Consumption by carnivorous birds in the Sylt-Rømø Wadden Sea, in the Königshafen (both calculated from values given in Tab. 3.1 and 3.2) and in the Dutch Wadden Sea (Smit 1981a; recalculated with assumptions used in this paper); values are in g AFDW * m^{-2} * $year^{-1}$

	Sylt-Rømø Wadden Sea	Königshafen	Dutch Wadden Sea
Sub- + intertidal area	3.4	19.2	3.9
Intertidal area	8.7	17.6	6.6
Subtidal area	0.93	23.3	1.4
Without Eider			
Sub- + intertidal area	2.1	7.7	2.5
Intertidal area	6.7	10.0	5


Sylt-Rømø Wadden Sea

Königshafen

Fig. 3.4: Seasonal pattern of consumption by carnivorous birds in the Sylt-Rømø Wadden Sea (top) and the Königshafen (bottom, + 1 SE, 4 - 6 years per month)

low level (Beukema 1981, Asmus 1982, 1987). Only waders migrating through the area in May and August/September profit from the seasonal pattern of benthic production.

Discussion

Comparing the results from the Sylt-Rømø Wadden Sea with the Königshafen, it appears that the size of an intertidal area has a strong impact on consumption by birds, as consumption is 50 % higher in the Königshafen than in the whole Sylt-Rømø Wadden Sea. Even in the light of a higher benthic biomass within the Königshafen, compared to that of the entire Sylt-Rømø Wadden Sea, a higher proportion of biomass is consumed by birds in the Königshafen. Probably, this is an effect of the sheltered bay with a large proportion of sandflats at mean tide level. Furthermore, short distances between high-tide roosts and low-tide foraging areas might be a criterion for habitat selection (cf. Swennen 1984), since, even within the Königshafen, tidal flats near the high-tide roost were preferred for foraging (Scheiffarth & Nehls 1995). In addition, the habit of many waders and gulls of foraging along the moving tideline for most of the year (Evans 1979, Nehls & Tiedemann 1993) enhances bird numbers in small bays with elongated tidelines as compared to a straight coastline (Evans & Dugan 1984). In all, it seems almost independent of scale, whether comparing two adjacent areas (this study), a larger region like eastern England (Prater 1981) or the entire East Atlantic Flyway (Hockey et al. 1992), that smaller intertidal areas face higher bird densities than larger areas.

For a large-scale comparison of consumption within the Wadden Sea, Smit's (1981a) estimates for the Dutch Wadden Sea for the seventies were recalculated on the basis of our assumptions. This resulted in an annual consumption of 6.6 g AFDW * m^{-2} * year^{-1} for the tidal flats of the Dutch Wadden Sea (Tab. 3.3), which is 34 % below the value calculated for the tidal flats of the Sylt-Rømø Wadden Sea in the nineties. Whether this difference really exists remains open, since for most species an increase in numbers in all parts of the Wadden Sea has been observed (Meltofte et al. 1994, Rösner 1994, Smit & Zegers 1994). This is most probably due to both improved registration and a real increase in bird numbers. At least for the Dutch Wadden Sea, increasing bird numbers are paralleled by increasing benthic biomass due to eutrophication of the tidal flats (Beukema 1989), so that the proportion of biomass taken by birds may not have changed. Whether or not there was an increase in benthic zoomass in the northern part of the Wadden Sea during the last 20 years is not yet clear (Jensen 1992, Reise et al. 1994).

At present the consumption by birds at the northern end of the Wadden Sea should not be lower than at the western end. As species richness and biomass of the macrobenthic communities in the Sylt-Rømø Wadden Sea are similar to those in the Dutch Wadden Sea (Reise et al. 1994, Lackschewitz 1995), consumption by birds equals 15 – 25 % of the mean annual zoobenthic biomass in both areas. The equal amount of absolute consumption per m^2 as well as predation rate on tidal flats is in contrast to the much lower densities of wintering waders in the northern part of the Wadden Sea than in the Dutch part (Zwarts 1988). Most of the smaller species leave the northern parts in winter. An equal level of consumption is not only achieved by higher numbers during spring or autumn, since the share of waders in total consumption reaches only 35 % in the Sylt-Rømø Wadden Sea as compared to 44 % in the Dutch Wadden Sea but also by the higher proportion of large and heavy birds, such as Shelduck, in the Sylt-Rømø Wadden Sea. Especially in late autumn and winter, Eider and Shelduck dominate the bird community. This can be regarded as a reaction to the harsher conditions in the northern part of the Wadden Sea as compared to the western parts, because large birds have lower thermostatic costs than small birds (Wiersma et al. 1993). Additionally, the phenology of consumption reflects the unfavourable winter conditions for most of the bird species in the northern Wadden Sea. A sharp drop in bird numbers appears from January to February, when the risk of ice-cover is highest. In contrast, consumption in the western Wadden Sea is high throughout winter and reaches a peak in February (Smit 1981a). This may reflect immigration from the northern parts of the Wadden Sea. Although differences in the climatic conditions apparently affect species composition as well as the seasonal patterns of consumption in the two subareas of the Wadden Sea, this has no negative impact on total consumption by birds. Consumption within the Wadden Sea seems to differ only on a local scale related to structural elements in the landscape, e.g. sediment composition, bays, etc.

The proportion of 15 – 25 % of mean annual biomass taken by birds as calculated in this study falls well within the range of the results from other studies conducted in temperate estuaries on the European continent (for a recent review, see Meire et al. 1994). Only in Great Britain have slightly higher values apparently been achieved (Baird et al. 1985). In contrast, a much higher proportion of the mean biomass (82.7 %) as well as production (42.6 %) are consumed by birds on the Banc d'Arguin, Mauritania (Wolff & Smit 1990). One major reason for this difference between temperate and tropical estuaries may be stability, with low annual variability and therefore long-term predictability of food resources on tropical mudflats (Wolff 1991b).

Until now the processes linking consumption by birds with production of their invertebrate prey are only marginally understood. Questions concerning whether or not bird numbers are limited by food resources in the Wadden Sea must be investigated on the species level, since different species have a different sensitivity to fluctuating food resources (Beukema et al. 1993).

Acknowledgements

First, we would like to express our greatest gratitude to the numerous people who have been counting birds over the years. The Danish National Environmental Research Institute made unpublished data available. We thank especially John Frikke for the aerial surveys, and Iver Gram and Lars Maltha Rasmussen for the counts from Margrethe Kog. Spring-tide counts on Sylt and in the Rickelsbüller Koog were co-ordinated by Hans-Ulrich Rösner from the WWF, who also made the data available. Furthermore, we would like to thank the Naturschutzgemeinschaft Sylt e.V., Birgit Andresen from the Amt für Land- und Wasserwirtschaft, Husum, and Ralph Tiedemann for co-ordinating and conducting counts in 'their' areas. The manuscript was improved by the comments of Franz Bairlein, Hermann Hötker and an anonymous reviewer. This study was supported by the BMBF and is publication no. 225 of the project 'Ecosystem Research Wadden Sea'.

4. Bar-tailed Godwits (*Limosa lapponica*) in the Sylt-Rømø Wadden Sea: which birds, when, from where, and where to?

Gregor Scheiffarth

Abstract

In the Sylt-Rømø Wadden Sea, a tidal catchment area in the northern Wadden Sea, Bar-tailed Godwits of two different populations stop over on migration between wintering and breeding areas. The Afro-Siberian population, which winters in West Africa and breeds in Siberia, uses roosts on the mainland coast only for one month each in spring and summer, whereas the European population, with wintering areas in Western Europe and breeding grounds in Fennoscandia, occurs mainly for three months in spring on the islands. Some birds also stay from autumn until late January. The European population was studied in detail in the Königshafen area at the northern end of the island of Sylt. Morphometric as well as ringing data confirmed that birds belonged to the European population with 13 out of 15 ringing recoveries in or from Great Britain. During the spring stopover, birds moulted from winter to breeding plumage in 43 days. On autumn migration, Bar-tailed Godwits arrived already with ¼ winter plumage. Moult back into complete winter plumage took 28 days. Sex ratio was 1:1 throughout the year apart from i) the second half of May, when males left before females and ii) winter, when more males than females left the study area to overwinter in milder regions like the Dutch Wadden Sea or Great Britain. However, birds identified by colour rings in winter did not differ in size from all other birds colour ringed and not wintering in the Königshafen area. In spring, most colour marked birds arrived before the 24th of March and left after 30 – 40 days on the 3rd or 4th of May. A higher turnover of birds was observed in May as compared to March and April when Bar-tailed Godwits from other areas seem to concentrate in the northern Wadden Sea before final departure to the Fennoscandian breeding grounds. In autumn most marked birds arrived before 14th August. However, some birds arrived in early September, when a high turnover of birds occurred, since a proportion of the early arriving birds left for other wintering areas. On spring migration Bar-tailed Godwits seemed to be highly site-faithful whereas in autumn less than 25 % of the birds ringed in spring were resighted. Assuming 100 % site faithfulness in spring, maximum mortality rates ranged between 17.4 and 26 % for adults which is far below previously published figures.

Introduction

The seasonal occurrence of large numbers of birds in the Wadden Sea and their migration between southern wintering and northern breeding sites fascinates natural scientists for more than a century (e.g. Droste-Hülshoff 1869, Homeyer 1880). Some 10 – 12 million waterbirds use the Wadden Sea during their annual cycle. For 41 species of waterbirds, the area is an internationally important stopover or wintering site (Meltofte et al. 1994). The Bar-tailed Godwit (*Limosa lapponica*), a long-distance migrant, on an annual average contributes 4 – 5 % in numbers to this waterbird community (Smit 1981b, Scheiffarth & Nehls 1997). Two different populations (classified as subspecies by Engelmoer & Roselaar 1998) of the species occur in the Wadden Sea. The European population breeds in Fennoscandia and winters around the North Sea, mainly in the western part of the Wadden Sea and Great Britain (Smit & Piersma 1989, Drent & Piersma 1990, Engelmoer & Roselaar 1998). The Afro-Siberian population has breeding areas on Taymyr and Yamal and wintering sites in West Africa, mainly the Banc d'Arguin, Mauritania and Guinea-Bissau (Smit & Piersma 1989, Drent & Piersma 1990, Wymenga et al. 1990, Engelmoer & Roselaar 1998).

As a basis for the understanding of the stopover ecology of Bar-tailed Godwits, parameters describing the birds present in a study area have to be known. In particular a classification with different populations is important since different constraints act on the different populations, resulting in distinct behavioural patterns (Scheiffarth et al. 1993, Scheiffarth & Bairlein 1998a). This paper summarizes basic population parameters, as the seasonal occurrence, morphology, moult into breeding and back into winter plumage, turnover and return rates for Bar-tailed Godwits using the Sylt-Rømø Wadden Sea as a stopover and win-

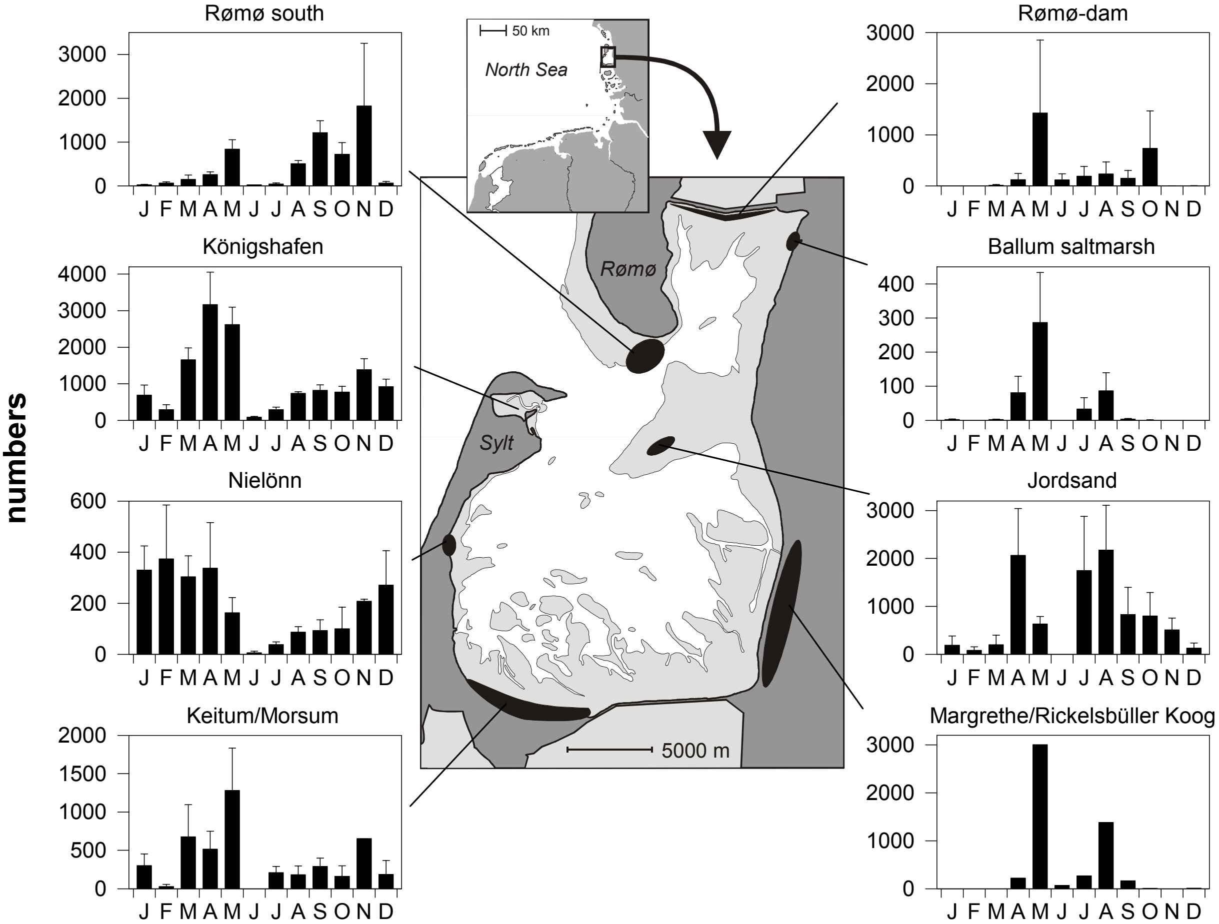


Fig. 4.1: Seasonal occurrence of Bar-tailed Godwits at different high-tide roosts in the Sylt-Rømø Wadden Sea. Monthly means + SE from 2 – 5 years.

tering area in the northern Wadden Sea, where both populations occur.

Material and methods

Study area

This study was carried out in the Sylt-Rømø Wadden Sea, a tidal basin in the northern part of the Wadden Sea in the German-Danish borderland with an area of 411 km^2 (Fig. 4.1). The islands of Sylt and Rømø, which protect the area from the North Sea, are both connected to the main land by causeways. Detailed studies were carried out in the Königshafen, a shallow tidal bay at the northern end of Sylt with a total area of ca. 6 km^2. For a detailed description of the area, see Gätje & Reise (1998).

Bird counts

Birds were counted during high-tide at each spring-tide (approx. every 15 days) from dikes, dams or dunes between 1989 and 1995 (for a description of the spring-tide counts, see Rösner & Prokosch 1992). Additional, counts were conducted during the migration periods in the subareas Königshafen and Nielönn (s. Fig. 4.1 for location of the subareas). During some periods, birds in the Königshafen were counted daily. Phenologies are presented on a monthly or fortnightly basis. For each time interval, first the mean number of birds per year was calculated and in a second step for each time interval the mean across all years. This method of calculation accounts for the variation between years and eliminates the variation within years for each time interval.

Moult of body feathers

To follow the progress of body moult in spring and autumn, males in foraging flocks were scanned with telescopes. Extension of breeding plumage was recorded on a 7 point scale (Pienkowski 1980, see also Prokosch 1988, Piersma & Jukema 1993) for each male in the flock (1: winter plumage, 2: traces of breeding plumage, 3: ¼ breeding plumage, 4: ½ breeding plumage, 5: ¾ breeding plumage, 6: traces of winter plumage, 7: complete breeding plumage). On average, flocks consisted of 72 males (range: 12 – 258

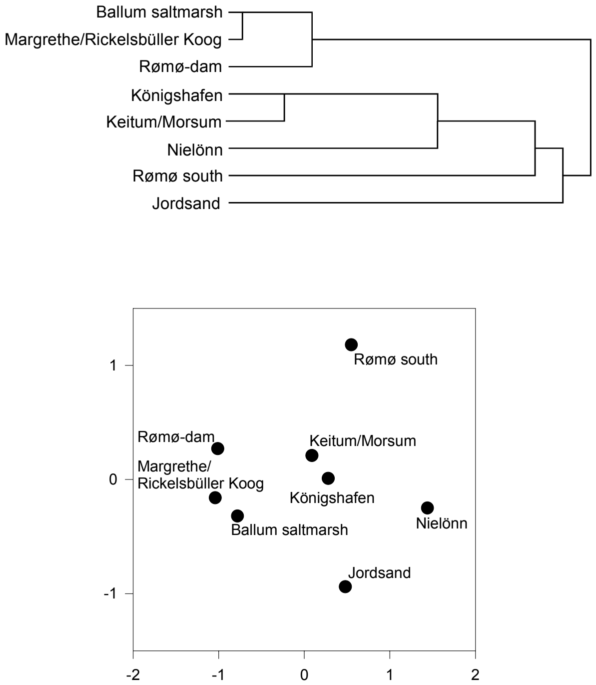


Fig. 4.2: Cluster analysis and Multiple Dimensional Scaling (MDS) plot to demonstrate similarities between the phenologies at different high-tide roosts in the Sylt-Rømø Wadden Sea. Similarities were calculated with the cosine measure (Backhaus et al. 1990). Stress of MDS plot: 0.061; $r^2 = 0.976$.

males). For each sample a mean plumage score was calculated.

Catching, measuring, marking, and resighting of birds

Between 1991 and 1993 a total of 129 adult and 18 juvenile Bar-tailed Godwits were caught by cannon nets (Ireland et al. 1991, see also Prokosch 1988) at the water line in the Königshafen area. Birds were aged and sexed according to Prater et al. (1977). Wing length was measured to the nearest mm as described in Engelmoer & Roselaar (1998). Tarsus+toe was also measured to the nearest mm, excluding the claw from total length (Prater et al. 1977, in contrast to Engelmoer & Roselaar 1998). Bill length (culmen, from bill tip to feathering) was measured to the nearest 0.1 mm with a vernier calliper according to Prokosch (1988) and Engelmoer & Roselaar (1998). Body mass was recorded to the nearest gram with an electronic balance.

Besides metal rings, 120 adult birds got individual colour ring combinations for subsequent identification in the field. Additionally, 88 adult birds were marked with a yellow dye (picric acid) in March 1992 to enhance the chance of resighting as well as the determination of the number of marked birds in a flock. Mainly during the migratory periods in spring (March – April) and autumn (August – October), flocks of foraging Bar-tailed Godwits or birds moving from or to the high-tide roost were controlled for marked individuals.

Since Bar-tailed Godwits show a strong sexual dimorphism (Fig.. 4.5, Prokosch 1988, Engelmoer & Roselaar 1998), the sexes can easily be distinguished in the field. To determine the sex-ratio of the local population, flocks of foraging Bar-tailed Godwits were scanned with a telescope and the sex of each individual was determined on the basis of the relationship between estimated bill length and body size (cf. Zwarts et al. 1990). Mean size of observed flocks was 241 birds (range: 46 – 530 birds).

Results

Phenology and distribution of Bar-tailed Godwits in the Sylt-Rømø Wadden Sea

Bar-tailed Godwits used eight areas in the Sylt-Rømø Wadden Sea as main high-tide roosts (Fig. 4.1). Two types of roost sites can be distinguished on the basis of the phenologies (Fig. 4.2): i) sites along the mainland coast, which are only used during migratory stopover in May and August to October ('Ballum saltmarsh', 'Margrethe/Rickelsbüller Koog', 'Rømø-dam'). According to the phenologies, Bar-tailed Godwits occurring at these sites are supposed to belong to the Afro-Siberian population (Prokosch 1988, Piersma & Jukema 1990). ii) sites on the islands, which are attended during the entire year apart from the breeding season in summer. On Sylt in particular, highest numbers occurred during the spring migration, which lasts for three months from March to May in contrast to the mainland. The sites on Sylt show the typical phenology for the European population (Prokosch 1988). Within this second group of roosts representing the islands, 'Jordsand' and 'Rømø south' each form a distinct subgroup with phenologies showing a mixture of the patterns on the mainland and on Sylt.

Phenology, moult, sex ratio and morphology of Bar-tailed Godwits in the Königshafen

In August, after the breeding season, bird numbers in the Königshafen increased only moderately and stayed on a constant level from mid-September until mid-January (Fig. 4.3). In mid-February, birds returned with increasing numbers until the end of April/early May. Bird numbers decreased rapidly during May, resulting in low numbers in June. Owing to this phenology, Bar-tailed Godwits in the Königshafen

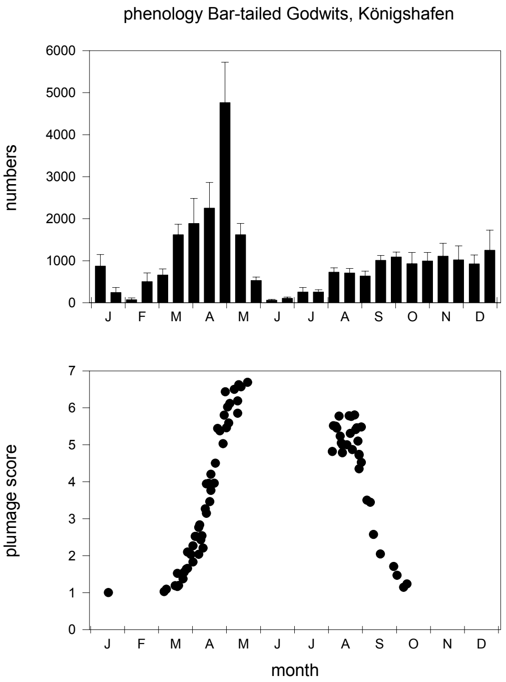


Fig. 4.3: upper graph: Phenology of Bar-tailed Godwits in the Königshafen 1990 – 1995 as fortnight means (+ SE). Lower graph: Progress of moult into breeding resp. winter plumage of male Bar-tailed Godwits in the Königshafen area. Plotted are mean plumage score of flocks of birds scanned with a telescope (mean number of males in flocks: 72). Extent of breeding plumage was recorded on a 7 point scale from 1: winter plumage to 7: complete breeding plumage (Pienkowski 1980).

were studied in detail being considered as representative of the European population.

Male Bar-tailed Godwits in the Königshafen moulted from winter plumage to breeding plumage during their stopover in spring (Fig. 4.3). The first bird with traces of breeding plumage appeared on 7th March and the first male with a complete breeding plumage was observed on 12th April. On 27th March 50 % of the males showed traces of breeding plumage whilst by 8th May 50 % of the males present were in complete breeding plumage. Taking the two 50 % dates as the average start and endpoint of moult for the population, this results in an average moult duration of 43 days in spring.

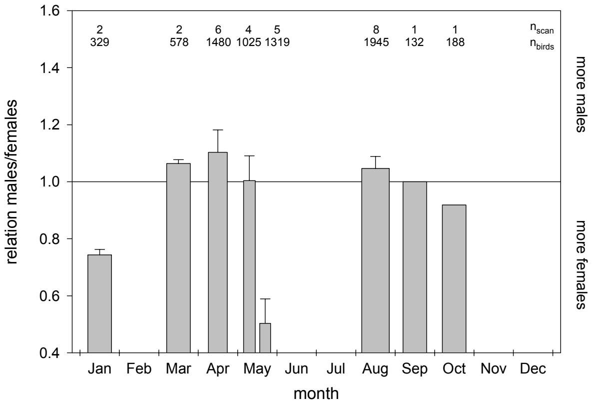


Fig. 4.4: Sex ratio (n males/n females) of Bar-tailed Godwits in the Königshafen area (x + SE). Flocks (mean flock size: 241) of birds were scanned with a telescope.

When Bar-tailed Godwits arrived in the Königshafen in August, more than 50 % of the birds already had started to moult into the winter plumage. Furthermore, mean plumage score fluctuated largely in August, indicating a high turnover rate of birds in the Königshafen. From the end of August onwards, a continuous moult of the male population into winter plumage could be observed. Although the first male in complete winter plumage was seen on 29th August, on 28th August 50 % showed still ¾ or more of the breeding plumage. On 1st October 50 % of the male Bar-tailed Godwits were in complete winter plumage resulting in an average duration of 35 days from more than ¾ of breeding plumage to winter plumage. This period is slightly longer than in spring, when birds needed 28 days for moult from winter to more than ¾ of the breeding plumage.

During most of the year the population present in the Königshafen consisted of similar numbers of males and females (Fig. 4.4). There were only two exceptions: In the second half of May many more females were present than males since males left the area earlier than females (cf. Prokosch 1988), and also in January more females than males were present.

Bar-tailed Godwits caught in March showed a strong sexual dimorphism, with females being larger (Fig. 4.5). They had 5.7 % longer wings (K-S test, $D_{76,42} = 0.826$, $p < 0.01$), 23 % longer bills (K-S test, $D_{76,43} = 0.964$, $p < 0.01$), 7.2 % longer ‘legs’ (tarsus+toe, K-S test, $D_{73,43} = 0.681$, $p < 0.01$), and 21.4 % more mass than males (K-S test, $D_{59,34} = 0.954$, $p < 0.01$).

No Bar-tailed Godwits were caught in winter but since birds were individually marked with colour rings, it was possible to check whether Bar-tailed Godwits staying in winter in the northern part of the Wadden Sea differed in morphology from the average of birds caught in spring and not controlled in January/February (Fig. 4.6). For all morphometric variables tested, no differences were found in either males or females (bill, wing, tarsus+toe, K-S test, for all variables $p > 0.1$). Thus, birds staying in January/February in the area are supposed to be of the same size as migrants present in March.

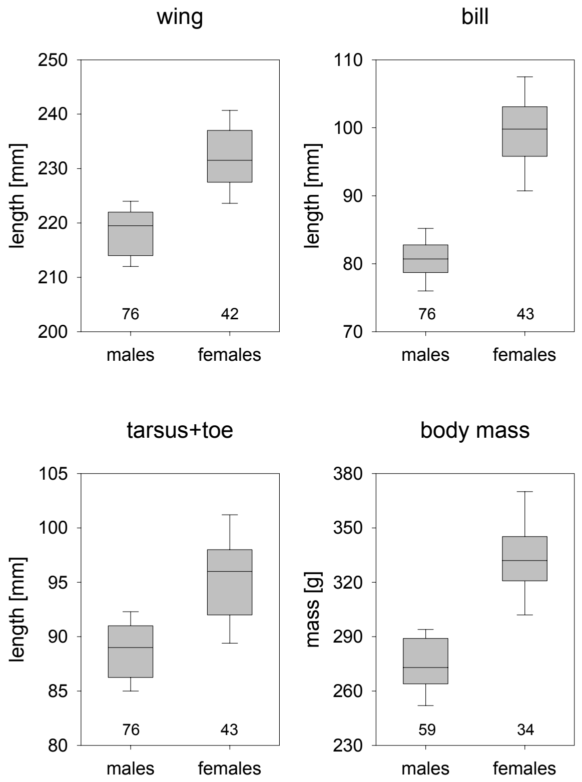


Fig. 4.5: Box plot (line = median, box = 50 % interval, error bars = 90 % interval) of morphometric parameters of Bar-tailed Godwits caught in March in the Königshafen. Numbers below boxes denote number of birds measured.

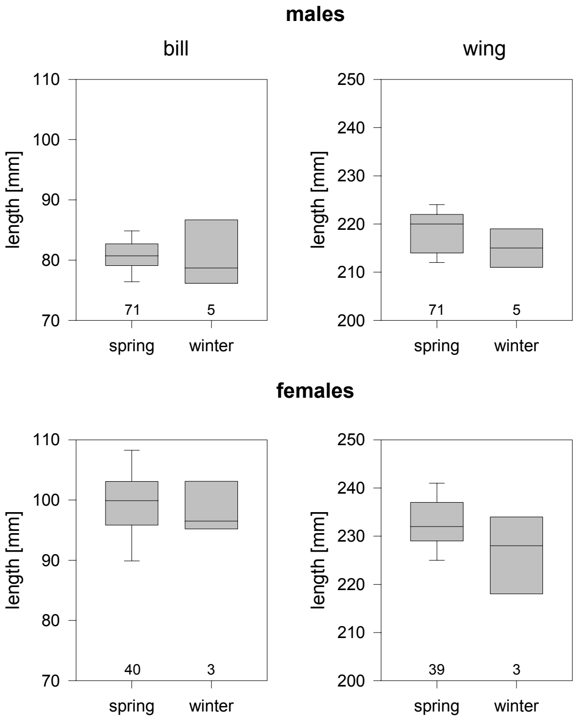


Fig. 4.6: Comparison of bill and wing length between Bar-tailed Godwits caught in March and present in January/February (winter) and all other birds caught in March and not observed in winter in the Königshafen area. See Fig. 4.5 for statistics.

Controls of ringed birds outside the Sylt-Rømø Wadden Sea

From 137 Bar-tailed Godwits marked with metal or colour rings, 11 were recorded in other areas. Four birds ringed as adults and one as juvenile with metal rings in Britain were controlled during the catches in the Königshafen and colour ring combinations from two other birds ringed as juveniles in England were identified (Fig. 4.7).

The majority of controls (15 out of 18) originated from Great Britain, most of them from the British east coast. Six of these birds were either ringed or controlled in winter, one in early spring, three in early autumn and the remaining five birds in late autumn. Additionally, one bird was found dead in the Dutch Wadden Sea in March and another bird was controlled in July in southern Norway.

Turnover and residence time of migratory Bar-tailed Godwits in the Königshafen area

The proportion of marked birds in the local population fluctuated between 4.2 % and 0.3 % (Fig. 4.8). The maximum proportion of marked birds observed in the field depended on the number of birds actually marked

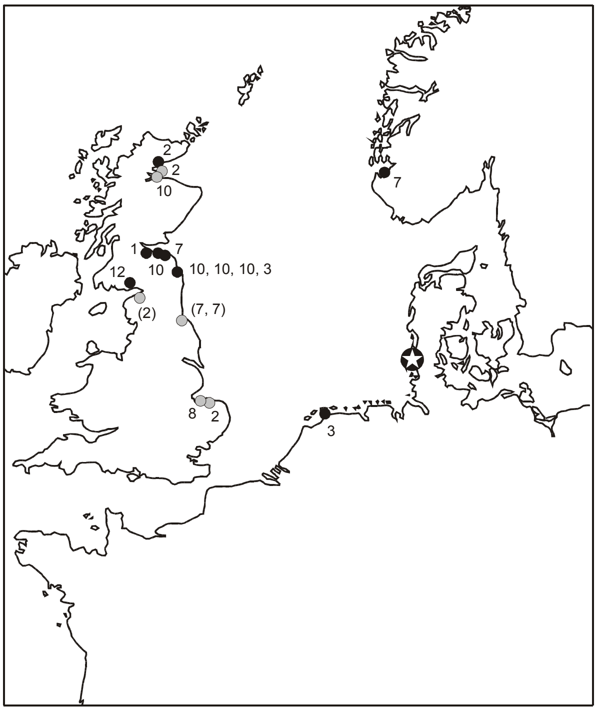


Fig. 4.7: Controls of Bar-tailed Godwits ringed outside the Sylt-Rømø Wadden Sea (grey dots) and birds ringed in the Königshafen (star) and controlled elsewhere (black dots). Numbers denote month of ringing or control, bracket around numbers for birds ringed as juveniles.

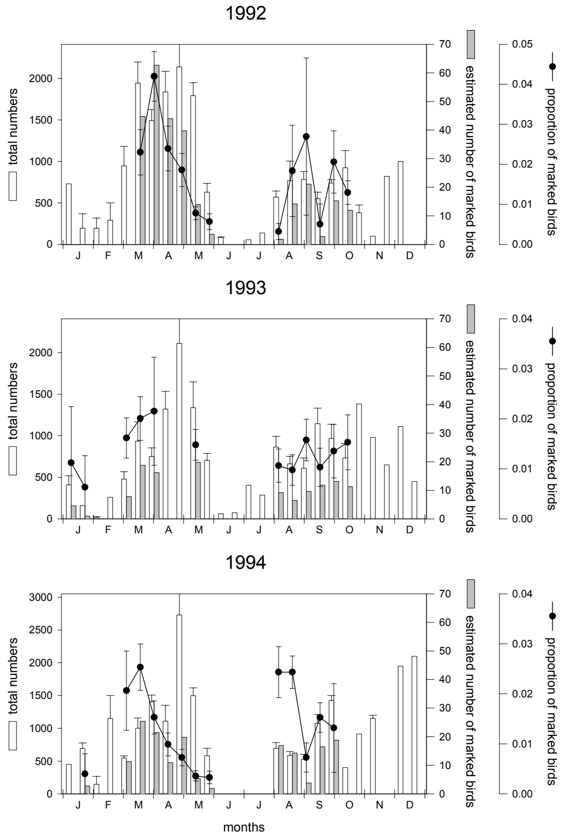


Fig. 4.8: Proportion of colour marked birds in the Königshafen area (± SE) and estimated number of colour marked birds (proportion of colour marked birds * total number of birds present).

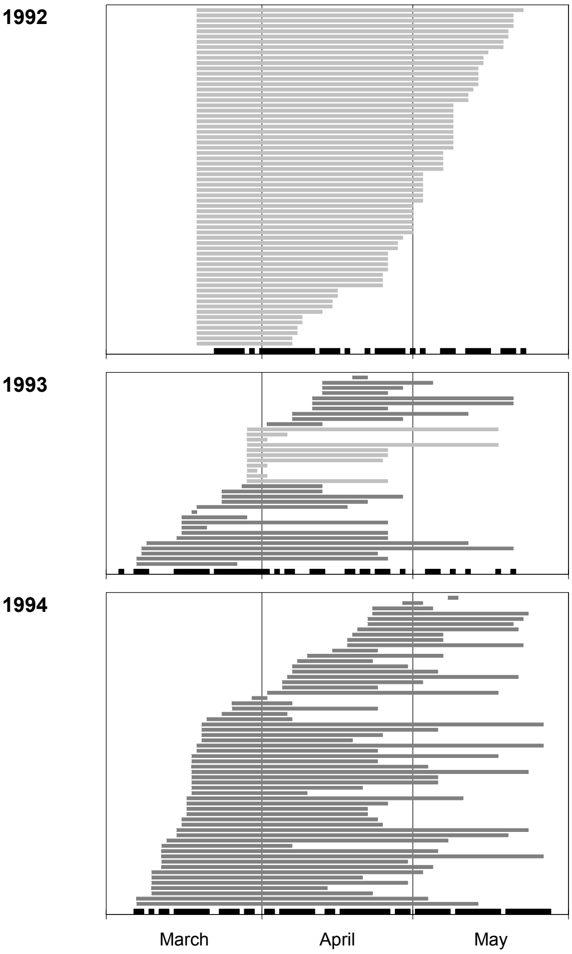


Fig. 4.9: Length of stopover of individually colour ringed Bar-tailed Godwits in the Königshafen area in spring. Light grey bars denote birds caught in the respective season, dark grey bars in previous years, small black bars denote days when flocks were controlled for colour ringed birds.

and on the resighting efforts which both differed between seasons. Thus, proportions between years and seasons are not comparable. Apart from spring 1993, within one season the resighting effort was, however, on the same level. In spring, the proportion of marked birds in the local population decreased from April onwards, indicating that most of the marked individuals arrived and left earlier than the phenology of total numbers suggests. In autumn the proportion of marked birds showed a pronounced decrease between the end of August and the middle of September with a subsequent increase in the following fortnight period indicating some turnover of the marked birds.

In spring, most of the individually marked birds arrived in the Königshafen area before the 24th March (Fig. 4.9, 4.10, Tab. 4.1). In spring 1994 with a high effort for controls, most birds were observed for the first time in a rather short period in March. However, birds kept arriving until the beginning of May. They stayed in the area for 30 – 40 days until 3rd or 4th May (median day of last observation in 1992 and 1994; the days of the last observation in 1993 are not reliable since efforts to identify colour marked birds in April and May were too low). Marked birds started to leave the area already in the first half of April. Even though the total number of birds continued to increase or remained on a high through the end of April/early May, most of the marked individuals had already left the Königshafen, indicating a high turnover of individuals (Fig. 4.10).

With the data from spring 1994, it was possible to estimate the number of birds migrating through the Königshafen area. For the period from mid-February to end of May, a total of 140,345.23 bird days resulted from the phenology of fortnightly means. If each bird would stay for the mean stopover length of 37.8 days (Tab. 4.1), a total of 3,713 Bar-tailed Godwits would have used the Königshafen area as a stopover site during the spring migration of 1994. However, unmarked birds arriving late in the area stayed for a shorter time as phenology in relation to departure of marked individuals suggests, so that the total number of birds passing through must be higher. In fact, the maximum

Tab. 4.1: First and last day of observation and length of stay of Bar-tailed Godwits around List/Sylt in the northern part of the Wadden Sea. For length of stay and date of first observation per season, birds caught in the respective season and year were excluded. n_{birds}: number of individuals observed; $n_{readings}$: number of identifications; $n_{field\ days}$: number of days with reading attempts.

	mean	SE	median	n_{birds}	$n_{readings}$	$n_{field\ days}$
spring						
first day of observation						
1992						
1993	26.3.	2.8	24.3.	26	151	43
1994	26.3.	2.1	19.3.	59	320	66
last day of observation						
1992	2.5.	1.6	2.5.	64	325	44
1993	22.4.	2.8	26.4.	37	151	43
1994	2.5.	1.9	4.5.	59	320	66
length of stay						
1992						
1993	28.7	3.6	25	26	151	43
1994	37.8	2.4	36	59	320	66
autumn						
first day of observation						
1992	31.8.	5.7	29.8.	15	82	44
1993	15.8.	3.5	10.8.	17	98	46
1994	14.8.	2.5	13.8.	21	170	44
last day of observation						
1992	12.10.	4.0	19.10	17	82	44
1993	24.9.	4.0	27.9.	18	98	46
1994	17.9.	3.1	20.9.	21	170	44
length of stay						
1992	40.1	6.5	42	15	82	44
1993	38.6	4.2	42	17	98	46
1994	32.7	3.7	36	21	170	44

number of birds counted early May was 4020 individuals which might come close to the actual number of birds passing through.

In autumn, most individually marked birds returned before 14th August to the area (Fig. 4.11, 4.12, Tab. 4.1). Only a few birds were observed for the first time in September. Observations from 1992 were not as reliable as in 1993 or 1994 since the 44 days with attempts to read colour rings were scattered over a longer period than in the latter years. Unfortunately, the median day of last observation of marked individuals correlates with the end of the field season, so that no reliable estimate of the departure time can be made. However, some birds left the area already between late August and mid-September. Together with an increase in numbers from mid-September onwards, a higher turnover of individuals than at other times of autumn migration can be assumed in the first half of September (Fig. 4.12).

Return rates of Bar-tailed Godwits

To test for site fidelity of Bar-tailed Godwits, return rates of birds to the area around List were analysed (Tab. 4.2). Return rates depend on the efforts made to identify colour marked birds, since more Bar-tailed Godwits ringed in spring 1992 were resighted in spring 1994 (68 %) than in spring 1993 (53 %) when flocks were searched for colour ringed birds on less days (35 %) as compared to spring 1994. Obviously, not all birds present in spring returned to the area in autumn, whereas return rates in spring are much higher. Considering only the return rates in spring 1994, the year with highest field efforts, and assuming 100 % site fidelity, annual adult mortality ranges between 17.4 % for the birds ringed in 1992 and 25.9 % for the birds

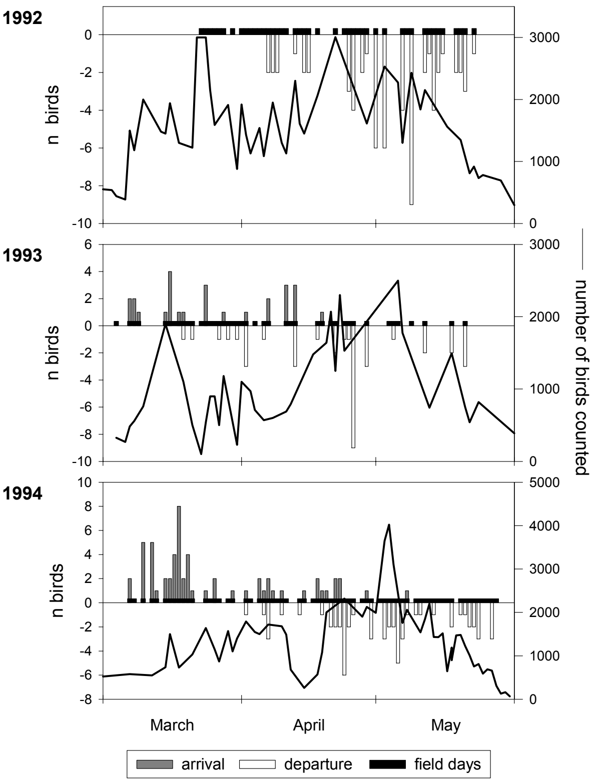


Fig. 4.10: First (‘arrival’) and last (‘departure’) day of observation of individually colour ringed Bar-tailed Godwits in the Königshafen area in spring. Small black bars denote days when flocks were controlled for colour ringed birds, white line shows total number of Bar-tailed Godwits present at the high-tide roost in the Königshafen.

ringed in 1993. If Bar-tailed Godwits are not 100 % site faithful, these rates would be even lower.

Discussion

Mortality of European Bar-tailed Godwits

Boyd (1962) calculated an annual mortality of 39.5 % for adult Bar-tailed Godwits. For the similar sized Black-tailed Godwit (*Limosa limosa*) mortality rate estimates for adults range between 30.3 % (Boyd 1962) and 36.9 % (Glutz et al. 1986). Even the lower mortality estimate of 30.3 % for Black-tailed Godwits is higher than the estimated mortality in spring 1994 and matches exactly the number of birds resighted in 1997, when field effort was low and most probably some birds were missed. In conclusion, European Bar-tailed Godwits i) seem to be highly site faithful on spring migration and ii) most probably have lower mortality rates than estimated before.

Migration routes of European Bar-tailed Godwits

Bar-tailed Godwits of the European population are considered to breed in northern Fennoscandia and to winter mainly around the North Sea (Smit & Piersma 1989, Drent & Piersma 1990) whereas birds from the Afro-Siberian population winter in West Africa (Mauritania and Guinea-Bissau) and breed in Siberia (Taymyr and Yamal, Smit & Piersma 1989, Drent & Piersma 1990, Wymenga et al. 1990). Comparison of morphometric data from birds caught in the Königshafen with birds from the different breeding areas gives strong indication that the birds occurring in the Königshafen breed in northern Fennoscandia (Tab. 4.3): no difference was found in bill length and wing length (t-test for both measurements and sexes, $p > 0.05$). Additionally, birds breeding in central Siberia have shorter bills and wings than the Königshafen birds (t-test for both measurements and sexes, $p < 0.05$). As shown by ringed birds, wintering areas for Bar-tailed Godwits using the Königshafen as a stopover site are located in Great Britain and the Wadden Sea. Furthermore, morphometric data from birds wintering in West Africa indicated that these Bar-tailed Godwits were smaller and thus do not belong to the European population (Wymenga et al. 1990). Thus,

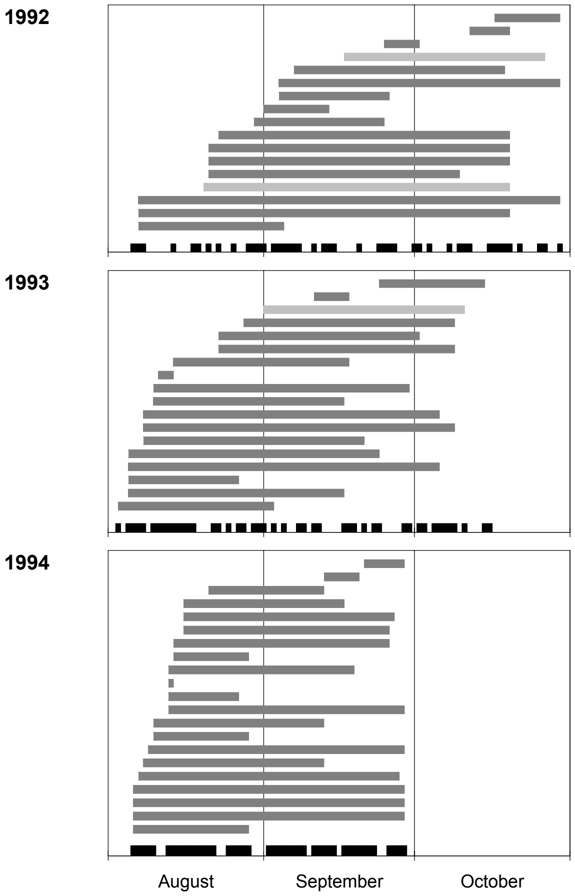


Fig. 4.11: Length of stopover of individually colour ringed Bar-tailed Godwits in the Königshafen area in autumn; see Fig. 4.9.

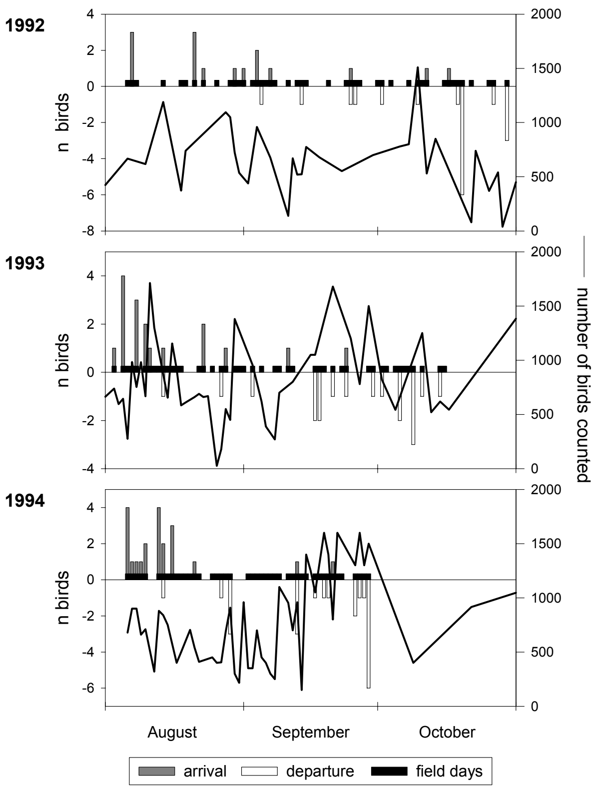


Fig. 4.12: First (‘arrival’) and last (‘departure’) day of observation of individually colour ringed Bar-tailed Godwits in the Königshafen area in autumn, see Fig. 4.10.

Bar-tailed Godwits occurring in the Königshafen and most probably at other roosts with similar phenology on the island of Sylt, belong to the European population.

For European Bar-tailed Godwits the following migration pattern emerges (Fig. 4.13): birds winter around the North Sea with the Sylt-Rømø Wadden Sea as one of the northeasternmost wintering sites (Smit & Piersma 1989, Meltofte et al. 1994). In late January or February, most Bar-tailed Godwits leave the northern part of the Wadden Sea. This decrease in numbers is paralleled by a slight increase in the western parts and a large increase on the Wash (Meltofte et al. 1994, Atkinson 1996), so that birds move to these areas for a short period of time to escape high thermostatic costs (Scheiffarth & Nehls 1998). In March, birds return to the Wadden Sea; some of these birds fly directly to the northern part of the Wadden Sea whereas others seem to stopover for a brief period in the western part (Meltofte et al. 1994). In late April, almost all Bar-tailed Godwits from the European population seem to gather in the Danish and northern German Wadden Sea, similar to the nearctic Knot (*Calidris canutus islandica*) which overwinters in western Europe (Meltofte et al. 1994, Piersma et al. 1994). In the first half of May, European Bar-tailed Godwits depart to their Fennoscandian breeding sites where they could be observed from mid May onwards (Byrkjedal et al. 1989). In autumn, migration seems to be more complex. Numbers of Bar-tailed Godwits in the Wadden Sea are lower than in spring (Meltofte et al. 1994) which can be caused by shorter stopover times and/or by birds not visiting the same stopover areas as in spring. In contrast to the high stopover site fidelity in spring, less than half of these birds used the Königshafen area in the northern Wadden Sea during autumn migration. Ringing controls, as well as the phenology on the Wash (Atkinson 1996), indicate that some birds migrate directly from the breeding area to Great Britain. Others arrive in the northern Wadden Sea in August but move on to further sites in September, indicating that some European migrants may use shorter stopover times than in spring. Another group of birds arrives in August and September and stays in the northern Wadden Sea until late autumn, or even overwinters in the area.

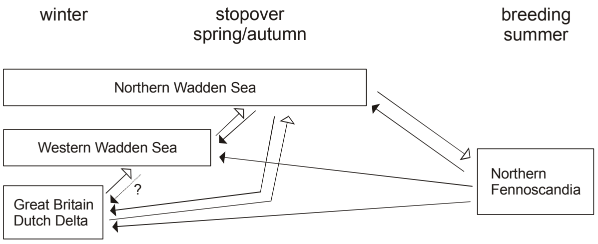


Fig. 4.13: Proposed migration patterns of European Bar-tailed Godwits. Open arrows represent spring migration, black arrows autumn migration.

Differential migration in European Bar-tailed Godwits?

Several authors state an excess of males in the Bar-tailed Godwit populations wintering along the East Atlantic flyway (Cramp & Simmons 1983, Piersma & Jukema 1990, 1993, Zwarts et al. 1990, Atkinson 1996). This is in contrast to what has been found in the northern Wadden Sea during spring migration, where equal numbers of males and females were observed (this study, cf. Tab. 4 in Prokosch 1988). There are two points to keep in mind when determining sex ratios in Bar-tailed Godwits. Males and females may use different habitats for foraging and roosting or occupy distinct positions within flocks (Smith & Evans 1973, Zwarts et al. 1990, own obs.), so that unequal sex ratios could be an effect of catching method or place as stated by Cramp & Simmons (1983). Furthermore, one has to distinguish between populations, since there is no reason to assume that the sex ratio is the same in all

Table 2: Return rates of Bar-tailed Godwits in the area around List/Sylt. Given are the number of identified birds per season and the percentage of birds resighted from the number of ringed adult birds per season. Birds were caught in the Königshafen near List. Birds with unknown season of ringing were individuals with incomplete colour ring combinations due to loss of rings. For effort to identify birds, number of days with reading attempts are given in the second row of the column heads.

season of ringing	number of birds ringed	autumn 1992 44	spring 1993 43	autumn 1993 46	spring 1994 66	autumn 1994 44	spring 1997 7
spring 1992	88	23 (26.1 %)	47 (53.4 %)	22 (25 %)	60 (68.2 %)	33 (37.5 %)	14 (15.9 %)
autumn 1992	4		2 (50 %)	2 (50 %)	1 (25 %)	1 (25 %)	1 (25 %)
spring 1993	27			6 (22.2 %)	20 (74.1 %)	9 (33.3 %)	5 (18.5 %)
autumn 1993	1				1	1	1
unknown							5
sum	120	23 (26.1 %)	49 (53.3 %)	30 (63.3 %)	82 (36.7 %)	44 (36.7 %)	26 (21.7 %)

populations. In particular, this may be the case if different selection pressures act on these populations, as is evident for European and Afro-Siberian Bar-tailed Godwits (Drent & Piersma 1990).

For the Afro-Siberian population, most estimates of sex ratio resulted in an excess of males. In particular, in the main wintering area in Mauritania two different methods came up with similar results (Piersma & Jukema 1993). In Guinea-Bissau, another important wintering area along the African West coast, where 23 % of the Afro-Siberian population overwinters (Smit & Piersma 1989), sex ratio equals 1 (Zwarts 1988). Taking the numbers of both wintering areas together, there might be a real excess of males in the Afro-Siberian population. Thus, the equal sex ratio in Guinea-Bissau indicates differential use of wintering areas by males and females, with females migrating further south.

For European Bar-tailed Godwits in the northern Wadden Sea, no male bias could be established (Prokosch 1988, Fig. 4.4). In winter, even the opposite is the case, with an excess of females being present. In contrast, in the Wash in all months a male bias in catches exists with an increase in the proportion of males in January and February, which is not considered to be an artefact of the catching method (Atkinson 1996). This complementary picture of sex ratios between European wintering sites suggests a differential migration of Bar-tailed Godwits, which is not unusual for a species with such a strong sexual dimorphism (Ketterson & Nolan 1983). Females, as the larger sex, may prefer to stay in the northern Wadden Sea as close to the breeding areas as possible, whereas males emigrate to milder wintering areas in Great Britain which might be related to the higher thermostatic costs of males compared to females (Scheiffarth 1996).

Tab. 4.3: Comparison of wing and bill length of birds caught in March in the Königshafen with measurements from potential breeding areas. Data for birds from Northern Fennoscandia including the White Sea and the Kanin peninsula (N. Fennoscandia) as well as Yamal and Taymyr (Taymyr) were taken from Engelmoer & Roselaar (1998).

	wing	SD	n	bill	SD	n
males						
Königshafen	218.6	5.3	76	80.7	3.3	76
N. Fennoscandia	218.1	5.8	33	81.4	4.2	33
Taymyr	214.9	4.5	41	78.8	3.9	41
females						
Königshafen	231.8	6.3	42	99.3	5.9	43
N. Fennoscandia	230.8	6.1	23	101.6	5.3	23
Taymyr	227.0	4.4	29	96.0	4.4	29

Acknowledgements

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5. The diet of Bar-tailed Godwits *Limosa lapponica* in the Wadden Sea: combining visual observations and faeces analyses

Gregor Scheiffarth

Abstract

Estimating diet composition of Bar-tailed Godwits *Limosa lapponica* by visual observations was hampered by large amounts of unidentified prey items. Therefore, additional analyses of faeces were conducted. Overall, 17 prey species were found in the droppings, but only four polychaetes, the Lugworm *Arenicola marina*, the Estuary Ragworm *Nereis diversicolor*, the Catworm *Nephtys hombergii*, *Scoloplos armiger* and one crustacean, the Shore Crab *Carcinus maenas* were taken regularly by the birds. In faecal samples the number of polychaete chaetae, hooks, jaws and bivalve umbos were estimated, which allowed in the case of *Nereis diversicolor*, *Nephtys hombergii*, *Scoloplos armiger* and the Baltic Tellin *Macoma balthica* an estimation of the minimum number of prey individuals per dropping. The ratios of these prey species to each other in the faeces were used to correct for the unidentified prey taken during observations. The diet of Bar-tailed Godwits showed a seasonal pattern, as well as differences between males and females. Diet was similar between the sexes in winter with *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger* comprising 99 % of the prey items taken. In spring 20 % of the prey items of males were *Macoma balthica*, whereas females took the Sand Mason *Lanice conchilega* instead. In late summer *Arenicola marina* was an important prey for females but its importance decreased with decreasing prey availability in autumn. Towards winter the proportion of small polychaete species like *Scoloplos armiger* and *Nereis diversicolor* increased in the diet.

Introduction

The knowledge of diet composition of predators is fundamental for the understanding of their foraging ecology. For birds, several methods have been proposed to quantify diet composition (e. g. Hartley 1948, Pienkowski et al. 1984, Duffy & Jackson 1986, Rosenberg & Cooper 1990). However, each method has its drawbacks, so that relying on one method alone may lead to biased results. Indirect methods such as analyses of stomach contents, regurgitates, pellets, or droppings have in common that prey organisms have already entered the digestive tract before analysis. Thus, problems with differential digestibility or detectability in the samples have to be taken into account when estimating the composition of the consumed diet (e. g. Greenwood & Goss-Custard 1970, Jenni et al. 1990, Rosenberg & Cooper 1990). On the other hand, direct visual observations of foraging birds often yield large amounts of unidentified prey, even for waders which forage in open, accessible habitats and are relatively easy to observe (e. g. Goss-Custard et al. 1977, Evans et al. 1979, Altenburg et al. 1982, Kalejta 1993, Peréz-Hurtado et al. 1997). For a quantification of the diet two possibilities are feasible: (a) a recalculation of the diet from indirect methods on the basis of feeding experiments (e. g. Green 1978 & 1984, Galbraith 1989, Jenni et al. 1990) which can go as far as the calculation of intake rates on the basis of faecal analysis (Dekinga & Piersma 1993). Analyses of pellets, droppings, or stomach contents often have the advantage that prey size can be calculated, if any indigestible parts of the prey species exist which relate to the size of the individual prey eaten. (b) The correction of visual observations by means of the indirect methods. Until now this has not been carried out and results of both methods have been presented separately.

In this paper seasonal and sexual differences in diet composition of Bar-tailed Godwits *Limosa lapponica* are presented on the basis of the combination of visual observations and dropping analysis, as visual observations alone resulted in 64 % unidentified prey items.

Bar-tailed Godwits breed from northern Scandinavia to Siberia and winter mainly in the western Wadden Sea, Great Britain, and West Africa (Cramp & Simmons 1983, Drent & Piersma 1990). During their stop-over in the Wadden Sea in spring birds increase their body mass, fuelling up for their up to 4000 km long-distance flights (Prokosch 1988, Drent & Piersma 1990). Individuals that winter in the Wadden Sea must cope with highly seasonal fluctuations of prey availability (Zwarts & Wanink 1993). Furthermore, Bar-tailed Godwits are highly sexually dimorphic (Prokosch 1988), so that differences in prey choice between the sexes are expected.

Methods

Study area

Collection of droppings and observations were carried out at tidal flats near List, Sylt in the northern European Wadden Sea (55°01'N, 8°26'E). Sediments consist mainly of coarse sand (Austen 1994, see Reise 1985 for a further description of the study area). On an annual average, Bar-tailed Godwits make up 17 % of the bird community of this area (Scheiffarth & Nehls 1997). The phenology of Bar-tailed Godwits shows the typical pattern of a stopover and wintering site for arctic breeding waders with high numbers from March to May, a low in June/July during the breeding season with almost no Bar-tailed Godwits present in the study area, and again higher numbers form August onwards to mid January (Scheiffarth 2001a).

Analysis of droppings

Droppings were collected during low tide at least once per month from August 1991 to April 1992. Radio tracking data confirmed that the median time Bar-tailed Godwits foraged on the same patch is 1 hour (Scheiffarth unpubl. data). Observations of captive Bar-tailed Godwits showed that the mean time between the start of feeding and the production of the first dropping took 28 min (Scheiffarth unpubl. data), which makes it likely, that at least part of the droppings collected on the mudflats represent local prey. Droppings were found and identified by following the tracks of Bar-tailed Godwits on the mudflats (cf. dit Durell & Kelly 1990). Entire droppings were scraped off the surface and preserved in 70 % ethanol. For analysis the samples were treated with ultrasound for at least for 10 min, resulting in a separation of sand and soft parts. After sedimentation for 1-2 min the supernatant was put over a 64 µm sieve and the parts retained were analysed in a 25 cm^3 cylindrical chamber with a diameter of 25 mm. All chaetae and aciculae of polychaetes were identified to species level (Friedrich 1938, Hartmann-Schröder 1971) by means of an inverted microscope (x 25 - 400). All parts were counted on three transects which allowed a calculation of the number of chaetae per species in the entire sample (see Tab. 5.1 for species and parts counted). Specific identification of the chaetae was facilitated by a reference collection of specimens from the study area (see also Dernedde 1993). Chaetae for the reference collection were obtained by digesting the worms in a bath of pepsin (from porcine gastric mucosa, 700 FIP-U/g, 0.7 Ph Eur-E/mg, Merck, Darmstadt) and HCl (10 % pepsin concentration in fresh water, pH 1.6).

Tab. 5.1: Parts of species counted in droppings.

Species	parts counted
Nereis diversicolor	jaws, aciculae, chaetae
Nephtys hombergii	jaws, aciculae, chaetae
Arenicola marina	chaetae, thoracic hooks
Lanice conchilega	chaetae, thoracic hooks
Scoloplos armiger	chaetae, thoracic hooks
other polychaetes	chaetae
Macoma balthica	umbos

The sand fractions were searched for hard parts of crustaceans and molluscs, and polychaete jaws with a stereo-microscope (x 8 - 64). For the umbos of the Baltic Tellin *Macoma balthica*, the jaws of the Estuary Ragworm *Nereis diversicolor* and the Catworm *Nephtys hombergii* calibration curves were constructed from locally collected specimens (Fig. 5.1) which allowed the estimations of body lengths (shell length or worm length) from these parts. For the calculation of calibration lines the function giving the best fit for the available data were used. Worm lengths were taken, after anaesthetising the worms with $MgCl_2$ (80 g l^{-1}, Hulings & Gray 1971), from relaxed individuals without stretching them to maximum length. The umbos of *Macoma balthica* were measured according to Zwarts & Blomert (1992). The jaws of *Nereis diversicolor* were measured from the base of the proximal ‘tooth’ to the distal end of the jaw, which differs from the method applied by Zwarts & Esselink (1989). They measured from the tip of the proximal ‘tooth’ to the distal end of the jaw, resulting in slightly shorter jaw lengths. From *Nephtys hombergii* maximum jaw length was measured from the base to the distal end. As this method was developed in parallel to the analysis of the droppings, length estimates for this species are only available for spring samples.

As a control, on each sampling date and place a 0-sample was taken, which consisted only of surface sediment and was treated in the same way as the droppings. Usually no prey remains were found in the 0-sample, otherwise a species was only counted in a

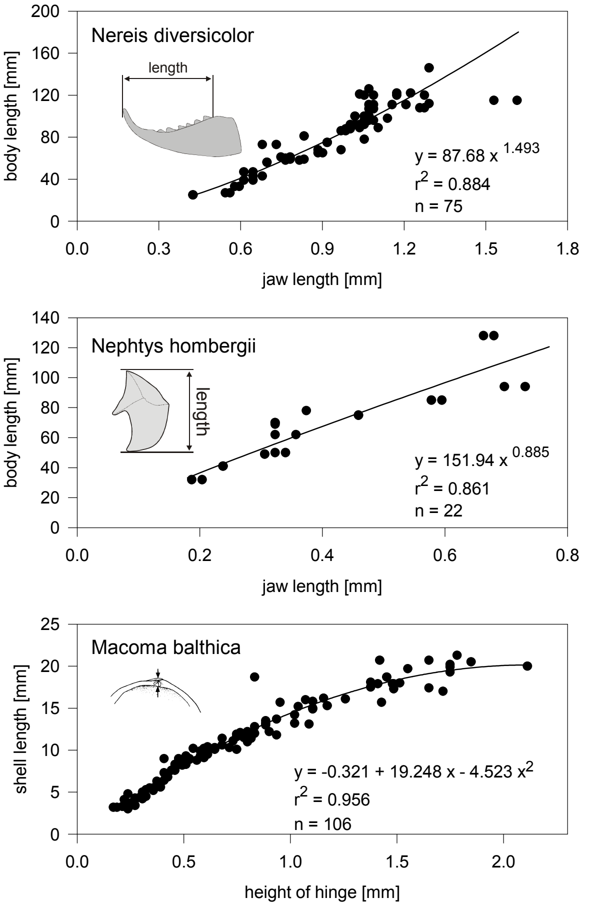

Fig. 5.1: Regressions for estimating worm lengths of *Nereis diversicolor* and *Nephtys hombergii* on the basis of jaw length, and the shell length of *Macoma balthica* on the basis of umbo width. Regression statistics for *Nereis diversicolor* and *Nephtys hombergii* were calculated with ln-transformed data.

sample, when the number of chaetae or other parts was larger than in the corresponding 0-sample.

Although usually more than one type of fragment per species was counted in one sample, the most obvious part which was easiest to count was chosen to be representative in all samples. If instead only other parts were counted in a sample, for comparability the numbers of the 'representative' part was calculated on the basis of the regressions from Tab. 5.2. For all calculations, only droppings with at least one identifiable part were considered. Empty droppings were discarded. After some practise with the identification of chaetae, the entire procedure for analysing one sample took 2 - 3 hours.

Counting all different parts in a sample, especially small ones like hooks, aciculae, and chaetae was not always possible, therefore the contents of all samples could not be quantified. Depending on the difficulty of the identification of various parts, the proportion of quantified parts differs between species. Counting chaetae and hooks of *Scoloplos armiger* proved to be particularly difficult, since these parts require a high microscopic magnification to identify. If large amounts of undigested flesh, pieces of carapaces or other undigested remainings of food made visibility poor, it was impossible to count these small parts. However, for most prey species in 85 – 95 % of all samples collected at least one body part could be quantified.

Calculation of the number of individuals in a sample

The number of individuals per sample could be determined for *Nereis diversicolor*, *Nephtys hombergii*, *Macoma balthica*, and *Scoloplos armiger*. In all other species either no unique body part was found in the droppings (e.g. Shore Crab *Carcinus maenas*) or these species have no parts which allow the calculation of the number of individuals represented in the droppings. For *Nephtys hombergii* and *Nereis diversicolor* the number of jaws in a sample divided by two was taken as the minimum number of individuals. If no jaws were found, regressions between the number of jaws and the number of chaetae or aciculae (Tab. 5.2) were used to estimate the number of jaws. Similarly, the minimum number of *Macoma balthica* was calculated by dividing the number of umbos by two.

Tab. 5.2: Relation between different countable parts in droppings within species.

species	regression	r^2	p	n
Nereis diversicolor	# aciculae = 0.0517* # chaetae + 35.08	0.395	0.001	28
	# jaws = 0.0265 * # aciculae + 0.11	0.742	< 0.001	56
	# jaws/# chaetae		n.s.	
Nephtys hombergii	# aciculae = 0.159 * # chaetae - 11.5	0.659	< 0.001	30
	# jaws = 0.0171 * # aciculae - 0.294	0.605	< 0.001	54
Arenicola marina	# chaetae/# thoracic hooks		n.s.	
Scoloplos armiger	# thoracic hooks = 0.348 * # chaetae + 89.1	0.658	< 0.001	34

Since *Scoloplos armiger* has no jaws or other indigestible structures which allow a direct conclusion on the number of individuals, a different approach was used. *Scoloplos armiger* has 12 - 22 thoracic segments (Hartmann-Schröder 1971). Each segment has 40 thoracic hooks, hence each individual should have 480 - 880 thoracic hooks. Usually, in faecal analysis not all chaetae or other soft parts are retained for analysis, so that a correction has to be made (e. g. Jenni et al. 1990). Since no feeding experiments with *Scoloplos armiger* were carried out, the probability that a thoracic hook was found in the faeces was based on a calculation with the chaetae of *Nereis diversicolor*. Moreira (1995) gives a regression between the length of *Nereis diversicolor* and the number of setigers. Furthermore, he estimated the mean number of chaetae per setiger as 28.2. Alternatively, the calculation can be carried out with the number of aciculae per setiger (4; Hartmann-Schröder 1971), which provides the same final result. Since the length of the *Nereis diversicolor* in the faeces was known from the relationship between jaw-length and worm-length and furthermore the minimum number of *Nereis diversicolor* in the droppings was known, the number of chaetae or aciculae which should be present in a dropping could be calculated. According to these calculations, 17.5 % of *Nereis diversicolor* chaetae were retained in the sample. Assuming the same proportion for the thoracic hooks of *Scoloplos armiger*, 84 - 154 hooks per individual should be in a sample. In order to calculate the number of *Scoloplos armiger*, an intermediate number of 119 thoracic hooks per individual was used. If visibility for *Scoloplos armiger* thoracic hooks as a result of their smaller size is poorer than for *Nereis diversicolor* chaetae, this calculation would lead to an underestimate of *Scoloplos armiger* in the diet of Bar-tailed Godwits.

Tab. 5.3: Species found in droppings and mean percentage (x) of droppings with occurrence per sampling date. CV = Coefficient of Variation; n date: number of sampling dates with occurrence of species; total number of droppings: 131; total number of sampling dates: 10.

species	x	CV	n date
Arenicola marina	38.0	83.0	8
Nereis diversicolor	48.1	40.8	9
Nephtys hombergii	60.6	54.1	9
Scoloplos armiger	78.1	31.1	10
Lanice conchilega	9.0	122.2	6
Anaitides spec.	3.0	234.9	2
Pygospio spec.	2.3	173.9	3
Eteone longa	2.4	216.0	2
Lumbricus spec.	2.1	316.2	1
Harmothoë impar	2.8	223.3	2
Carcinus maenas	14.3	84.8	9
Crangon crangon	6.9	117.6	5
Gammarus spec.	0.8	316.2	1
Crustacea spec.	5.5	152.0	4
Cerastoderma edule	1.7	235.8	2
Macoma balthica	17.5	155.0	6
Ensis spec.	2.1	216.0	2
Pisces spec.	1.9	213.5	2

Visual observations

From August 1991 to October 1993 individual birds foraging on tidal flats were observed for as long as possible and behaviour was recorded on a continuously running tape recorder (focal animal sampling, continuous recording; Martin & Bateson 1986). Observations were conducted from observation towers, dikes, and by following flocks of foraging Bar-tailed Godwits on foot. All ingested species and their estimated sizes were recorded. Ingested prey were converted into biomass according to Scheiffarth (1995). Only birds observed longer than 270 s were included in the analysis. Sex of the birds was determined through a telescope by the relationship between bill length and body size which is different for males and females (Scheiffarth 2001a, Zwarts et al. 1990).

For statistical analysis of diet composition, the proportion of the different prey organisms in the diet was calculated for each bird. Thereafter the mean proportion per sex and month for each prey organism was calculated. Before testing for differences in diet composition, all proportions were arcsine transformed (Sachs 1984). With these data a two-factorial MANOVA was performed. As test criterion Pillai's Trace statistic, transformed to approximate the F distribution was taken (Norusis 1986).

Results

Overall, 17 prey species were found in droppings of which 10 were polychaetes (Tab. 5.3). Only the polychaetes Lugworm *Arenicola marina*, *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger*, as well as the crustacean Shore Crab *Carcinus maenas* were regularly taken by Bar-tailed Godwits. The other species showed low frequencies of occurrence in the droppings and/or a high coefficient of variation. The occurrence of most of these species was restricted to autumn.

The occurrence of major prey species in droppings likewise showed a distinct monthly variation within the

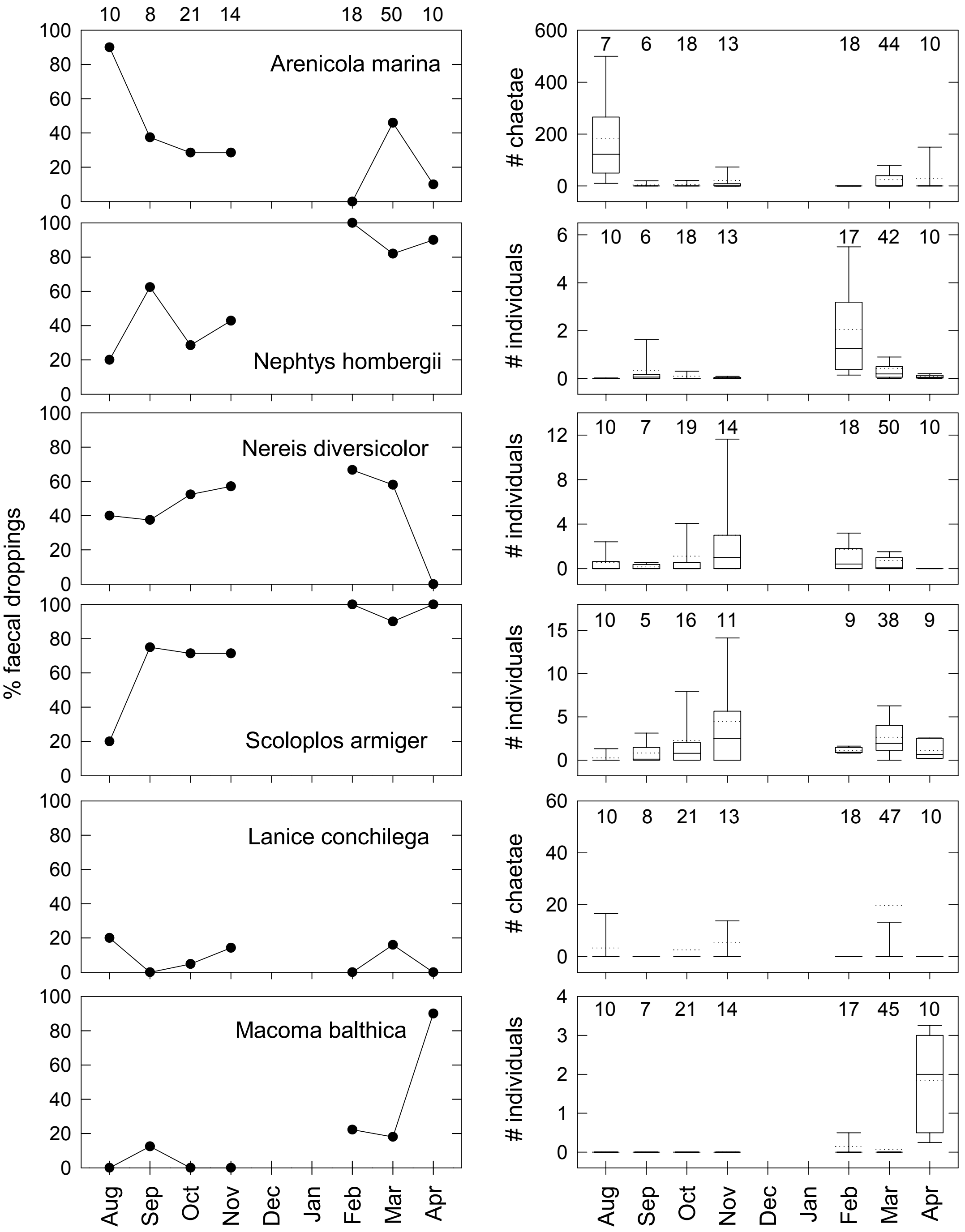

Fig. 5.2, left: Monthly variation of occurrence of main prey species in droppings, 100 % = all droppings collected each month with at least one identifiable part. right: Box plots of seasonal variation of number of chaetae or minimum number of individuals per dropping; box represents 50 %, error bars 90 % of the data, straight line in 50 % box denotes median, and dotted line the mean. Numbers represent the number of samples analysed.

study year (Fig. 5.2, left). In August Bar-tailed Godwits took relatively many *Arenicola marina*. Towards winter, the proportion of droppings with small polychaete species, namely *Nephtys hombergii*, *Nereis diversicolor*, and *Scoloplos armiger*, increased in concurrence with a decrease of the proportion of *Arenicola marina*. In February these small polychaetes dominated the diet. In spring *Scoloplos armiger* and *Nephtys hombergii* were taken regularly and the importance of *Macoma balthica* rose sharply, whereas *Nereis diversicolor* disappeared.

For most prey species a similar monthly pattern in the study year emerged if the mean numbers of individuals or chaetae per dropping are considered (Fig.

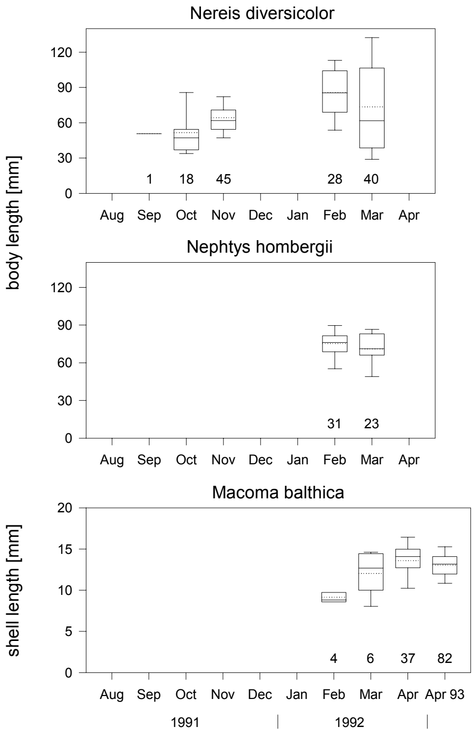

Fig. 5.3: Variation of prey size for *Nereis diversicolor*, *Nephtys hombergii*, and *Macoma balthica*. Prey-size was calculated from contents of droppings using the regressions from Fig. 5.1. Box represents 50 %, error bars 90 % of the data, straight line in 50 % box denotes median, and dotted line denotes mean. Numbers represent the number of parts measured. Note that *Macoma balthica* was found both in April 1992 and April 1993.

5.2, right). However, there are also marked differences between the two patterns. Although the proportion of droppings containing *Nephtys hombergii* remained high during spring, the number of individuals decreased from 2.05 ind. dropping^{-1} to 0.08. The number of *Scoloplos armiger* per dropping remained low throughout winter and spring despite the fact, that this species was present in almost every dropping.

Besides the seasonal pattern in prey choice also the sizes of prey taken by the birds varied between the months studied (Fig. 5.3). In *Nereis diversicolor* the mean worm length increased from 51.7 mm in September/October to 85.6 mm in February (Kruskal-Wallis, $\chi^2 = 21.12$, df = 4, $P < 0.01$). In February the same mean worm size as in *Nereis diversicolor* was taken in *Nephtys hombergii* (M-W U-Test, U = 561, $p > 0.05$). In both species no change in prey size between February and March could be detected (M-W U-Test, *Nereis diversicolor*: U = 704, $p > 0.05$, *Nephtys hombergii*: U = 286, $p > 0.05$). *Macoma balthica* taken by Bar-tailed Godwits increased in average shell length from 9.2 mm in February to 13.6 mm in April (Kruskal-Wallis, $\chi^2 = 7.9$, df = 2, $p < 0.05$). The same Macoma sizes were taken as prey one year later, in April 1993, the only month when samples containing *Macoma balthica* were collected in that year (M-W U-Test, U = 1851, $p > 0.05$).

The results from faecal analyses were used to correct the visual observations. For a correction of the prey category '*Nereis*/*Nephtys*' for each month the relative proportions of the two species in the droppings were used. Likewise, for the prey category 'unidentified' it was assumed that it consisted of *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger*. All other prey species detected in the faeces were either considered to be insignificant (Scaleworm *Harmothoë impar*, *Eteone longa*, Paddleworm *Anaitides sp*., *Pygospio sp*., Earthworm *Lumbricus sp*., gammarids *Gammarus sp*., American Jackknife Clam *Ensis directus*, fish *Pisces sp*.) or showed a similar pattern between observations and droppings, so that a correction was not considered to be necessary. Thus, the relative proportions of *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger* were calculated for each month. For each individual bird observed, the categories '*Nereis*/*Nephtys*' and 'unidentified' were multiplied with the corresponding proportions.

Prey composition based on the corrected number of individuals taken during observations (Fig. 5.4) showed a clear difference between months (MANOVA, $F_{56,1449} = 11.14$, $p < 0.001$), as well as, a marked difference between males and females (MANOVA, $F_{8,201} = 4$, $p < 0.001$). Furthermore, the monthly patterns differed between the two sexes (two-way interactions, MANOVA, $F_{56,1449} = 1.7$, $p < 0.01$). Overall, 94 % of all prey items taken by Bar-tailed Godwits were polychaetes (males 91 %, females 96 %), of which the largest proportion comprised *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger*. The importance of these polychaetes was most pronounced in winter, with an increasing importance of *Scoloplos armiger* in autumn and a large proportion of *Nephtys hombergii* in February. Crustaceans played a minor role, and only so in autumn which is related to the availability of these species on intertidal flats (Boddeke 1976, Beukema 1991 & 1992, Herrmann et al. 1998). Sex differences in diet composition were due to *Arenicola marina* and Sand Mason *Lanice conchilega*, which were more often taken by females than by males (ANOVA, *Arenicola marina*: $F_{1,208} = 14.33$, $p < 0.001$, *Lanice conchilega*: $F_{1,208} = 13.02$, $p < 0.001$). For females *Arenicola marina* was an important prey species in August, but towards winter it nearly disappeared from the diet (ANOVA, $F_{7,97}$

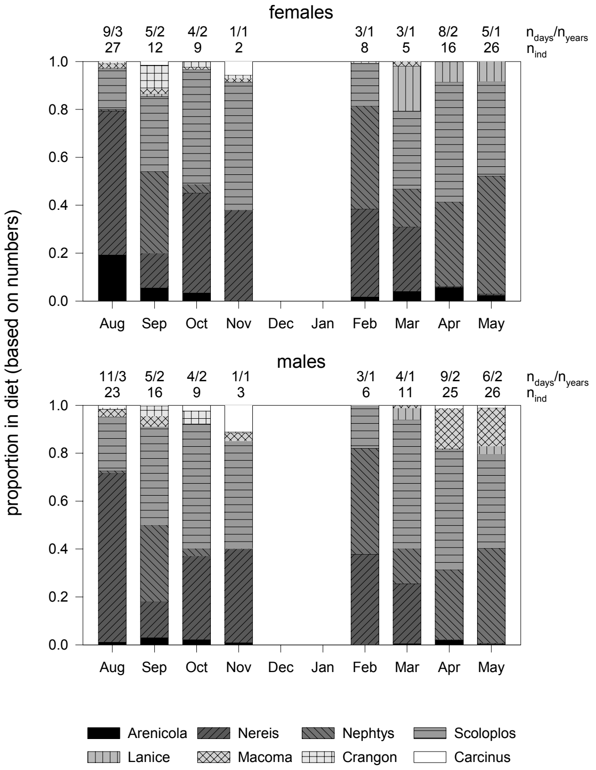

Fig. 5.4: Seasonal variation of diet composition (by numbers) for female and male Bar-tailed Godwits as determined by corrected visual observations on the basis of faeces analyses. Numbers above bars represent number of birds observed (n_{ind}), number of years with observations (n_{years}) and number of days with observations (n_{days}).

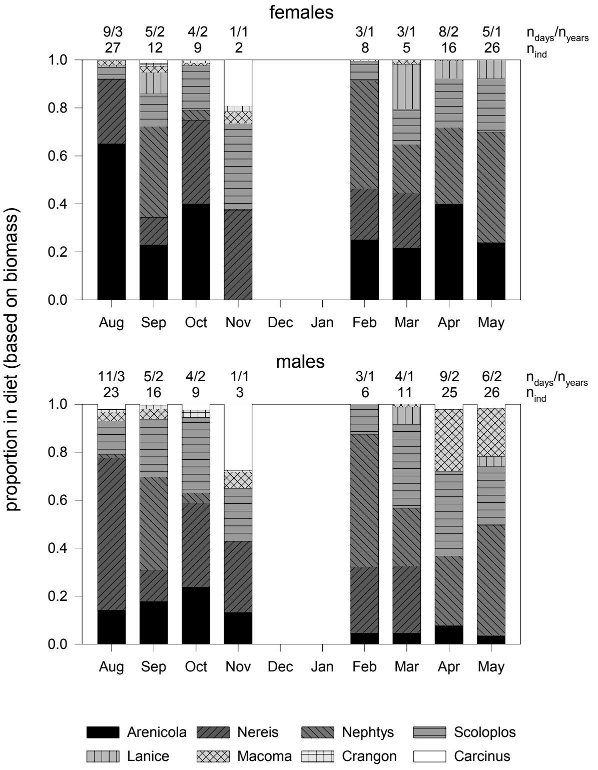

Fig. 5.5: Seasonal variation of diet composition (by biomass) for female and male Bar-tailed Godwits as determined by corrected visual observations on the basis of faeces analyses. Numbers above bars as in Fig. 5.4.

= 4.68, $p < 0.001$), whereas *Lanice conchilega* was most often taken in spring (ANOVA, $F_{7,97} = 2.66$, $p < 0.02$). On the contrary, *Macoma balthica* was an important prey for males in spring (ANOVA, $F_{7,111} = 2.88$, $p < 0.01$). Diet composition differed most strongly between sexes in August and became more similar towards winter. In February the diet of males and females was almost identical, *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger* together comprising 99 % of all prey by numbers. From March onwards, diet composition differed again between the sexes with the largest differences within the annual cycle in April and May.

When considering prey biomass composition, the importance of *Arenicola marina* in the diet of females becomes even more pronounced, particularly in August (65 %, Fig. 5.5). Even for males the proportion of *Arenicola marina* comprised up to 24 % of the diet. Although overall prey composition based on biomass differs between the two sexes (MANOVA, $F_{8,201} = 3.94$, $p < 0.001$), *Arenicola marina* is the only species where a significant difference can be found (ANOVA, $F_{1,208} = 10.9$, $p < 0.01$). In contrast to *Arenicola marina*, the importance of *Scoloplos armiger* is much lower as compared to the proportions based on numbers (see Fig. 5.4). Nevertheless, this species still makes up 25 % of the diet of males and 17 % of the diet of females, by mass.

Discussion

Like in many other wader studies (e. g. Goss-Custard et al. 1977, Altenburg et al. 1982, Kalejta 1993, Peréz-Hurtado et al. 1997), a high proportion of the prey remained unidentified during the observations. However, for the construction of energy budgets (Scheiffarth 1995, Scheiffarth & Bairlein 1998a), prey intake has to be estimated with the highest possible precision and diet composition must be known quantitatively. Goss-Custard (1973) recommended, that ‘as much as possible should be described by the observations and any gaps should be filled by the analysis of pellets and droppings’. Many alternatives for determining diets, based on the examination of contents or remainings from the digestive tract, exist (Pienkowski et al. 1984, Duffy & Jackson 1986, Rosenberg & Cooper 1990). In the case of Bar-tailed Godwits the analysis of faeces has several advantages over other methods (see Verkuil 1996). Bar-tailed Godwits are difficult to catch on the feeding grounds, so that stomach flushing is no serious alternative. Since Bar-tailed

Tab. 5.4: Diet composition of Bar-tailed Godwits in different stop-over and wintering sites: Banc d'Argiun (Mauretania), Cádiz Bay (Spain), The Wash, Tees and Lindisfarne (Britain) and Königshafen (Germany). Figures are percentages of occurrence of prey species in gizzards or proventriculus, pellets, and faeces or the percentage of the total number of prey ingested, as determined by visual observations. If more than one area or period was available, the mean percentage was calculated.

Species	Banc d'Arguin observ. [a]	Cádiz Bay faeces[b]	Cádiz Bay observ.[b]	Wash faeces, pellet, gizzard[c]	Wash observ.[c]	Tees observ.[d]	Lindisfarne oesoph., proventr.[e]	Lindisfarne observ.[e]	Königs-hafen corr. observ.[f]
Coleoptera spec.		5.5							
Mollusca spec.	9.5	16.6			13.8				
Macoma balthica				95.7		2	52.4	2.6	3.3
Cerastoderma edule				16.3			9.5		
Scrobicularia plana							4.8		
Tellina tenuis							4.8		
Hydrobia ulvae			9.3	9.8					
Nereis diversicolor		83.3	61.7	13.0		80	9.5	1.4	27.6
Nephtys hombergii				1.1					21.6
Lanice conchilega					15.2			0.9	2.9
Arenicola marina					1.2		66.7	37.7	3.3
Scoloplos armiger							14.3	57.4	38.2
Diopatra spec.		11.1							
Polychaeta spec.	13.5				21.0				
Crangon crangon									1.6
Carcinus maenas				12.0	0.1	2			1.5
Seeds		38							
unidentified	77		29	9.8	48.8	16			

[a] Piersma 1982, [b] Peréz-Hurtado et al. 1997, [c] Goss-Custard et al. 1977, [d] Evans et al. 1979, [e] Smith 1975, [f] this study

Godwits seldom produce pellets and have never been observed doing so during this study, the vast majority of the indigestible remainings of prey organisms must pass the gut and leave the birds within the faeces. Furthermore, analysing droppings is a non-invasive method and samples are easy to collect (dit Durell & Kelly 1990, Verkuil 1996).

The analysis of faeces only by means of a binocular microscope is insufficient for detecting the remains of all prey species. Many small parts may be missed in this way and a compound microscope with a x 250 magnification or a phase contrast microscope (Moreira 1995) must be used. At least all polychaetes have some indigestible parts (chaetae, hooks) which are detectable in this way (see Moreira 1995). The method used in this study, using an inverted microscope, has the advantage that the entire sample can be surveyed and no extra preparations have to be made nor do subsamples have to be taken.

Assessing the numbers of different parts in a dropping goes one step further than determining the percentage of samples with the occurrence of a prey species. Counting parts offers the opportunity to estimate the minimum number of individuals per prey species and dropping, and seasonal changes in the relative importance of prey species can be determined (see Mouritsen 1994). When presenting both the frequency of occurrence and the mean number of parts per dropping, as recommended by Duffy & Jackson (1986) and Rosenberg & Cooper (1990), it becomes obvious that these are not always correlated (contrary to Goss-Custard & Jones 1976). As shown by the example of *Scoloplos armiger*, some prey species are taken regularly by most of the birds (a high proportion of droppings contain this species) but the importance in the diet varies seasonally (the mean number of individuals per dropping fluctuates). Although *Scoloplos armiger* is also the prey of *Nephtys hombergii* (Schubert & Reise 1986, Beukema 1987) and therefore parts of *Scoloplos armiger* may have entered the birds via *Nephtys hombergii*, observations have shown that *Scoloplos armiger* was regularly taken by Bar-tailed Godwits as prey in all months of observation.

Nevertheless, the method of analysing the droppings as presented here still has some shortcomings. The number of jaws, chaetae, or hooks counted must be in some way related to the number of prey organisms actually ingested, but this relationship is yet unknown. The processes which act on these parts during digestion have not been studied in detail, so that feeding experiments are needed for the interpretation of the number of parts found in the faeces (Green 1978 & 1984, Galbraith 1989, Jenni et al. 1990, Robinson & Stebbings 1993). Furthermore, different prey species are digested at various rates or have different detection rates. This might result in a different relation of the indigestible parts to each other in the faeces as compared to the ingested prey (e. g. Greenwood & Goss-Custard 1970, Jenni et al. 1990).

As Carss & Parkinson (1996) concluded from feeding trials, analysing faeces gives a good estimate of the ranks of different prey species in the diet but offers a poor indicator for the true proportions consumed. This problem was circumvented in the present study. By combining observations and faeces analyses the true proportions of the staple food species could be estimated. Only prey of minor importance were missed by the observations, so that the entire spectrum of prey organisms was not covered by this method, resulting in only 8 prey species as opposed to 17 by faecal analysis. However, the missing 9 prey species in the observations were taken so rarely, that they can be considered insignificant in the diet of Bar-tailed Godwits.

For further progress it would be desirable to distinguish between the faeces from males and females. In this study a distinction between droppings of both sexes was impossible, so that a single correction factor for the observations had to be used. A solution to this problem could be the measurement of steroid hormones in the faeces (Totzke, pers. comm.) or the distinction of the size of footprints between males and females on the mudflat.

In this study several prey species have been described for the first time in the diet of Bar-tailed Godwits, but most of these were of minor importance. Like in most other studies, polychaetes form the main prey (Tab. 5.4, see Piersma 1982). In Europe *Nereis diversicolor*, *Lanice conchilega*, *Arenicola marina*, and *Scoloplos armiger* are the most important ones. Additionally, some molluscs are taken, in Europe mainly *Macoma balthica*. Compared to other waders, the prey choice of Bar-tailed Godwits appears relatively constant between areas and between seasons.

Although some 94 % of the diet of Bar-tailed Godwits around List consisted of polychaetes, some seasonal variation was apparent, but the total proportion of polychaetes in the diet never dropped below 85 %. Furthermore, an apparent difference existed between males and females which was based mainly on the choice of large polychaete species like *Arenicola marina* and *Lanice conchilega* by females and the bivalve *Macoma balthica* by males in spring.

Males and females were not equally separated in prey choice throughout the year. Prey choice differed most in late spring and summer but became similar towards winter. The differentiation in diet composition coincided with a separation in habitat choice. In late spring and summer males utilised exposed mudflats, while females tended to feed at the waterline instead, as all Bar-tailed Godwits do in winter (own obs., C. Both pers. comm.). This partitioning of the sexes in spring may be density related. As densities of Bar-tailed Godwits increase in spring, the smaller males may avoid competition with females (C. Both pers. comm.). Alternatively, it may also be that when temperatures rise in spring, *Macoma balthica* and small polychaetes become available on the exposed mudflats, which for some reason can be exploited in a profitable way by the males.

In all, the results show that quantitative dropping analyses offer the opportunity for the reproducible correction of observations and therefore result in a more complete picture of diet composition of birds. Especially, when the major interest lies in the calculation of energy intake or male-female differences, the combination of both approaches should be favoured to a separate presentation of droppings and observations.

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6. Migratory strategies and stopover ecology of European Bar-tailed Godwits (*Limosa lapponica*) in the northern Wadden Sea: consequences for winter distribution

Gregor Scheiffarth

Abstract

Bird numbers in the Wadden Sea show pronounced seasonal variations. In contrast to long-distance migrants with wintering areas in Africa and breeding grounds in the Arctic, phenologies of birds wintering in the Wadden Sea must depend on local conditions. By means of an energy budget for the European population of Bar-tailed Godwits was investigated whether i) birds are constrained by energy intake on spring migration and ii) in how far thermostatic costs influence winter distribution of the birds in Europe. With 0.0083 W g^{-1} Bar-tailed Godwits of the European population had a higher BMR than expected by allometric equations which is supposed to be an adaptation to wintering in cold areas. T_{lc} was 16.1°C and conductance amounted to 0.000334 W g^{-1} $°C^{-1}$ which is in the expected range. Thermostatic costs were estimated with 'heated taxidermic mounts'. Due to the sexual size dimorphism in Bar-tailed Godwits, males always had higher thermostatic costs than females, with M_{maint} varying seasonally between 1.6 and 2.9 * BMR. For females M_{maint} varied between 1.4 and 2.4 * BMR. Additionally, birds invested between 27.3 and 54.5 kJ day^{-1} to heat ingested food to body temperature. When foraging at tidal flats, average peck rate was 18 pecks min^{-1}. Peck rate did not differ between males and females, however males showed a seasonal pattern in peck rate in contrast to females. Average success rate differed between the sexes with 3.6 prey min^{-1} for males and 2.5 prey min^{-1} for females. Nevertheless, average energy intake rate varied seasonally but with 1.4 kJ min^{-1} again did not differ between males and females. Therefore, males and females differed in prey choice. Foraging time fluctuated between 48 % in February and 24 % in May. Taken together, these parameters resulted in an calculated energy intake of 500 kJ day^{-1} with a higher energy intake in April and August when birds moulted and prepared for migration. The patterns of energy intake and basic energetic costs (without e.g. activity) were closely correlated. The costs for activity must either be on the same, low level throughout the year or a high degree of compensation for thermoregulatory costs must exist. Birds regulated energy intake on a low level by reducing foraging time as soon as energy intake rate increased. A higher energy intake and therefore weight gain than observed should have been possible. This finding was interpreted as part of a energy minimizing migration strategy. Winter numbers of Bar-tailed Godwits in the study area were not influenced by ice cover, however thermostatic costs of females had a significant influence. Males left the study area earlier than females due to higher thermostatic costs. In the northern Wadden Sea these costs are high in relation to energy intake. The relation between energetic costs and gains appeared to be much better in the main wintering areas. However, some birds stay in the northern Wadden Sea, which might have the advantages of wintering as close to the breeding area as possible, no cost of movement and settling in a new area in mild winters, and probably lower rates of competition as well as predation.

Introduction

The seasonal change of bird numbers and communities is one of the pronounced phenomena in temperate wetlands like the European Wadden Sea (e. g. Droste-Hülshoff 1869, Meltofte et al. 1994, Nehls & Scheiffarth 1998). For the European Wadden Sea these changes are the result of migratory movements of birds between their northern breeding and southern wintering areas along the East Atlantic Flyway (e. g. Smit & Wolff 1981, Ens et al. 1990). Depending on the type of migration (Piersma 1987a) different bird populations use the European Wadden Sea to different extends. On the one hand long distance migrants use the Wadden Sea as a stopover site only for a short period of time on their migration between Africa and Siberia (e. g. Smit & Wolff 1981, Ens et al. 1990). Their phenology in the Wadden Sea does not depend on the local situation since they are constrained by a tight time schedule to reach their destination in time (Piersma 1987a). On the other hand bird populations use the Wadden Sea both as a stopover and wintering site. Their seasonal phenology could depend on the suitability of the area to cover energetic demands by a sufficient food intake.

Two populations of Bar-tailed Godwits occur in the Wadden Sea. The Afro-Siberian population spends the winter in Africa and breeds in Siberia. Birds of this population use the Wadden Sea twice a year for approximately one month as a stopover site on their long-distance migration between breeding and wintering site. The European population breeds in Fennoscandia. It winters mainly in Great Britain and the western parts of the Wadden Sea, but some birds stay the northern part of the Wadden Sea. To reach their wintering quarters, some birds migrate in autumn through the Wadden Sea, whereas others fly directly to the British Isles (Scheiffarth 2001a). In spring most birds of this population move into the Wadden Sea to prepare for a migration of 1500 - 2000 km to their breeding areas (Drent & Piersma 1990).

In this study two aspects of migratory ecology of the European population will be addressed. In contrast to the Afro-Siberian population, birds of the European population increase in weight with a rather slow rate in spring (Prokosch 1988, Drent & Piersma 1990). By means of an energy budget and the comparison of energetic costs with energy intake it is investigated whether during spring migration birds are constrained by energy intake or whether they follow the strategy of energy minimizing as one of the migration strategies proposed by the optimal bird migration theory (Alerstam & Lindström 1990). Furthermore, it is investigated, in how far thermostatic costs influence the seasonal pattern of occurrence in the northern Wadden Sea and whether thermostatic costs play a role in the winter distribution of Bar-tailed Godwits in Europe as was proposed for the winter distribution of passerines in the USA (Root 1988).

Methods

Study area

All field observations were carried out at the northern end of the island of Sylt near List (55°01'N, 8°26'E) in the European Wadden Sea. Observations were conducted mainly in the Königshafen, a shallow tidal bay with an intertidal area of 4.32 km^2 and on sandflats east of the village List. In the centre of the Königshafen bay a peninsula is situated with the main high-tide roost for Bar-tailed Godwits. A small weather station was placed on this peninsula which operated during most of the observation time and during trials with heated taxidermic mounts. The German Weather Service (DWD) operated a synoptic weather station on a dune near List from which data were available. For a further description of the study area, s. Reise (1985) and Gätje & Reise (1998).

Respirometry

Metabolic rates were measured in an open flow system with the ambient air drawn through respiratory chambers (28 l) at a rate of 55 - 60 l h^{-1} (Scheiffarth & Bairlein 1998b). The chambers were placed in a climatic room (Fig. 6.1) and contained a platform of wire mesh, so that faeces could fall on the floor covered by a plastic foil. Chamber walls were covered with black paper to minimize thermal reflections (Porter 1969). Air leaving the boxes was dried over 3 Å molecular sieve (Merk, Darmstadt). Air flow was measured continuously by a mass flow controller (DK 38 DT, Krohne, Duisburg), CO_2 was measured by a IR analyser and O_2 by a paramagnetic oxygen analyser (Hartmann & Braun, Frankfurt; s. Hill 1972). Analysers were calibrated before each session with two known gas mixtures (1.: 20 % O_2, 2 % CO_2; 2.: 99.99 % N_2) and controlled with the same mixtures after each session.

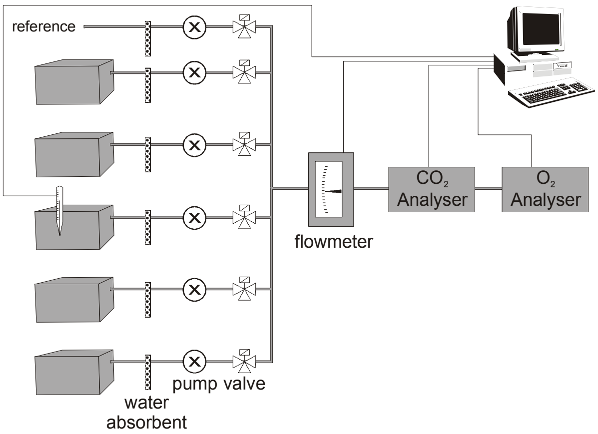

Fig. 6.1: Experimental set up of the open flow respirometry system for the measurement of metabolic rates.

Tab. 6.1: Abbreviations used in the text. Nomenclature follows as much as possible standards proposed by Bligh & Johnson (1973).

BMR	basal metabolic rate [W]
DEE	daily energy expenditure [W]
DME	daily metabolizable energy intake [W]
H_m	heat loss of mount [W]
H_{sm}	standardised heat loss of mount [W]
K_{es}	thermal conductance of live bird [W °C^{-1}]
K_{esm}	thermal conductance of mount [W °C^{-1}]
M_{maint}	maintenance metabolism [W]
O_{2e}	fractional concentration of Oxygen leaving metabolic chamber
O_{2i}	fractional concentration of Oxygen entering metabolic chamber
R_g	global radiation [W m^{-2}]
SMR	standard metabolic rate [W]
T_a	ambient temperature [°C]
T_b	body temperature [°C]
T_e	operative temperature [°C]
T_{es}	standard operative temperature [°C]
T_{lc}	lower critical temperature [°C]
T_m	mount temperature [°C]
u	windspeed [m s^{-1}]
VCO_2	rate of carbon dioxyde production [l h^{-1}]
VO_2	rate of oxygen consumption [l h^{-1}]

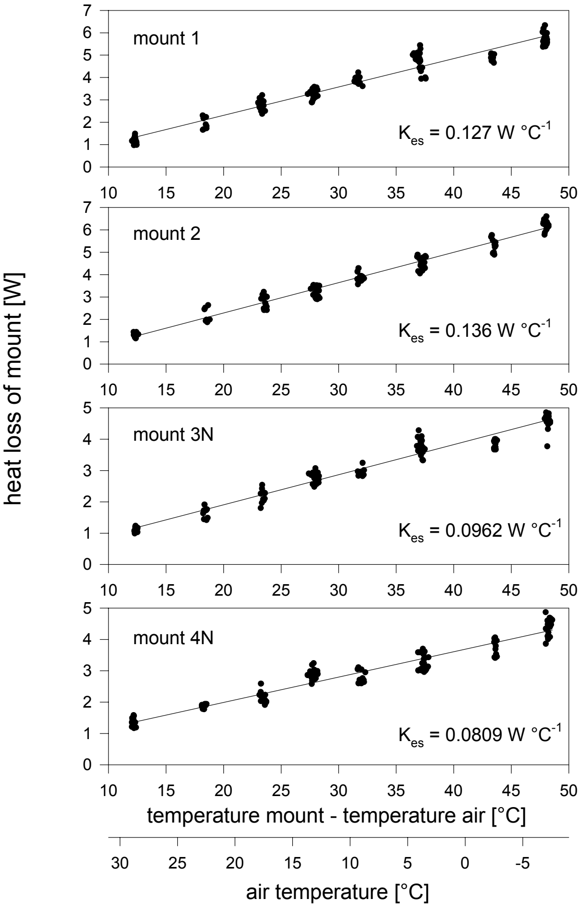

Fig. 6.2: Heat loss of mounts in relation to temperature difference between ambient temperature and mount temperature for the determination of the mounts' conductances. Mounts were placed in metabolic chambers with an air flow of 55 - 60 l h^{-1}. Axis with air temperature is drawn for rough orientation and does not represent exact temperatures during measurements.

The experimental set up allowed six channels to be measured sequentially. One channel was always used as reference with ambient air (climatic room), so that up to five animals could be measured in one session. After 150 s air of the next channel was directed over the flowmeter to the analysers, resulting in a cycle length of 15 min when all respirometry chambers were in use. To consider the dead volume of the pneumatic system, measurements during the first 30 s after switching to a new channel were discarded. This resulted in a recording period of 2 min every 15 min for each channel (respirometry chambers and ambient air). Since the ambient air was measured each cycle, gas concentrations of the chamber air could be related directly to ambient gas concentrations. Depending on the number of animals to be measured, not always all chambers were used, which resulted in a shortening of cycle length. Additionally, air temperature of one respirometry chamber was recorded with a thermistor (NTC). Since all chambers were placed close together and air mixing in the climatic room was sufficient, this temperature was considered representative for all the chambers. Flow rate, CO_2 concentration, O_2 concentration, and chamber temperature were recorded on a PC with the software system DIA/DAGO (Gesellschaft für Stukturanalyse, Aachen).

One male and one female bird from the European population were kept in outdoor aviaries where they had food and water ad libitum. Respirometric measurements were conducted during winter, when birds had been in captivity for 2 ½ years. Birds were placed in the respirometry chambers between 19:00 hh and 20:00 hh without previous deprivation of food and stayed there until 8:00 hh the next morning. Before and after the sessions birds were weighted to the nearest gram and the mean of these two values was taken as body weight. Oxygen consumption was calculated after Withers (1977):

$$VO_2\ [l\ h^{-1}] = (flow*(O_{2i}-O_{2e})-VCO_2*O_{2i})/(1-O_{2i})$$

Metabolic rate (in Watt [W]) was calculated from oxygen consumption assuming an energetic equivalent of 20 kJ l^{-1} O_2 (for abbreviations used, s. Tab. 6.1). The largest error resulting from the use of this figure for all nutrients would be 6 % (Schmidt-Nielsen 1983). However, since the respiratory quotients indicated a high proportion of fat oxidized during the measurements, any error introduced by this value is negligible. As the aim of this study was the estimation of standard metabolic rate (SMR, s. Aschoff & Pohl 1970a for the conditions to be met for the measurement of SMR) at different temperatures, only one temperature per night was tested with the highest temperature presented in the first night and subsequent lowering of the temperature in the following nights (temperature range: 30°C to -7°C). For analysis, only measurements after midnight were considered. The minimum of the running mean of 1 h was taken as SMR. A constant respiratory quotient of 0.75 after midnight was taken as evidence that the time lag between the last access to food and the first measurements analysed was sufficient to assume that birds were in a postresorptive state.

Heated taxidermic mounts

Heated taxidermic mounts are hollow copper models covered by the skin or plumage of the animal under investigation and heated to the corresponding body temperature. They serve as T_{es} thermometers (Bakken 1992), which allow an extension of the Scholander model (Scholander et al. 1950) to a general thermal environment (Bakken et al. 1985). After calibration with live birds they allow the calculation of thermostatic costs or maintenance metabolism (for the difference between the two terms, s. Dawson & O'Connor 1996) for different environmental situations. The general approach is to expose heated taxidermic mounts to a complex thermal environment, characterized by wind, air temperature, and solar radiation. By the help of heated taxidermic mounts a single temperature index is produced, which can be compared to a simpler environment (e. g. a metabolic chamber). The reaction of an animal to the simpler environment can be quantified and on the basis of T_{es} extrapolated to the complex situation (Walsberg & Wolf 1996).

The construction of heated taxidermic mounts was first described by Bakken et al. (1981) and modified by Wiersma & Piersma (1994). According to the latter instructions four heated taxidermic mounts were produced (2 males, 2 females, Fritzsche-Nehls & Nehls, Husum). In accordance with measurements of Knots (*Calidris canutus*), body temperature was set to 41°C (Verboven & Piersma 1995). Regulation of mount temperature and data recording was achieved by the software 'rs23moun' running on a laptop computer together with a hardware interface (Gesellschaft für Telemetriesysteme, Bordesholm). In the field the entire system was powered by a car-battery. Every 10 min the software recorded average temperature of mounts and power for heating the mounts. Concurrently, every 10 min a standard weather station recorded average air temperature (T_a), wind speed (u), and solar radiation (R_g, Lohse et al. 1993). Mounts were regularly waterproofed by a commercial tent spray, but measurements were stopped when it started raining. During measurements mounts were placed on open mudflats at different weather situations with a distance to each other of 1.5 m. Two situations were tested: a) mounts facing wind (64 h of recording) and b) mounts oriented 90° to wind direction (41 h). Before each measuring session, electric resistance of the mounts' heating wire was measured. Over the entire time only small changes in resistance occurred, with a coefficient of variation between 0.9 % and 2.7 %. Since the recording programme allowed an easy change of resistance for the calculation of heating power, always the actual values were used.

Heated taxidermic mounts do not resemble live birds (Bakken et al. 1985), they have to be calibrated to the heat loss of 'real' birds. Nevertheless, heat loss in Knot mounts occurred in the same parts of the body as in live birds (Wiersma et al. 1993, Wiersma & Piersma 1994). For calibration, thermal conductance of mounts was estimated under the same conditions and the same temperature range as for the respirometric measurements (Fig. 6.2). Mounts were placed in the same metabolic chambers and the pump of the system was operating (although no difference in conductance with the former situation was found when the pump was switched off; t-test for comparison of slope of two linear regression lines; for all four mounts $p > 0.05$). Two mounts were calibrated before and after the field season and no difference in conductance was found (t-test, $p > 0.05$). For standardization of the heat loss of each mount to the heat loss of live birds, equation 4 of Wiersma & Piersma (1994) was used:

$$H_{sm} = K_{es} (T_b - (T_m - H_m/K_{esm})).$$

One of the major goals of using heated taxidermic mounts was to calculate T_{es} or M_{maint} on the basis of standard weather registrations. For this purpose the model developed by Wiersma & Piersma (1994, equation 5) was used:

$$H_{sm} = (K_{es} + K_u * u^{exp}) * (T_m - T_a) - K_r * R_g$$

The parameters K_u, exp, and K_r were estimated by an iterative regression procedure (SPSS/PC+) on the basis of the standardized measurements of the mounts and the parallel weather registrations. During parameter estimation, all values of H_{sm} were used unless mount temperature dropped below 40°C. However, for the calculation of M_{maint} with the model on the basis of long-term weather data, for all cases when $T_{es} = T_{lc}$, BMR was used instead of the calculated H_{sm}. Most of the long-term weather data are available on a daily basis but with rising temperatures the chance increases that for some period of a day T_{es} rises above T_{lc}. Therefore, all values for H_{sm} were corrected on the basis of a regression between the relation of H_{sm}(day/10min) and T_{es} (Wiersma & Piersma 1994).

Behaviour of Bar-tailed Godwits in relation to weather

For birds foraging on mudflats, the orientation in relation to wind direction was recorded in three categories: head facing wind (0°), bird perpendicular to wind direction (90°), and wind from back (180°). Furthermore, distances between birds were recorded in relation to body length of the birds (24 cm). Distance estimation was once controlled with mounts of known distance placed on mudflats which gave a good accordance between estimated and real distance. Unfortunately, distance between individuals or density of birds in high tide roosting flocks could not be determined, since flocking was very tight and no suitable observation point with a good position in relation to the birds could be found. Therefore, only distances of foraging birds were analysed. Parallel to all observations, the actual weather situation was recorded by a standard weather station (GKSS, Lohse et al. 1993) within max. 2 km of the flocks.

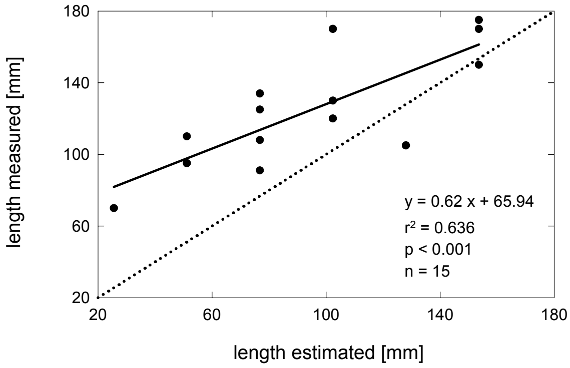

Fig. 6.3: Calibration of worm length estimations of *Arenicola marina*. Worms were held besides the bill of a stuffed Bar-tailed Godwit and length was estimated from an observation tower at 50 m distance from the stuffed bird. Dotted line denotes line of equality.

Quality of prey

The quality of different prey and energy intake was calculated from length-weight relationships of the main prey organisms. Individuals of the main prey species were collected from the tidal flats of the Königshafen at different seasons and in different years. Only fresh animals were used for biomass determination. Depending on the species, different methods were applied for the measurement of animal size or length. In *Macoma balthica*, maximal shell length was measured to the nearest 1/10 mm with a vernier calliper. For a standardization of length measurements *Arenicola marina* was kept at 15°C for several hours and then torn to maximum length along a ruler. Smaller polychaetes (*Nereis diversicolor, Nephtys hombergii, Scoloplos armiger*, *Lanice conchilega*) were anaesthetised with a solution of $MgCl_2$ ($80\ g\ l^{-1}$; Hulings & Gray 1971) and maximum length was measured to the nearest mm on a ruler without tearing the worms. For biomass estimation, all animals were oven-dried for three days at 75°C and weighted to the nearest µg or mg. Polychaetes were combusted for 4 h and *M. balthica* for 12 h at 510°C. For ash free dry mass (AFDM) the difference between dry mass and ash mass was taken.

Estimation of intake rates

Between August 1991 and October 1993 individual birds foraging on tidal flats were observed as long as possible and behaviour was recorded on a continuously running tape recorder (focal animal sampling, continuous recording; Martin & Bateson 1986). Observations were conducted in different parts of the Königshafen and on sandflats east of List from observation towers, dikes, and from small chairs on the sandflats. Birds foraging in these areas roost in the Königshafen during high tide. All activities, pecks, probes as well as ingested or rejected prey species were recorded. Size of the prey was determined in relation to bill length (females 99.7 mm, males 80.5 mm, Scheiffarth 2001a) or height of leg rings. Since prey size is a crucial factor in the calculation of energy intake, observations were calibrated in the field. For calibration of the size of polychaetes, main prey species (*Arenicola marina, Nereis diversicolor, Nephtys hombergii*, *Scoloplos armiger*) of different but for the observer unknown length were hold besides the bill of a stuffed Bar-tailed Godwit. To resemble the situation during observations, this mount was placed 50 m apart from an observation tower on a sandflat. As shown in Fig. 6.3 for *Arenicola* *marina*, small prey items were underestimated (cf. Goss-Custard et al. 1987, Zwarts & Esselink 1989). The resulting regressions were used for the corrections of prey size. For *Macoma balthica* a different approach was used. During the observation period in spring 1993 droppings containing *Macoma balthica* were collected around the observation tower. On the basis of the relation between umbo height to shell length (Scheiffarth 2001b), a size frequency distribution of *Macoma balthica* taken by the birds was calculated. This distribution was compared to the distribution of size classes on the basis of the observations (Fig. 6.4, cf. Zwarts & Blomert 1992). All estimated prey sizes were converted into biomass on the basis of the length-weight relationships (Tab. 2). For months when no relationship was available, either the relationships closest by or from the same season but a different year were used. If for any prey species no own length-weight relationship was obtained, equations from Zwarts & Wanink (1993) were used. Biomass (AFDM) was converted into energy with energy densities given by Zwarts & Wanink (1993). Prey not identified during the observations was corrected on the basis the diet composition as determined by a dropping analysis (Scheiffarth 2001b). If prey size was unknown, the mean or median prey size of identified prey of the same species was taken. Additionally, for *Nereis diversicolor* and *Nephtys hombergii* the size distributions calculated from jaw size were compared to the size distributions based on observations. Peck, success, and energy intake rates were calculated on the basis of the entire time the observed bird was engaged in foraging activity. Only observations with foraging behaviour lasting longer than 270 s were analysed so that it was assured that intake rates of all observed birds showed a constant level.

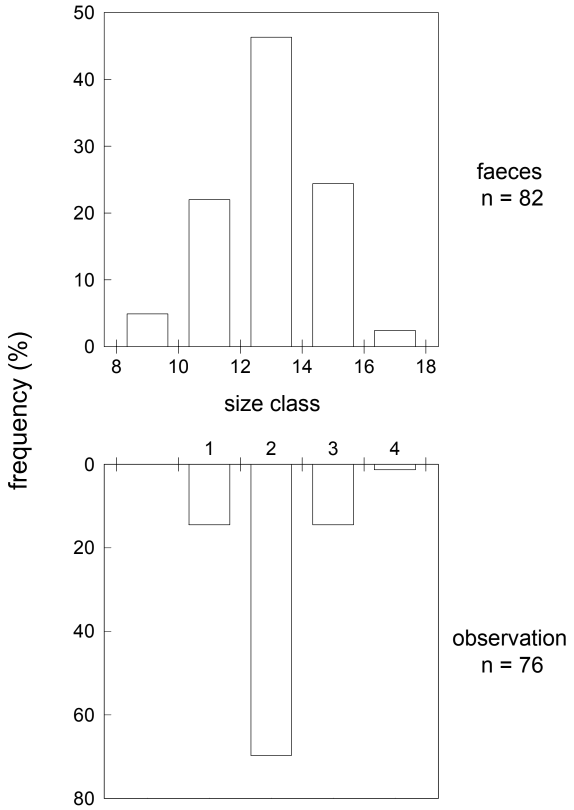

Fig. 6.4: Comparison of size frequency distribution of *Macoma balthica* in faecal samples and size classes determined during observations. Size classes for faecal samples are in mm shell length, for observations in relation to height of a colour leg ring.

For statistical analysis, peck, success, and energy intake rates were square root transformed to reach homogeneity of variances. To test for seasonal changes within one sex, a one-way analysis of variance was performed. Influence of sex was tested by a two-way analysis of variance with the factors sex and month. All values for November were excluded from the analysis because of small sample size and unreliable observation conditions.

Foraging time

Foraging time was quantified by scan sampling in connection with instantaneous recording (Martin & Bateson 1986). Flocks of Bar-tailed Godwits were followed and every 5 min the behaviour of 50 birds was recorded. When possible, flocks were followed for an entire tidal cycle. In this case, the proportion of time foraging per tidal cycle was calculated as the average proportion of all 5 min intervals. When flocks could not be followed for an entire tidal cycle, per month the mean proportion of foraging birds from all observations was calculated for each 5 min interval of the tidal cycle. Missing intervals were filled by linear interpolation between the last and the first nonmissing value. From this, the monthly proportion of foraging time was calculated as the mean of all averaged 5 min intervals of a tidal cycle. In this case, no variance of the foraging time was calculated since this would only represent the variance within one tidal cycle and cannot be used for the comparison of foraging time between months. Additionally, every 30 min the number of Bar-tailed Godwits on the high tide roost was counted. The percentage of birds attending the roost site in relation to the daily maximum was calculated on a day to day basis.

Calculation of daily energy intake

To estimate assimilated energy per day the proportion of time spent foraging was recalculated to minutes

Tab. 6.2: Length-weight relationships of main prey species sampled in the Königshafen/Sylt. Regressions were calculated with ln-transformed data: ln(afdm[g])=a*ln(length[mm])+b.

species	sampling date	a	b	r^2	p	n
Nereis diversicolor	Aug/Sep 1991	1.861	-11.801	0.8318	0	35
	Apr 1992	1.758	-11.357	0.9417	0	16
	Aug 1992	2.079	-12.731	0.9635	0	25
	Feb 1992/Feb 1993	1.776	-11.809	0.8070	0.015	6
Nephtys hombergii	Jan 1992	2.402	-13.781	0.9975	0	9
	Apr 1992	2.416	-13.745	0.9364	0	28
	Aug 1992	2.281	-13.213	0.9598	0	23
	Feb 1993	2.117	-12.421	0.9384	0	16
	Apr 1993	2.231	-13.050	0.9812	0	20
Scoloplos armiger	Sep 1991	1.546	-11.740	0.7135	0	23
	Feb 1992	1.792	-13.110	0.9231	0	25
	Apr 1992	1.578	-11.584	0.8577	0	16
	Aug 1992	1.679	-12.597	0.6897	0.0029	10
	May 1993	1.187	-10.354	0.8635	0	26
Arenicola marina	Jan 1992	1.940	-10.546	0.8033	0	22
	Apr 1992	2.249	-11.862	0.8911	0	53
	Aug 1992	2.248	-12.204	0.8390	0	50
	Feb 1993	2.517	-14.162	0.9033	0	25
	May 1993	2.446	-13.136	0.8820	0	25
Lanice conchilega	May 1992	0.853	-6.717	0.6762	0	40
	Sep 1992	0.522	-4.683	0.1545	0.0121	40
	Feb 1993	0.532	-6.097	0.5370	0.159	5
	May 1993	1.875	-11.932	0.6940	0.0015	11
Macoma balthica	May 1992	3.241	-11.432	0.9644	0	38
	Sep 1992	3.551	-12.583	0.9686	0	42
	Feb 1993	3.059	-11.495	0.9810	0	37
	Mar 1993	3.018	-11.402	0.9917	0	29
	Apr 1993	2.710	-10.299	0.9710	0	19

foraging per day. Since time spent foraging could not be determined for each sex separately, intake rates for males and females were pooled (no statistical difference between the sexes, see 'energy intake rate'). The seasonal pattern of assimilated energy intake was calculated by multiplying energy intake rate with foraging time taking into account an assimilation efficiency of 80 % (mean value of different sources: Kersten & Piersma 1987, Castro et al. 1989, Zwarts & Blomert 1990).

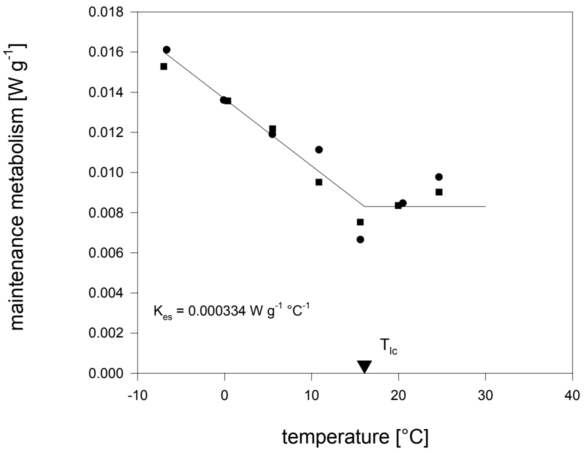

Fig. 6.5: Maintenance metabolism of Bar-tailed Godwits in relation to ambient temperature. Birds were measured under convection free conditions. ■ = male, ● = female.

Calculation of energy demands to heat ingested food to body temperature

Birds have to heat ingested food to body temperature. By assuming that the ingested food has a similar specific heat capacity as water (4.1868 J g^{-1} $°C^{-1}$) it is possible to calculate these energetic costs if the amount of ingested fresh mass (FM) is known. Since apart from *Macoma balthica* no FM was measured, this had to be estimated by conversion factors from dry mass (DM). In a first step ingested DM was calculated from the amount of ingested ash free dry mass (AFDM) for each prey species separately which in turn was estimated from the intake rates together with foraging time. For this calculation, as far as possible relationships between DM and AFDM from the Königshafen area were used. When this was not possible, conversion factors from DM to AFDM given by Rumohr et al. (1987) were taken. Further on, FM was calculated from DM with conversion factors from Rumohr et al. (1987). For *Macoma balthica* a relationship between FM and DM from the Königshafen was used. Prey organisms were supposed to have surface water temperature. Thus, for the calculation of the amount of

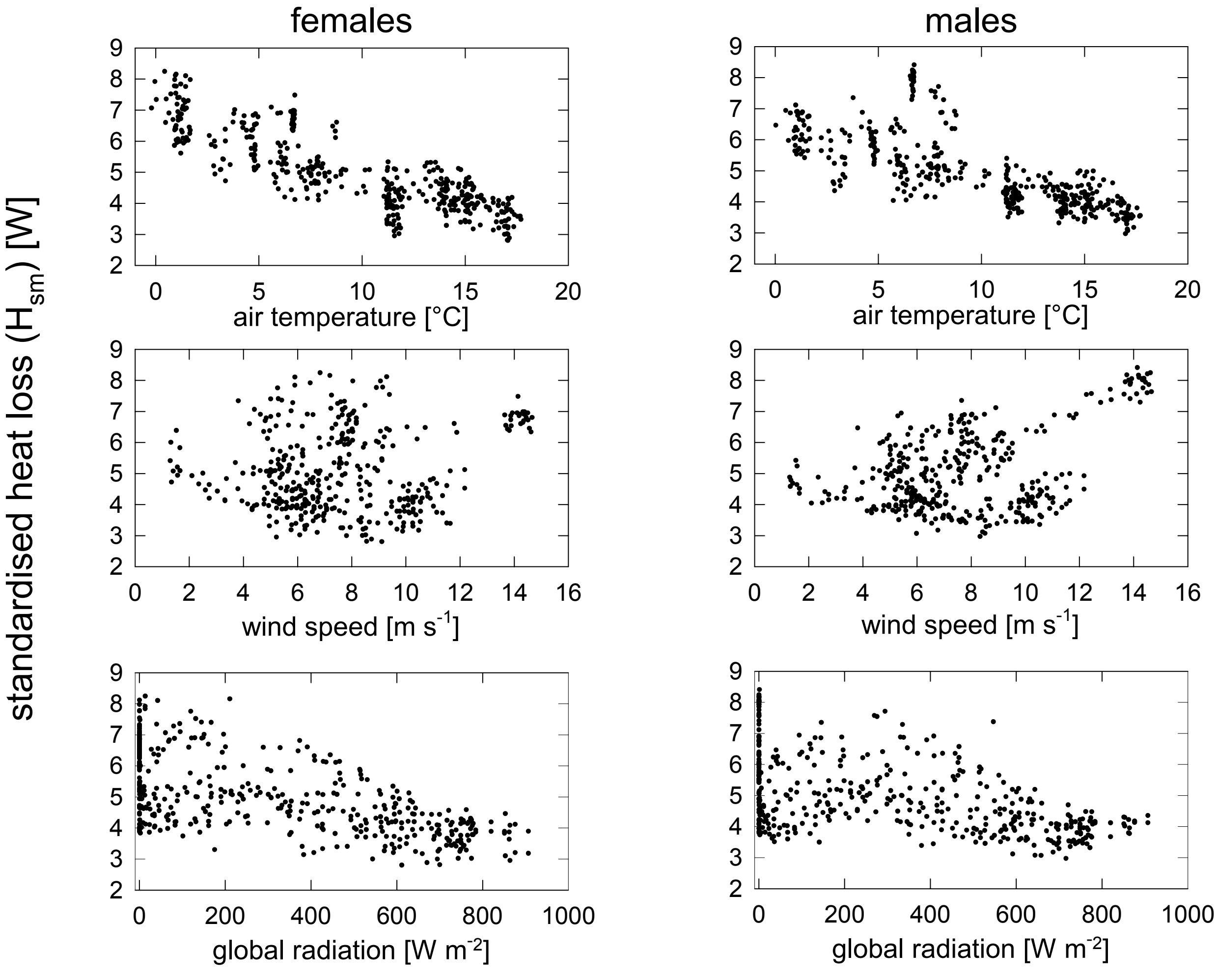

Fig. 6.6: Standardised heat loss (H_{sm}) of heated taxidermic mounts in relation to environmental parameters during measurements of mounts placed solitary on open mudflats.

Tab. 6.3: Parameters (± SE) estimated with iterative regression procedure for model relating weather data to M_{maint}: $SMR = (K_{es} + K_u * u^{exp}) * (T_b - T_a) - K_r * R_g$. Two situations were distinguished: mount facing wind (0°) and mount perpendicular to wind (90°).

parameter	males		females	
orientation	0°	90°	0°	90°
K_u	0.0189 ± 0.0014	0.011 ± 0.0012	0.0268 ± 0.0023	0.0134 ± 0.0018
exp	0.714 ± 0.032	0.897 ± 0.048	0.427 ± 0.040	0.639 ± 0.062
K_r	0.00097 ± 0.00009	0.00095 ± 0.00014	0.00118 ± 0.00009	0.00085 ± 0.00014
r^2	0.821	0.778	0.792	0.764
n	381	199	387	196
K_{es}	0.0914 W/°C		0.1111 W/°C	
BMR	2.27 W		2.76 W	
body mass (march)	274 g		333 g	

energy needed to heat the ingested food to body temperature, mean surface water temperatures from the Königshafen (Martens, unpubl.) were used.

Results

Maintenance metabolism in a standard laboratory environment

Measurement of SMR in relation to temperature with birds from the European population resulted in a BMR of 0.0083 W g^{-1}, a lower critical temperature of 16.1°C, and a conductance of 0.000334 W g^{-1} $°C^{-1}$ (Fig. 6.5). Because of the sexual size dimorphism in this species (Scheiffarth 2001a), for further calculations absolute BMR values based on the body weights in early spring were computed separately for males and females. For males BMR amounts 2.27 W and conductance 0.0914 W $°C^{-1}$. Corresponding values for females are 2.76 W for BMR and 0.1111 W $°C^{-1}$ for conductance (Tab. 6.3).

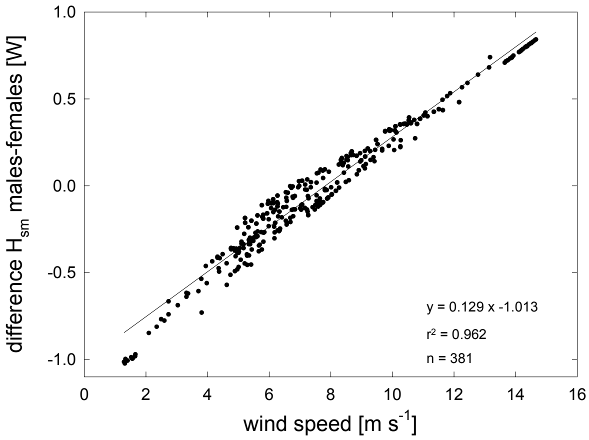

Fig. 6.7: Difference in H_{sm} between males and females in relation to wind speed. Difference in H_{sm} was calculated with results from H_{sm} predicted by the model of Wiersma & Piersma (1994) for weather situations during measurements.

Measurement of maintenance metabolism in the field with heated taxidermic mounts

After standardization of the heated taxidermic mounts with the conductances of live birds, heat loss (H_{sm}) of Bar-tailed Godwits could be related to weather parameters (Fig. 6.6). It became obvious, that apart from

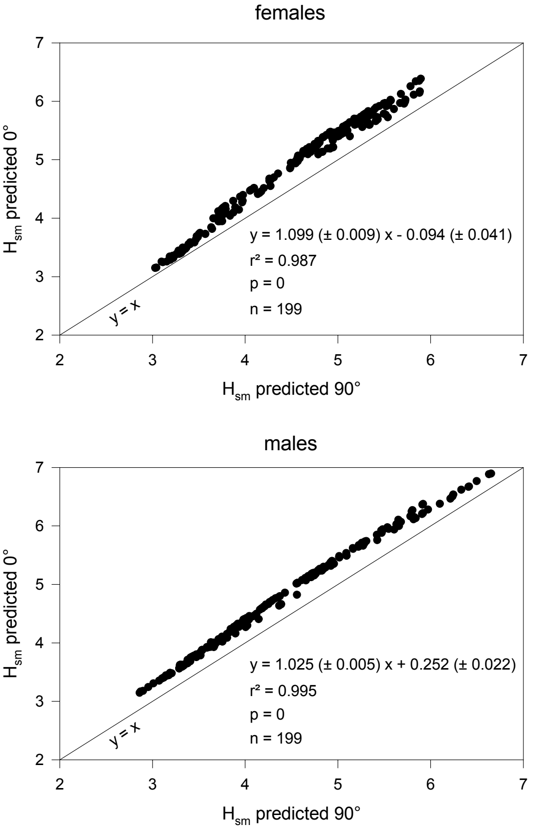

Fig. 6.8: Comparison of H_{sm} between mount facing wind and mount placed perpendicular to wind direction. Comparison is based on results from H_{sm} predicted by the model of Wiersma & Piersma (1994) for weather situations during measurements of mounts perpendicular to wind direction.

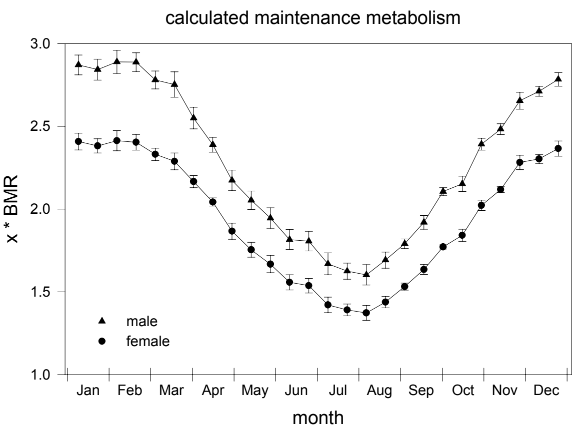

Fig. 6.9: Seasonal phenology of calculated maintenance metabolism of a male and female Bar-tailed Godwit standing solitary on open mudflats of the Königshafen facing wind. Phenology is based on daily weather registrations of the DWD (German Weather Service) of the station List form years 1988 - 1997. Calculated are fortnightly means (± SE) over 10 years.

ambient temperature also wind speed and global radiation influenced H_{sm}. Furthermore, influence of these parameters differed between males and females. Parameter estimation of the model for birds facing wind resulted in an explained variation in the data of 79 % and 82 % for females and males, respectively (Tab. 6.3). On average, the absolute values of M_{maint} did not differ between males and females (regression of males against females, slope ± SE: 1.002 ± 0.016, intercept ± SE: 0.049 ± 0.085), any existing difference (residuals of the regression of males against females) was related to wind speed (Fig. 6.7). This effect was due to the fact that wind speed had a higher impact on M_{maint} of males than females.

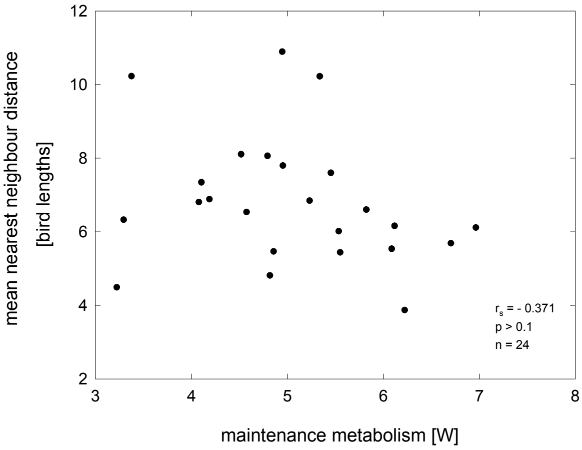

Fig. 6.10: Distance of foraging Bar-tailed Godwits in relation to calculated maintenance metabolism based on weather registrations during observations.

For mounts operated perpendicular to wind direction, after parameter estimation the model explained 76 % and 78 % of the variation in H_{sm} for females and males, respectively (Tab. 6.3). In comparison to mounts facing wind, mounts perpendicular to wind direction seem to have a lower H_{sm} in both sexes (Fig. 6.8, for both sexes slope > 1, p < 0.001). However, since the difference is marginal and the opposite result should be expected due to a greater surface area exposed to wind, it is assumed that under the conditions tested no difference in H_{sm} between the two orientations of the mounts exists. Therefore, for further calculations, only the results of the model fitted to the situation of a solitary mount facing wind are used.

Since males have a lower BMR than females, the same maintenance metabolism means higher thermostatic costs for males. Therefore, for further analysis maintenance metabolism is always expressed as a multiple of BMR. On the basis of long-term weather data a seasonal pattern of M_{maint} could be calculated (Fig. 6.9). Throughout the year males had a higher M_{maint} than females (ANOVA, p < 0.001). Furthermore, the difference between both sexes was larger in winter than in summer (ANOVA, two-way interactions, p <

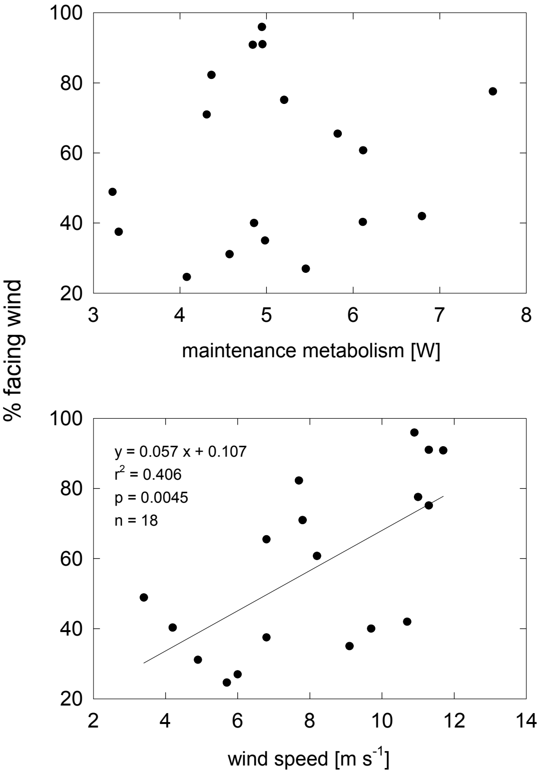

Fig. 6.11: Orientation of foraging Bar-tailed Godwits to wind direction in relation to calculated maintenance metabolism based on weather registrations during observations (top) and wind speed (bottom).

Tab. 6.4: Results of a multiple regression analysis of the orientation of Bar-tailed Godwits towards wind direction. Adjusted $r^2 = 0.369$, number of cases = 18.

parameter	B	SE B	p
wind speed	0.057	0.017	< 0.01
temperature			> 0.1
global radiation			> 0.1
constant	0.107	0.149	> 0.1

0.05) when thermostatic costs were on the lowest level. Highest thermostatic costs appeared in January and February. Especially for males at this time of year M_{maint} could reach up to 3 * BMR.

During foraging, Bar-tailed Godwits did not react to rising thermostatic cost with energy saving behaviours. They neither foraged in closer flocks at high levels of M_{maint} (Fig. 6.10), nor did they orient their longitudinal axis towards wind direction (Fig. 6.11). Orientation to wind direction was only dependent on wind speed (Fig. 6.11, Tab. 6.4).

Quality of prey

Biomass intake was estimated from length-weight relationships for the main prey species (Tab. 6.2, Fig. 6.12). *Arenicola marina*, *Scoloplos armiger*, *Lanice conchilega*, and *Macoma balthica* showed a strong variation in length-weight relationships between sampling dates (ANCOVA, for each species $p < 0.001$). On the contrary, *Nephtys hombergii* showed no difference in length-weight relationship between all sampling dates (ANCOVA, $p > 0.05$). Relationships for *Nereis diversicolor* were not different, when the winter sample was excluded from the analysis (ANCOVA, $p > 0.05$). When considering the biomass of the mean size taken by the birds, it becomes obvious, that besides a seasonal variation also variation between years exist (Fig. 6.13, cf. Zwarts & Wanink 1993). Hence, for large prey as *A. marina* quality may differ between years, whereas quality of smaller prey like *N. hombergii* is more predictable.

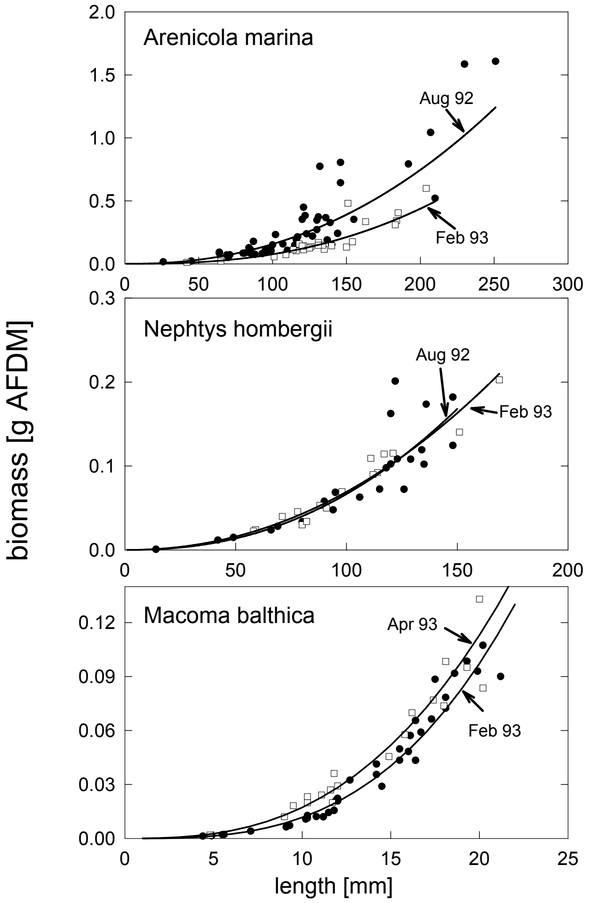

Fig. 6.12: Examples of length-weight relationships of polychaetes (s. Tab. 6.2). Curves are recalculated from ln-ln regressions.

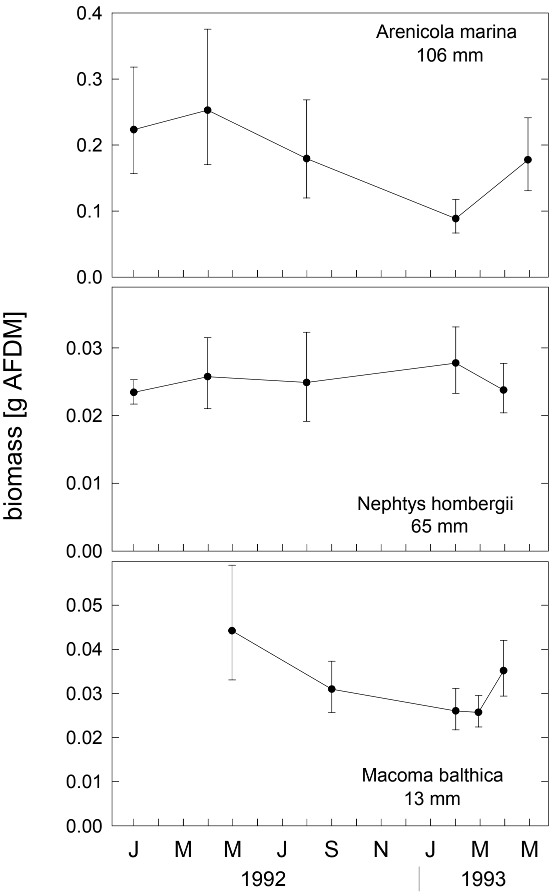

Fig. 6.13: Variation in biomass of preferred size classes of *Arenicola marina*, *Nephtys hombergii*, and *Macoma balthica* between sampling dates. Values are predicted biomasses (± SE) from regressions.

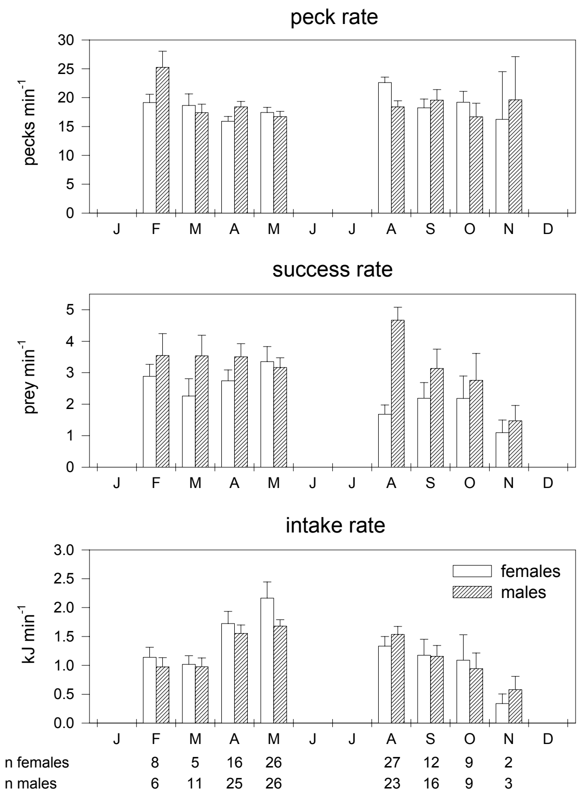

Fig. 6.14: Mean peck, success, and energy intake rates (+ SE) for male and female Bar-tailed Godwits on tidal flats around List.

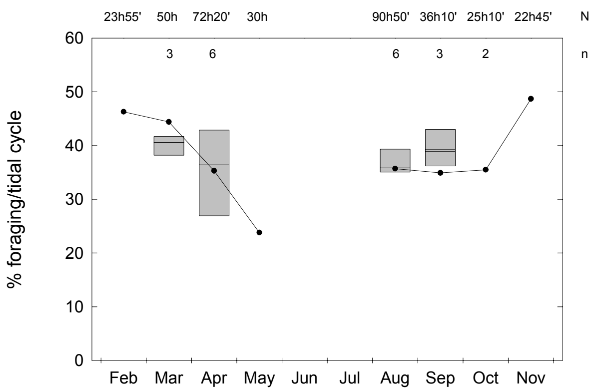

Fig. 6.15: Percentage of time spend foraging per tidal cycle. Box plots (line = median, box = 50 % interval, error bars = 90 % interval) represent days with observations of an entire tidal cycle. Dots connected by line result from the mean of all observations of a month, including observations lasting shorter than a tidal cycle (s. text). N = total observation time, n = number of complete tidal cycles observed.

Energy intake rate

Bar-tailed Godwits foraging on tidal flats pecked with an average rate of 18 pecks min^{-1} (Fig. 6.14). Males showed no seasonal variation (ANOVA, $p > 0.05$) in contrast to females (ANOVA, $p < 0.001$), which had the highest peck rate in August. Overall, no difference between males and females existed in peck rate (two-way ANOVA with sex and month, effect of sex, $p > 0.05$) but the seasonal patterns between the two sexes were different (two-way ANOVA, interaction between sex and month, $p < 0.05$).

In contrast to peck rate, success rate (prey min^{-1}) differed between males and females (two-way ANOVA with sex and month, effect of sex, $p < 0.001$) with males on average having a higher success rate than females (3.6 vs. 2.5 prey min^{-1}). Again, females showed a seasonal pattern in success rate with the lowest rate in August (ANOVA, $p < 0.05$), whereas males did not (ANOVA, $p > 0.05$). Consequently, seasonal patterns differed between the two sexes (two-way ANOVA, interaction between sex and month, $p < 0.01$).

Energy intake rate did not differ between males and females (two-way ANOVA with sex and month, effect of sex, $p > 0.05$). Both sexes showed a seasonal pattern in intake rate (for each sex ANOVA, $p < 0.01$) with elevated intake rates in April, May and August. The seasonal patterns did not differ between the sexes (two-way ANOVA, interaction between sex and month, $p > 0.05$).

In general, with the same peck rate males had a higher success rate than females which resulted in the same energy intake rate. This hints at smaller prey sizes chosen by males which becomes extremely obvious in August. During this month females fed on large *Arenicola marina*, whereas males had a higher proportion of smaller polychaete species like *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger* in the diet (Scheiffarth 2001b). Nevertheless, energy intake rate was still on the same level.

The increase of energy intake rate for males in spring is only based on a better quality of the prey (higher biomass per prey item), not on a higher success rate. In part this is paralleled by a switch in prey choice towards *Macoma balthica* in April and May (Scheiffarth 2001b). Also for females, energy intake rate rose in spring, but this was in part achieved by a parallel increase in success rate.

Foraging time

A comparison between foraging time calculated on the basis of observations covering the entire tidal cycle and foraging time calculated with the average of all observation intervals per month shows that the resulting proportions of time spend foraging do not differ (Fig. 6.15; t-test for comparison of an empirical mean with a

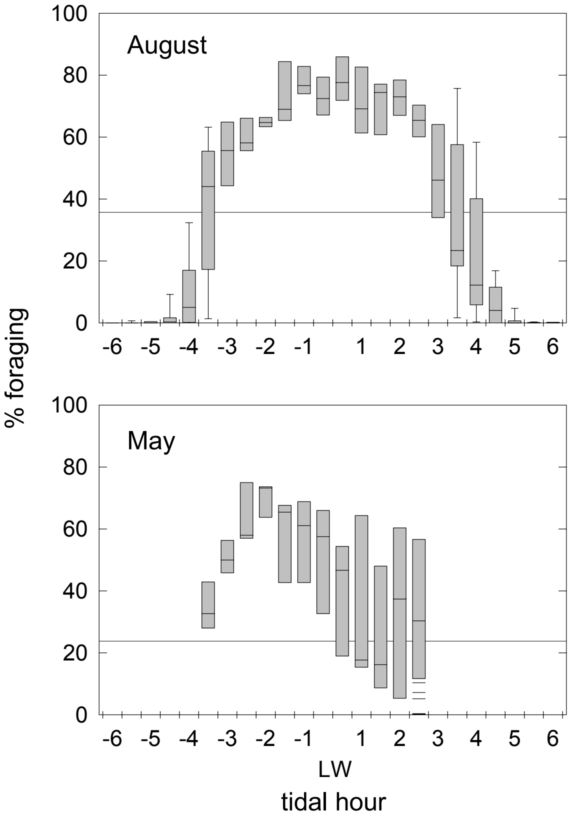

Fig. 6.16: Tidal pattern of foraging activity in August and May. Horizontal line represents mean percentage of time spend foraging calculated from the tidal pattern as presented in Fig 6.15; LW: low water.

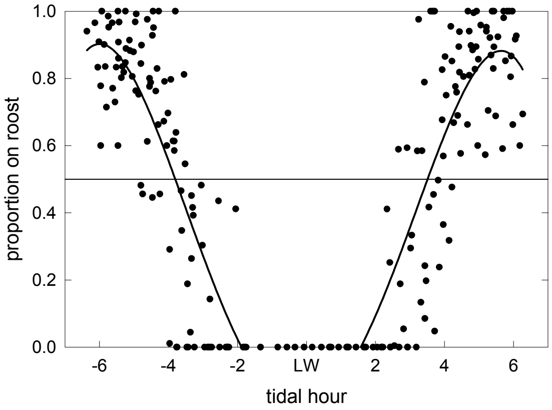

Fig. 6.17: Tidal pattern of roost site attendance. For each dot the proportion of the number of Bar-tailed Godwits on the roost relative to maximum number of birds per day was calculated. To lead the eye, a 4^{th} order polynomial was fitted to the data; data from all months pooled; LW: low water.

given mean, for each month $p > 0.05$). Because of no statistical difference between the two methods and since results of the second method are based on more observations, for further calculations the average of all observation intervals per month is used.

The highest proportions of foraging per tidal cycle were observed in November and February with 46 - 48 %. From February onwards, opposite to an increase in the quality of food (Fig. 6.13) as well as energy intake rate (Fig. 6.14), time spend foraging decreased towards a minimum in May with 24 % of the tidal cycle. From August to October the time spend foraging remained at about 35 % of the tidal cycle. Variation in the proportion of time spend foraging is not caused by a variation in the length of the tidal period used for foraging but by the level of foraging activity during low tide (Fig. 6.16). In August, for example, birds started foraging two hours after high water with the highest foraging activity around low water. They ceased foraging two hours before high water. This tidal pattern resulted in a mean foraging activity of 36 % per tidal cycle. Also in May birds started foraging two hours after high water. However, maximum foraging activity occurred already two hours before low water. Around low water Bar-tailed Godwits formed roosting flocks along the water line resulting in a reduced foraging activity in the second half of the tidal cycle. Foraging activity ceased two hours before high water, like in August. This tidal pattern resulted in a mean foraging activity of 24 % per tidal cycle. High tide roost attendance confirmed the general pattern of foraging activity with 50 % of the birds leaving the roost two hours after high water and 50 % of the birds returning to the roost site 2 - 3 hours before high water (Fig. 6.17).

Energy intake

Assimilated energy intake of Bar-tailed Godwits foraging on the tidal flats around List varied with season (Fig. 6.18). In most months Bar-tailed Godwits assimilated on average 500 kJ day^{-1}. Exceptions with an elevated energy intake were April and August when birds moulted into breeding and winter plumage, respectively, and prepared for migrations to breeding or wintering sites. A slightly elevated energy intake was observed in February, when birds had the highest energy demands for thermoregulation. The November value is on an extremely low level due to shortcomings in the observations of intake rates (see methods) and therefore seems unreliable.

Energy intake however has to be considered in relation to energy expenditure. Compared to M_{maint} of a solitary Bar-tailed Godwit on open sandflats it appears that in April, May, August, and September a surplus of energy is available (Fig. 6.19). Nonetheless, birds stay for several hours in a tight flock at the high tide roost,

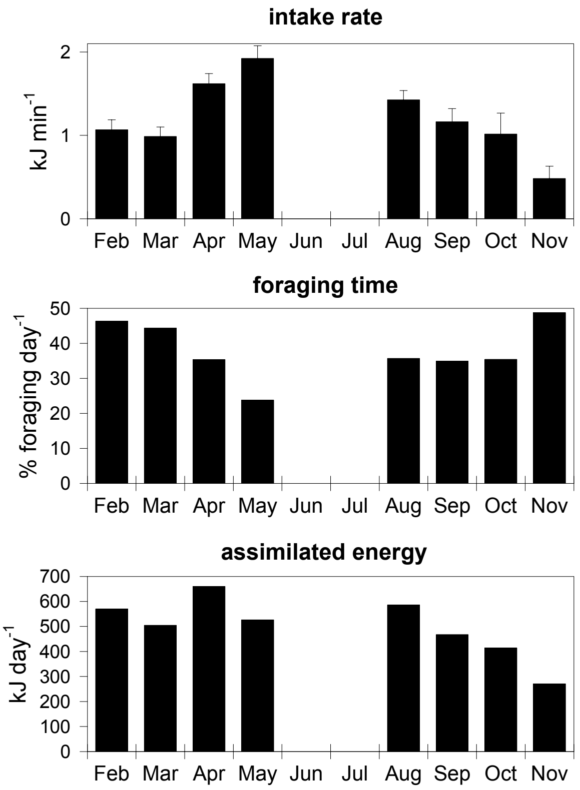

Fig. 6.18: Seasonal patterns of intake rate (mean + SE for all birds observed per month), foraging time and calculated energy intake. For calculation of assimilated energy, an assimilation efficiency of 80 % was assumed.

where thermostatic costs are reduced (Wiersma & Piersma 1994). Furthermore, calculation of energy intake is based on many steps with several assumptions so that the absolute level of energy intake might be on a higher level (s. ‘errors in calculating energy intake’). Outside the migratory and moulting season energy intake seems to be closely related to M_{maint}. Thus, although only a small margin for additional energy expenditure is left in October, birds should be able to cope with the rising M_{maint} towards January by an increase of the time spent foraging as can be seen for February.

Additionally to thermostatic costs, birds have to heat the food to body temperature (Fig. 6.20). Depending on water temperature and amount and type of food ingested, energy to warm up the food to body temperature varied between 27.3 kJ and 54.5 kJ per day. These values represent between 12.5 % and 25 % of the BMR, with high values in winter and early spring. In relation to the assimilated energy, birds had to spend between 5.6 % and 8.3 % of the energy gained from the food to warm it up. The highest amount of energy had to be invested in April, when energy intake was on the highest level within the annual cycle but water temperatures were still relatively low.

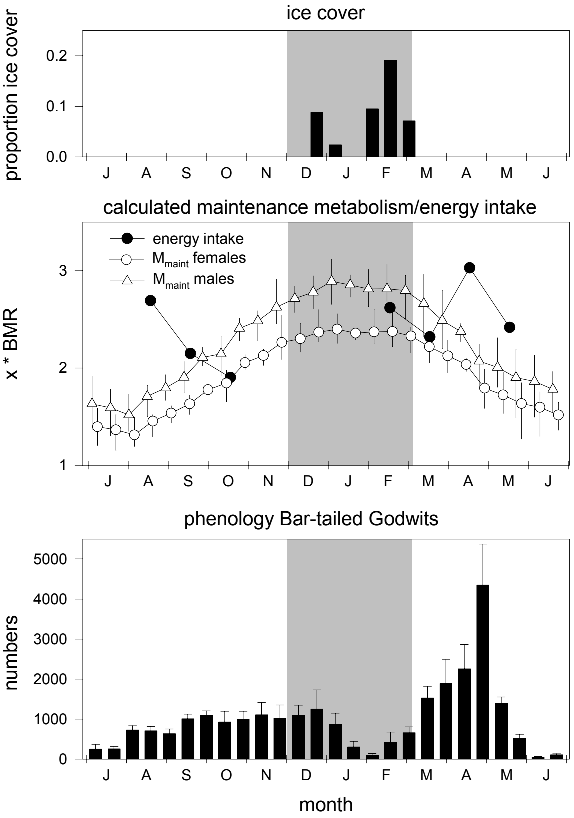

Fig. 6.19: Seasonal pattern of ice cover, maintenance metabolism, assimilated energy intake, and occurrence of Bar-tailed Godwits around List. For ice cover mean proportion of days with ice per fortnight interval at Amrum in the years 1990 - 1995 was calculated (Koslowski 1990 - 1993, Strübing 1994 - 1996). Maintenance metabolism (mean + range per fortnight) was calculated on the basis of daily weather registrations of the DWD (German Weather Service) at List in the years 1990 - 1995. Phenology of Bar-tailed Godwits (mean + SE) is based on spring tide counts in the Königshafen 1990 - 1995 (1 - 6 counts per fortnight interval). Shaded area denotes winter period; data within this period was used for a multiple regression analysis (s. text).

In order to test whether thermostatic costs or ice cover of the mudflats influence migratory movements of Bar-tailed Godwits in winter, a multiple regression with M_{maint} and ice cover as independent and bird numbers as dependent variables for each sex was performed. Each fortnight interval from December to the beginning of March of the years 1990 - 1995 formed a data point. Ice cover had no influence on bird numbers, whereas M_{maint} of females had a significant influence (r^2 = 0.141, $p < 0.05$, n = 29). Thus, birds leave the area as a consequence of high thermostatic costs, with males leaving earlier than females (Scheiffarth 2001a). Males have to leave the area since they have higher thermostatic costs than females. Bar-tailed Godwits

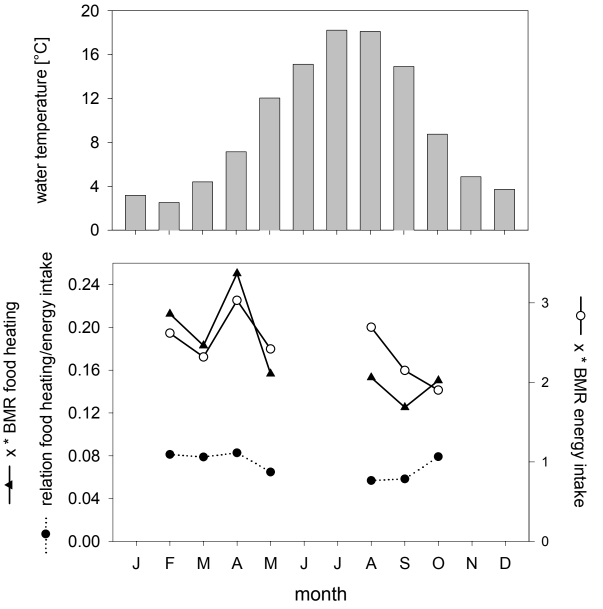

Fig. 6.20: Seasonal variation in energy demands for ingested food to body temperature in relation to BMR and metabolisable energy intake (lower graph). Energy demands were calculated on basis of water temperatures near List (upper graph, mean temperatures 1991 - 1994; Martens, unpubl.) and water content of prey ingested.

return to the study area by the end of February or the beginning of March, when thermostatic costs decrease and a good relation between M_{maint} and energy intake is to be expected.

Discussion

Heated taxidermic mounts as a tool for estimating the maintenance metabolism of Bar-tailed Godwits

Several possibilities exist for the estimation of thermostatic costs of homeotherm animals in the field. The use of T_a alone is the worst alternative and has not proved satisfactory for linking laboratory investigations to the field because it does not take into account the effects of wind and radiation (Wiersma et al. 1993, Dawson & O'Connor 1996). In particular, wind has a strong effect on birds living in open habitats (Wiersma & Piersma 1994) like Bar-tailed Godwits do. Therefore, three serious alternatives exist: modelling heat transfer between the animal and its environment (e.g. Porter & Gates 1969, O'Connor & Spotila 1992, Cartar & Morrison 1997), measuring T_e and wind speed (Bakken et al. 1985, Bakken 1990), and the use of T_{es} thermometers like heated taxidermic mounts (Bakken et al. 1985, Bakken 1992, Wiersma & Piersma 1994).

Modelling heat transfer involves the estimation of many parameters and is based on many assumptions (O'Connor & Spotila 1992) so that this way is often unpractical and may lead to biased results just as any empirical method may do. The measurement of T_e instead of the complete modelling of heat transfer is critical, if wind is expected to have a large influence on thermostatic costs (Wiersma & Piersma 1994). In this case, T_{es} is usually calculated from measured T_e by modelling the influence of wind on T_e. Here again, besides the measurements, parameters of the heat transfer model have to be estimated like in the complete modelling of heat transfer.

The third alternative, measuring T_{es} by means of heated taxidermic mounts, has the advantage that mounts resemble the shape of the target species and that heat loss of heated taxidermic mounts can directly be calibrated against the heat loss of live birds in the laboratory. Additionally, heated taxidermic mounts serve as a model to calculate the influence of wind on a warm body (Wiersma & Piersma 1994). With heated taxidermic mounts, empirical measurement of heat loss can be used to estimate parameters of a physically realistic model which allows the calculation of M_{maint} on the basis of widely available weather data (Wiersma & Piersma 1994).

However, mounts cannot simulate the change in conductance of the insulation like pilomotoric movements of the feathers (Biebach 1978, Marsh & Dawson 1989) or changes in cutaneous circulation which results in a change of heat transfer (Walsberg & Wolf 1996). Nevertheless, these differences should be minimized due to the calibration of mounts with a sufficient range of temperatures. The most critical part of the method is the calibration of the mounts only against a temperature gradient. For more reliable results, calibrations should also be made against wind and radiation (Walsberg & Wolf 1996) since e.g. thermal resistance of birds and mounts can change with wind speed (Walsberg & Wolf 1996). Furthermore, Walsberg & Wolf (1996) found substantial variation in T_{es} between different mounts. However, since mounts were calibrated, T_{es} was standardized on the basis of live birds. Despite all these shortcomings of the way heated taxidermic mounts are used at present, a comparison between the results of the modelling of heat transfer of Knots (*Calidris canutus*) and results of an empirical model developed with heated taxidermic mounts were in close agreement for the weather situations of the Canadian arctic (Cartar & Morrison 1997).

In this study conductance of Bar-tailed Godwits as well as of the mounts were determined under standard conditions which means with free convection in the respirometry boxes. However, Bakken (1976) recommended that these measurements should be conducted with forced convection at a standard wind speed of 1 m s^{-1}. This would result in a higher conductance for the birds as well as the mounts (s. Wiersma & Piersma 1994) which in turn would result in a higher M_{maint} for Bar-tailed Godwits than presented in this study. Changes in K_{es} had the highest effect of all parameters on M_{maint} in a sensitivity analysis of a modelling approach (Cartar & Morrison 1997) so that this point might be critical also for heated taxidermic mounts. On the other hand, M_{maint} was calculated for birds standing solitary on open sandflats. However, Bar-tailed Godwits spent 50 % of the tidal cycle in roosting flocks. Within flocks of Knots a reduction of wind speed up to 51 % resulted in a reduction in M_{maint} of 6 - 9 % (Wiersma & Piersma 1994). For Avocets (*Recurvirostra avosetta*) M_{maint} calculated for birds in a flock was reduced by up to 5 % compared to birds standing solitary on open sandflats (Hötker & Scheiffarth in prep.). In all, since the errors certainly do not cancel out each other, the exact level of M_{maint} as presented in this study may be questionable but should be in a correct order of magnitude. Comparisons between seasons and sites as well as between different species should be possible by means of this method.

Errors in calculating energy intake

The calculation of net energy intake is based on several assumption as well as a multistep procedure which can each introduce its own errors. Assimilation efficiency had to be taken from literature and the parameters energy intake rate and foraging time per day were estimated from observations and benthic sampling.

Calculation of net energy intake was based on the assumption of a constant assimilation efficiency of the ingested energy of 80 %. This is a rather conservative estimate, since in some studies higher assimilation efficiencies were measured for carnivorous birds (Castro et al. 1989). Furthermore, assimilation efficiency can vary throughout the year depending on the status of the bird (Bairlein 1985, Karasov 1996) and a change in the size of digestive organs as one possible prerequisite of a change in assimilation efficiency was shown for waders (Piersma et al. 1996, Piersma & Lindström 1997). Therefore, assimilated energy of Bar-tailed Godwits can be on a higher level, e. g. in winter or during preparation for migration.

To estimate the effect of errors in the estimated parameters foraging time and energy intake rate on net energy intake, sensitivity of the final result to changes in the parameters was tested. Most of the calculations for estimating net energy intake are linear so that a change in these values has the same proportional effect in the resulting energy intake. E.g. an increase of 20 % in foraging time results in a 20 % increase in net energy intake. The only non-linear calculation was the estimation of energy per prey item because all length-weight relationships were exponential functions. A 20 % reduction in the length of all polychaetes taken by the birds results on average in a 11 % reduced net energy intake, a 20 % increase in the length of all polychaetes results on average in a 11.9 % increase in net energy intake. For a 50 % increase or decrease in estimated worm length the mean changes in net energy intake are 31.9 % and 26.4 %, respectively.

The most uncertain value is the estimated foraging time per day from population means. A basic assumption was that birds forage for the same time and with the same intensity day and night. Telemetric data showed that Bar-tailed Godwits were foraging during the night (pers. obs.) although intake rates and exact foraging times are yet unknown. However, a large error in the estimate of foraging time is rather unlikely since i) the tidal patterns of foraging and roost site attendance were inverse, indicating that with scan sampling a reasonable tidal pattern of foraging activity can be obtained with a satisfactory estimate of the start and end of foraging activity, when birds fly between foraging sites and roost sites, ii) foraging activity of flocks around low tide is much easier to observe than during the periods when birds fly to and from the roost, making any bias introduced by the observation method during this part of the tidal cycle small, iii) birds could not forage longer than the maximum observed time in February because the foraging habitat was not available for longer time, iv) in months with a shorter proportion of foraging than in February, the daylight period was longer so that birds could be observed for a higher proportion of the day minimizing the error introduced by the assumption of equal foraging times day and night. Also an error of 50 % in the length estimates of the prey is rather unlikely, since these estimates were calibrated with stuffed birds. In summary, calculated net energy intake should lie in the presented order of magnitude.

BMR of Bar-tailed Godwits: why is it that high?

Measured BMR of Bar-tailed Godwits of the European population was higher than predicted by all allometric equations available relating BMR to body weight (Tab. 6.5). The measurements were conducted with birds which had been in captivity for 2½ years. Thus, internal organ structure might have changed and resulted in

Tab. 6.5: Comparison of BMR of Bar-tailed Godwits from the European population measured during this study with predicted BMR from several equations scaling BMR to body weight. BMR values were calculated with a weight of 275 g, the mean weight of the birds during measurements in the thermoneutral zone. When applicable, equations for non-passerine birds were taken.

BMR [W]	relation (measured BMR)/ (predicted BMR)	Source
2.28		measured, this study
2.05	1.11	Prinzinger & Jackel 1986
1.97	1.15	Kersten & Piersma 1987
1.77	1.28	Daan et al. 1990
1.72	1.32	Reynolds & Lee 1996
1.57	1.45	Kendeigh et al. 1977
1.49	1.53	Lasiewski & Dawson 1967
1.38	1.65	Aschoff & Pohl 1970b
1.17	1.91	Bennett & Harvey 1987
mean	1.43	
SD	0.28	

a lowering of BMR (Piersma et al. 1996, Weber & Piersma 1996). However, Weathers et al. (1983) found no difference in BMR between freshly caught Apapanes (*Himatione sanguinea*) and birds which had been in captivity for one year. Nevertheless, if any influence of long-term captivity exists on the BMR of Bar-tailed Godwits, BMR in the wild should even be higher than the values presented in this study.

For the calculation of M_{maint} the same BMR was used throughout the year. At least for birds of the Afro-Siberian population no difference in weight specific BMR between summer and winter was found (Scheiffarth et al. 2002). Unfortunately, for the birds of the European population no reliable results for summer were available, since the measurement equipment failed. However, the few data available suggest a similar BMR in summer and winter. Furthermore, on basis of an equation presented by Weathers (1980), the same BMR for summer and winter would be predicted for the bird of the size of a Bar-tailed Godwit. So far, any changes in weight specific BMR, namely a rise in response to winter acclimatization seem questionable or largely absent in wild birds (Dawson & Marsh 1989, Dawson & O'Connor 1996). Piersma et al. (1995) found seasonal differences in BMR in Knots. However, these changes were related to migratory seasons, when Knots were accumulating nutrients at a rather fast rate and therefore a large metabolic machinery was necessary (Piersma et al. 1996). Since European Bar-tailed Godwits gained weight at a comparatively low rate in spring (Prokosch 1988), the increase in the size of the metabolic machinery and therefore a rise in BMR should not be as pronounced as in long-distance migrants with short stopover times.

Is a high BMR adaptive for wintering at northern or temperate latitudes? Birds wintering in open habitats at temperate sites have high thermostatic costs as compared to conspecifics wintering in more southerly areas (Hötker & Scheiffarth in prep., Piersma et al. 1991, Wiersma & Piersma 1994). Since sustainable metabolic rate (SusMR) is supposed to be coupled to BMR, for a high SusMR a high BMR is needed, which is achieved by a mass increase in energy supplying organs (Hammond & Diamond 1997). Thus, a high BMR is determined by a relatively large metabolic machinery, which evolved in adjustment to episodes of maximal energetic demands (Daan et al. 1990). For temperate wintering waders, overwintering might be the episode of maximal energetic demands (Piersma et al. 1996) and their metabolic machinery should be adapted to this situation. Besides an increased thermogenic capacity, a high BMR may lead to a lowering of T_{lc}, the protection of peripheral tissues, and an increased cold resistance (Dawson & O'Connor 1996).

The energy budget: energy intake in relation to basic energetic costs

Whether a stopover or wintering site is suitable depends to a large extent on the relationship between energetic costs and gains. For energetic costs the following parts were considered as basic, which had to be afforded in any case: M_{maint}, the heating of ingested food from water temperature to body temperature, costs for moult, and costs for body mass increase due to preparation for migration. These costs cannot substitute for each other or any other costs, so that they are additive. Other costs like specific dynamic action (SDA) and activity produce heat, which can compensate for either thermostatic costs (Masman et al. 1989, Zerba & Walsberg 1992, Chappell et al. 1997, Bruinzeel & Piersma 1998) or the costs of heating food to body temperature (Nehls 1995). Thus, although to a certain extent obligatory, they do not build an additive part in the energy budget. The amount of heat from these activities which can be used for thermoregulation is still a matter of debate and may vary from species to species (s. Bruinzeel & Piersma 1998).

For the calculation of basic energetic costs, several assumptions had to be made. Since energy intake could not be calculated for males and females separately, for all parts of the energy budget the mean of males and females was taken. For the population mean this should come close to the real situation, since for most time of the year both sexes were present in the study area in equal proportions (Scheiffarth 2001a). Besides M_{maint} and the cost of heating food which were determined in this study, costs of moult and weight increase had to be estimated. During April females increase 2.2 g d^{-1} and males 1.6 g d^{-1} in weight (Prokosch 1988). Assuming that 35 % of this mass increase consists of wet protein with an energetic density of 6 kJ g^{-1} and the remainder of fat with an energetic density of 39 kJ g^{-1} (Lindström & Piersma 1993) and furthermore, that deposition efficiency amounts 80 % (cf. Piersma & Jukema 1993), additional metabolizable energy demand would be 55 kJ d^{-1} and 75 kJ d^{-1} for males and females, respectively. For the calculation of the energy budget a constant weight increase with a mean cost of 65 kJ d^{-1} for April and May was assumed, because until the beginning of May an influx of birds into the study area was observed (Scheiffarth 2001a) and these birds were also supposed to increase in weight at the same rate as birds in April. Unfortunately, nothing is known about weight changes in autumn so that for August and September the same costs for the deposition of nutrients required for migration as in spring were assumed. According to Piersma & Jukema (1993), Bar-tailed Godwits are supposed to moult half of the dorsal and the entire ventral plumage in spring, which equals a dry feather mass of 6.54 g and 8 g for males and females, respectively. In autumn it is assumed that the entire dry feather mass is replaced, which results in a dry feather mass production of 9.2 g for males and 11.4 g for females (all values from Piersma & Jukema 1993). The cost of feather synthesis was calculated after Lindström et al. (1993) with the formula: C_f[kJ g dry $feathers^{-1}$] = 270 * BMR_m, where BMR_m = mass specific BMR [kJ d^{-1} g^{-1}]. With a moulting period of 45 days from mid March to the end of April (Scheiffarth 2001a) this results in an average feather production cost of 31 kJ d^{-1}. The corresponding value for autumn with a moulting period of 60 days from August to September (Scheiffarth 2001a) is 33.5 kJ d^{-1}.

Patterns of energy intake and calculated basic costs gave a close correlation (Fig. 21, $r = 0.83$, $p = 0.041$, $n = 6$; without August, s. below). However, since birds need energy for activity, metabolizable energy intake should be higher in relation to calculated costs. Besides the overestimation of M_{maint} or the underestimation of energy intake (s. 'errors in calculating energy intake'), a high rate of compensation of heat producing activities for thermoregulation could exist (s. Hötker in prep., Zerba & Walsberg 1992) so that the birds do not need extra energy for these activities. Only in August energy intake exceeded basic costs. During this month some Bar-tailed Godwits stopover in the study area only for a short time (Scheiffarth 2001a). Probably, these birds refill their energy stores as fast as possible, so that the assumed weight increase and therefore calculated costs might be too low. In all, basic costs seem to determine the seasonal pattern of the energy budget which implies, that costs for activity are more or less on the same level throughout the year.

The patterns of intake rate and foraging time were antiparallel. In spring, as soon as intake rate rose, foraging time decreased. Furthermore, the effort while foraging was on the same level for most of the year (a constant peck rate) so that birds seem to regulate their energy intake on a rather low level by the amount of time invested for foraging. Birds of the Afro-Siberian population gain weight at a much faster rate (Prokosch 1988) and their daily metabolizable energy intake (DME) is on a much higher level during spring migration than for birds of the European population (Scheiffarth et al. 2002). Even if DME would have been underestimated and relatively high activity costs are assumed, if compared to other migratory bird species metabolic scope of the European birds should lie much higher than the observed DEE (Fig. 6.21). A metabolic scope of 3.6 * BMR was estimated as a mean for parental investment of 26 altricial bird species (Daan et al. 1990). However, Lindström & Kvist (1995) calculated a metabolic scope of 4.6 * BMR for migratory passerines which might also be valid for waders. Thus, during migratory weight gain a higher metabolic scope might be possible than during parental care. Bar-tailed Godwits of the European population seem to be far under this metabolic ceiling during spring migration. Additionally, on the basis of a model proposed by Lindström (1991) a weight gain of 8-10 g d^{-1} would be the maximum theoretical rate, if Bar-tailed Godwits are not food limited. With a weight gain of 1.6 g d^{-1} and 2.2 g d^{-1} for males and females respectively, birds are far away from this limit. They should not be food limited, since in spring during the phase of weight gain, energy intake rate (kJ min^{-1}) increased while they reduced foraging time. In summary, on the basis of their energy turn-over as well as food supply a higher weight gain of European Bar-tailed Godwits should be possible in spring.

Migratory birds have three different strategies to optimize their migrations (Alerstam & Lindström

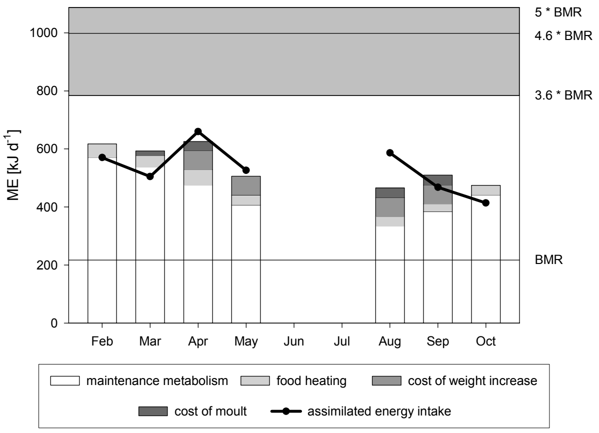

Fig. 6.21: Seasonal pattern of basic energetic costs (s. text) and metabolisable energy intake. Metabolic ceilings were calculated according to Daan et al. (1990, 3.6 * BMR, mean DEE_{par} of all species), Lindström & Kvist (1995, 4.6 * BMR, DME_{max} calculated for migratory passerines), and Kirkwood (1983, 5 * BMR, DME_{max}).

1990): minimize the total time on migration, minimize energy expenditure during migration, and minimize predation risk. Obviously, Bar-tailed Godwits of the European population do not follow the strategy of a time minimized migration since they neither forage nor depose energy at the maximum possible rate. If they adapt the energy minimization strategy, they should be indifferent to a superabundant food source and costs should be connected with either energy intake or energy expenditure (Lindström 1995). Whether departure fat load of European Bar-tailed Godwits is indifferent to superabundant food was not tested in this study, but the large reserves in weight increase rate connected with potential of a higher energy intake hint at this point. As a cost, a high energy expenditure or turn-over may have consequences on survival (Daan et al. 1996). A limit of approximately 4 * BMR is still considered as the upper level of maximum sustainable metabolic rate (Drent & Daan 1980), with higher metabolic rates, although physiologically achievable (s. Hammond & Diamond 1997), having consequences on fitness of the birds (Bryant 1991, 1997). For predation minimization, birds should have lower departure fat loads than with the other two strategies (Alerstam & Lindström 1990, Lindström 1995). Testing of this hypothesis in the field is difficult, if not impossible (Lindström 1995, Biebach 1996). Although this strategy cannot be ruled out, it does not explain why birds put on migratory reserves at such a low rate. In all, Bar-tailed Godwits of the European population seem to follow an energy minimizing migratory strategy, which may be connected to the high energetic costs of wintering in temperate latitudes. This might be the case if high energetic costs at one time of the year have to be balanced at other times. Furthermore, a slow but constant weight gain may be the safer strategy in early spring, when benthic food production varies between years (Zwarts & Wanink 1993).

If not for migration, did the high BMR and with it the related high metabolic scope evolve as an adaptation to adverse weather in winter? In particular males, which have higher thermostatic costs than females, may reach a physiological limit in DEE. At least in the northern part of the Wadden Sea birds seem to be food limited in winter, since they already forage for the entire time feeding grounds are accessible. Thus, especially for males, in cold winters a rise in energy intake to balance increased thermostatic costs appears to be impossible. Therefore, a high metabolic scope might be an advantage in the main wintering sites in Great Britain, where higher energy intake rates are achieved than in the northern part of the Wadden Sea (Smith & Evans 1973, Smith 1975) and therefore a high energy expenditure can be balanced.

Winter distribution of Bar-tailed Godwits in Europe: the influence of thermostatic costs

Phenology of Bar-tailed Godwits in spring, summer, and autumn in the Königshafen area was shaped by migratory movements of the birds between wintering and breeding sites. However, presence of the birds in winter at the northern end of their wintering range depended on the local situation of the area. Towards winter birds face two opposing trends: thermostatic costs increase and the prey situation becomes more and more unfavourable (s. Scheiffarth & Nehls 1998). The reaction of Bar-tailed Godwits was to rise foraging time, switch to smaller, easier accessible prey species (Scheiffarth 2001b), and in late winter emigrate to other wintering sites. In particular males left the area earlier than females (Scheiffarth 2001a) due to higher thermostatic costs (Fig. 6.9). Furthermore, females as the larger sex should be able to store more fat in relation to metabolic requirements than the smaller males which guaranties a longer survival time without food (Calder 1974, Biebach 1996) as an insurance when prey becomes inaccessible for some period in winter.

Which situation face birds migrating to other wintering sites than the northern Wadden Sea? Main wintering sites of the European Bar-tailed Godwit population are the Dutch Wadden Sea, the Dutch delta area, and estuaries on the British Isles along the North Sea and the Irish Sea (Fig. 6.22). A similar study on feed-

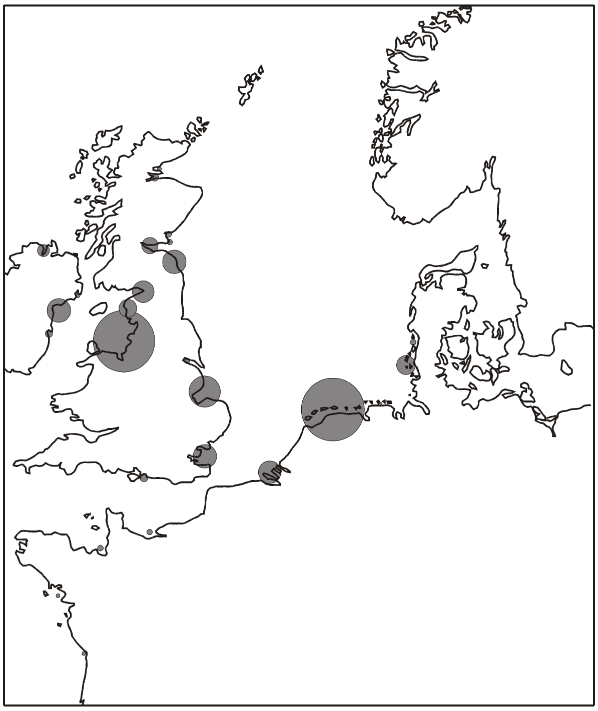

Fig. 6.22: January distribution of Bar-tailed Godwits in north-west Europe. Map based on data from Smit & Piersma (1989). For Great Britain data were taken from Cranswick et al. (1992, years covered: 1988 - 1992), for the Dutch delta area from Meiniger et al. (1994, 1995, 1996, years covered: 1988 - 1995), and for the Wadden Sea from Meltofte et al. (1994, years covered: 1980 - 1991).

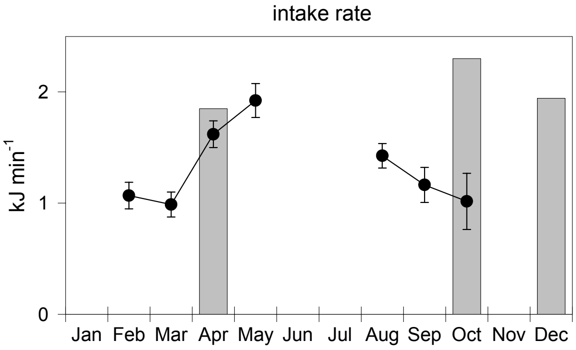

Fig. 6.23: Energy intake rates [kJ min^{-1}] of Bar-tailed Godwits near List/Sylt (dots ± SE) and at Lindisfarne, NE England (bars). Data for Lindisfarne from Smith (1975).

ing ecology of Bar-tailed Godwits was conducted in Lindisfarne, NE England (Smith 1975). There, in April Bar-tailed Godwits had a similar energy intake rate as in the Wadden Sea (Fig. 6.23). However, in winter energy intake rate was twice as high as compared to Sylt. Additionally, thermostatic costs are on a lower level in eastern and north-eastern England than on Sylt, especially for males (Fig. 6.24). Mean thermostatic costs in Great Britain should even be on a lower level than presented in Fig. 6.24 since M_{maint} was calculated on the basis of weather data from severe winters only (I. Mitchell, pers. com.). Even if the saving of thermostatic costs is marginal, in connection with the higher intake rates it should be easier for Bar-tailed Godwits to balance the energy budget in Great Britain than in the northern Wadden Sea. Only very few birds migrate further south to winter in France and Portugal (Smit & Piersma 1989) where they experience rather low thermostatic costs. However, nothing is known about the feeding situation in these areas.

If the wintering situation is much better elsewhere, why then do some Bar-tailed Godwits stay in the northern part of the Wadden Sea during winter? Since thermostatic costs are size dependent with smaller birds having higher costs than large birds (Wiersma et al. 1993, Scheiffarth & Nehls 1998) one might expect that individuals larger than the population mean would stay in the northern part of the Wadden Sea. However, in the Königshafen area colour marked birds resighted in winter were of the same size as birds which were present in spring (Scheiffarth 2001a). There must be a trade off between migrating to a wintering site with high intake rates together with relatively low thermostatic costs and staying as far north as possible during winter. Birds staying in the northern Wadden Sea face the risk of ice cover which can make foraging areas inaccessible. However, the chance that the entire Sylt-Rømø area is covered with ice is rather low since wind concentrates ice in one part of the area (pers. obs.). Therefore, ice cover had no influence on the phenology of Bar-tailed Godwits in this study (Fig. 6.19). Further costs of staying in the northern Wadden Sea are a low intake rate due to low prey availability and quality of prey (Zwarts & Wanink 1993) together with high thermostatic costs which might reach a physiological limit that cannot be supported by metabolism over longer periods. These costs have to be seen in connection with the advantage that no costs of movement arise in autumn and spring. Besides the pure flight costs there are also costs associated with arrival and establishment in a new and unknown area (Lindström 1995). Furthermore, the birds have the advantage in spring that they already know the area when others arrive. E. g. resident Oystercatchers (*Haematopus ostralegus*) are dominant to migratory birds arriving in a wintering area (Hulscher et al. 1996). Additionally, Bar-tailed Godwits wintering in the Sylt-Rømø Wadden Sea encounter low densities of conspecifics which might hint at a low level of competition in contrast to other areas with much higher densities, especially in the preferred British estuaries (Fig. 6.25). A further disadvantage of

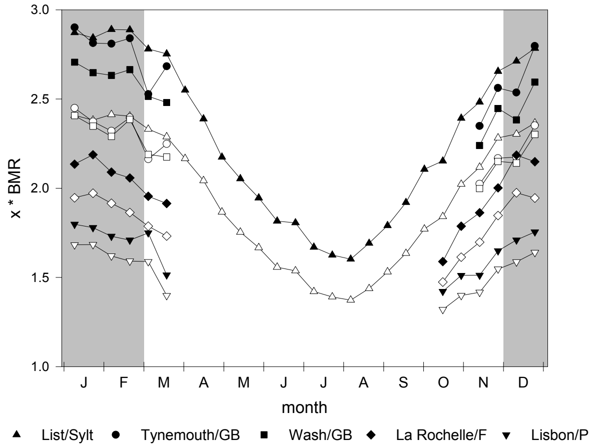

Fig. 6.24: Seasonal phenology of calculated maintenance metabolism in relation to BMR of a male (closed symbols) and female (open symbols) Bar-tailed Godwit standing solitary on open mudflats at different locations. Calculations based on daily weather registrations of the German Weather Service (DWD) for List (1988 - 1997), the British Meteorological Office for Tynemouth and the Wash (1978/79, 1981/82, 1984/85, 1985/86), Meteo France for La Rochelle (1985 - 1991), Instituto de Meteorologia, Portugal (1989 - 1995). Calculated are fortnightly means.

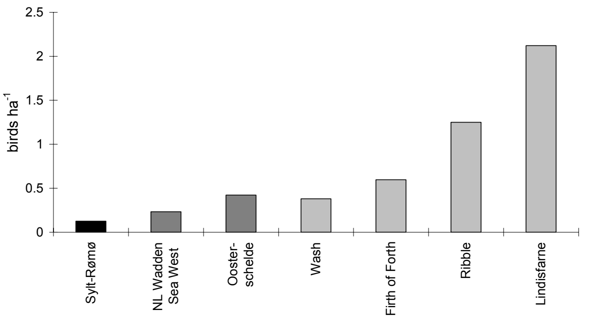

Fig. 6.25: Density [birds ha^{-1} intertidal area] of Bar-tailed Godwits in different wintering sites. Data source s. Fig. 6.22.

wintering in some narrow British estuaries might be a higher risk of predation (s. Cresswell & Witfield 1994) as compared to the open landscape of the Wadden Sea. For birds wintering in milder areas the advantage of lower thermostatic costs in connection with higher intake rates must outweigh the advantages birds have while staying in the northern Wadden Sea. The strategy of wintering as close to the breeding site as possible might be the riskier strategy of both, since in extremely harsh winters Bar-tailed Godwits have to leave the area.

Nonetheless, as shown in this study thermostatic costs can influence migratory and wintering strategies of birds. Due to these costs birds may either reach an energetic limit which cannot be supported by the metabolism over longer periods of time (Drent & Daan 1980, Kirkwood 1983), or thermostatic costs cannot be balanced by energy intake. Further hints of thermostatic costs playing a role in winter distribution of birds is the coincidence of the winter range of passerines in the USA with a limit of 2.5 * BMR (Root 1988) and the fact that DEE of Sanderlings wintering at different latitudes was determined by air temperature (Castro et al. 1992). Besides the influence on the overall pattern of winter distribution of Bar-tailed Godwits, thermostatic costs should also affect the distribution of males and females in winter with males choosing milder sites than females (Scheiffarth 2001a).

Acknowledgements

Conducting a 3 years study on energetics is impossible without the help of many people. First of all I would like to thank Wilhelm Gaul, Ingerlil Hertzler, Ralf Kammann, Georg Nehls, Claus Rüffler and Josef Wegge for their enthusiastic help in the field. Heated taxidermic mounts were constructed with great caution by Yvonne Fritzsche-Nehls and Georg Nehls. Popko Wiersma was always willing to discuss questions of heated taxidermic mounts and energetics in general. Horst Lohse from the research centre GKSS made a weather station available. Further weather data were provided by Hermann Hötker and Ian Mitchell. Klaus Strübing from the Bundesamt für Seeschiffahrt und Hydrographie introduced me to the world of sea ice and provided data of ice cover. The Wadden Sea Station List/Sylt of the Alfred-Wegener-Institut made its entire infrastructure available, which made fieldwork extremely comfortable. Thanks also to the staff of the Wadden Sea Station for support in many ways. For comments, as well as, patience during discussing various topics of the manuscript I would like to thank Franz Bairlein, Hermann Hötker, Christiane Ketzenberg, Georg Nehls and Uwe Totzke. This study was supported by the BMBF as part of the project 'Ecosystem Research Wadden Sea'.

7. Spring migration strategies of two populations of Bar-tailed Godwits (*Limosa lapponica*) in the Wadden Sea: time minimizers or energy minimizers?

Gregor Scheiffarth, Svea Wahls, Christiane Ketzenberg & Klaus-Michael Exo

Abstract

Birds can optimize their migration either by minimizing time of transport, energy expenditure, or predation risk during migration. For each of these optimization criteria different fattening and stopover strategies are predicted. The first two of these optimization criteria are examined here for the Bar-tailed Godwit (*Limosa lapponica*). In the European Wadden Sea two populations of Bar-tailed Godwits stopover during spring migration between their wintering and breeding areas. The European population winters mainly in Great Britain and the western part of the Wadden Sea and breeds in Fennoscandia. The Afro-Siberian population winters in West Africa and breeds in Siberia. The European wintering population migrates to the eastern parts of Wadden Sea in March where it stays until early May. During this time birds gain 1.9 g d^{-1} in body mass for a 1500 – 2000 km non-stop flight to the breeding areas. Afro-Siberian birds stay only for one month in May in the Wadden Sea where they gain on average 9.4 g d^{-1} in mass for a 4000 km non-stop flight. Intake rates in April/May did not differ between the two populations (1.5 kJ min^{-1} and 1.8 kJ min^{-1} for Siberian and European migrants, respectively) but total energy intake was higher for the Siberian migrants, since they spend 50 % of the day foraging vs. 30 % in the European birds. In contrast to European migrants, Afro-Siberian birds start to moult into breeding plumage already in their winter quarters. During their stopover in the Wadden Sea thermostatic costs are lower than at times when European birds are present. Thus, the higher energy demands of the Afro-Siberian birds seem to be fulfilled by a combination of physiological adaptations and a high working level. European birds seem to adopt an energy minimized migration strategy whereas Afro-Siberian birds appear to follow a time minimized migration.

Introduction

Migratory birds face several challenges during migration between their wintering and breeding sites. The migration period might be a bottleneck in the annual cycle of these animals (Piersma 1987a, 1994, Ens et al. 1994) during which resource limitations and competition at stopover areas even can restrict population sizes and distributions of migratory birds (Alerstam & Hedenström 1998). Migration itself is a costly activity, which can comprise up to 50 % of the annual energy budget (Drent & Piersma 1990), with the majority of time and energy spent on the ground for preparation of the flight (Hedenström & Alerstam 1997). To maximize reproductive output, long distance migrants have to optimize their journey with regard to timing of departure from the wintering ground and timing, as well as, rate of fuel deposition, and the choice of stopover sites (Piersma 1987a, Ens et al. 1994, McNamara et al. 1998). At least for Brent Geese (*Branta bernicla*) it has been proved that the amount of fuel accumulated at a spring stopover site can influence breeding success (Ebbinge & Spaans 1995). Migration can be optimized by saving time, energy or avoidance of predation (Alerstam & Lindström 1990, Lindström 1995, Alerstam & Hedenström 1998). This includes flight time, the stopover period, and the period in the wintering areas when birds prepare for return migration (Alerstam & Lindström 1990).

In waders which depend on coastal wetlands, three alternative travel schemes were proposed for their migration from the wintering areas to the breeding grounds (Piersma 1987a). They can either hop in small steps, skip in intermediate steps or jump in large steps of more than 10,000 km non-stop (Piersma & Gill 1998). Although energetically most costly, several wader species perform migrations of the latter type, probably owing to a lack in suitable stopover sites en route (Piersma 1987a). Under the assumptions of the optimal bird migration theory (Alerstam & Lindström 1990), by-passing suitable but low quality stopover sites is expected if birds adopt a time minimized migratory strategy (Gudmundsson et al. 1991). One example of such a long-distance migrant is the Bar-tailed

Godwit. On the East Atlantic Flyway two populations (or subspecies according to Engelmoer & Roselaar 1998) of this species form a leap-frog migration system (Drent & Piersma 1990). The ‘Afro-Siberian’ population winters in West Africa and breeds in Siberia (Cramp & Simmons 1983, Drent & Piersma 1990, Engelmoer & Roselaar 1998). In spring they conduct two 4,000 km non-stop flights with the European Wadden Sea as the only stopover site on the way to their breeding sites. In the Wadden Sea they stay for one month in May and show body mass gains of 5.6 - 11 g d^{-1} and 7.5 - 13.2 g d^{-1} for males and females, respectively (Prokosch 1988, Piersma & Jukema 1990). In contrast, the ‘European’ population winters in Europe around the North Sea with main wintering areas in Great Britain and the western parts of the Wadden Sea (Smit & Piersma 1989). They breed in northern Scandinavia and around the White Sea (Cramp & Simmons 1983, Drent & Piersma 1990, Engelmoer & Roselaar 1998). During spring migration they stay in the northern part of the Wadden Sea from March to early May (Meltofte et al. 1994) where males and females gain on average 1.6 and 2.2 g d^{-1} in mass, respectively (Prokosch 1988). From there they fly ca. 1,500 - 2,000 km non-stop to their breeding grounds.

The optimal bird migration theory (Alerstam & Lindström 1990) predicts the consequences for stopover ecology of different migration strategies. Birds following a time minimized migration have to devote as much energy as possible to fuel deposition and consequently avoid other time and energy consuming activities. Therefore, the time constraint must have consequences on the annual schedule, as well as, the behaviour at stopover sites. Birds following an energy minimized migration choose for a low energy turnover. According to the predictions of the optimal bird migration theory, their takeoff mass is independent of the intake rate and therefore they should be on the save side, always reaching the final takeoff mass. To reach the goal of an energy minimized migration during stopover they should reduce their energy expenditure as much as possible.

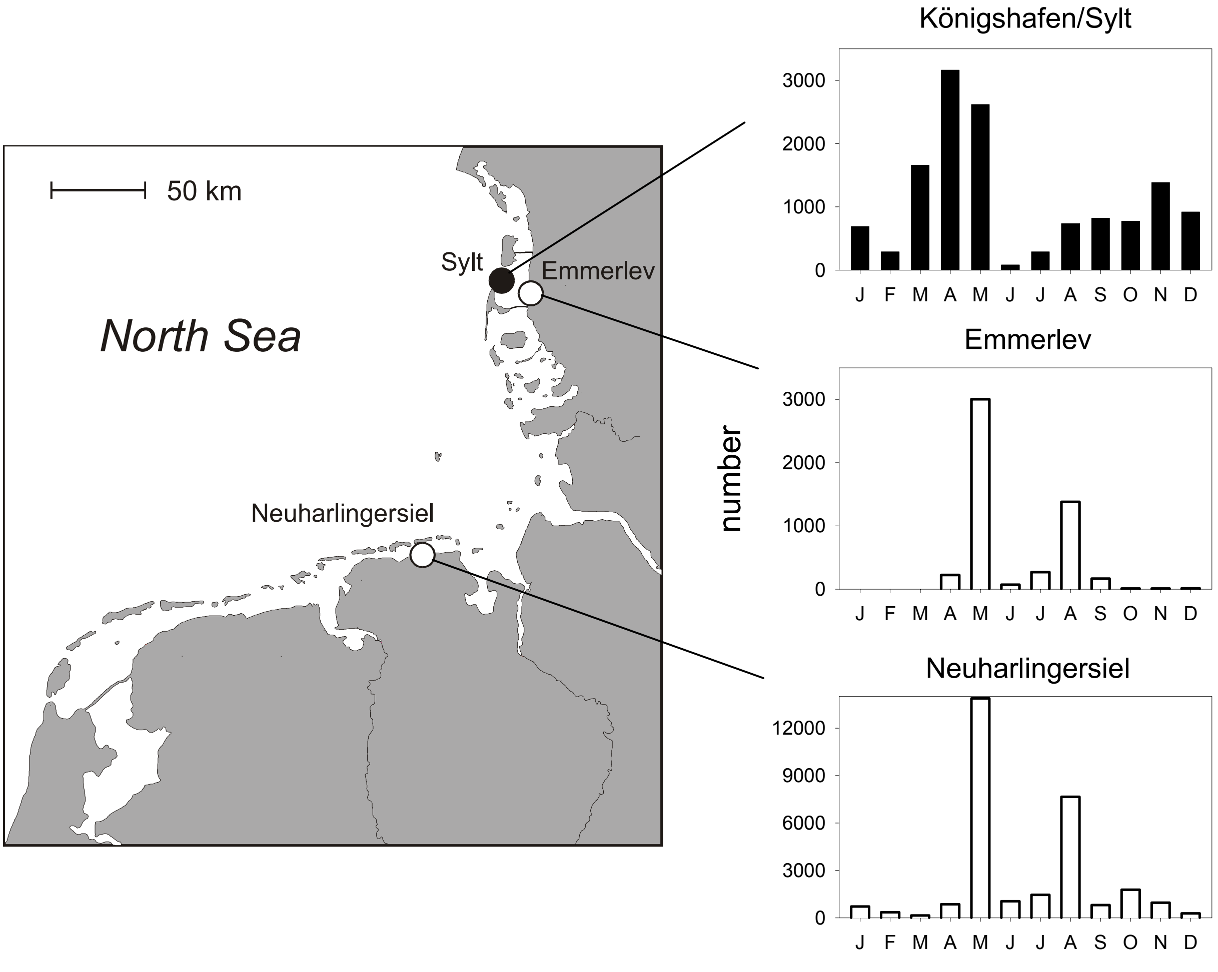

Fig. 7.1: Location of the study sites and phenologies of Bar-tailed Godwits at these sites. Phenologies are monthly means from 4 - 6 years. Open bars and symbols: Afro-Siberian population; black bars and symbol: European population. Note different scales of the y-axes.

Tab. 7.1: Parameters (± SE) estimated with iterative regression procedure for model relating weather data to M_{maint}: $H_{sm} = (K_{es} + K_u * u^{exp}) * (T_b - T_a) - K_r * R_g$ (Wiersma & Piersma 1994). Mass specific metabolic rates and conductances were transformed to individual based values by using mean body mass of birds when present in the Wadden Sea (for European birds own data., for Afro-Siberian birds Prokosch 1988).
Abbreviations used: M_{maint}: maintenance metabolism [W], H_{sm}: standardized heat loss of mount [W], K_{es}: thermal conductance of live bird [W °C^{-1}], u: wind speed [m s^{-1}], T_b: body temperature [°C], T_a: ambient Temperature [°C], R_g: global radiation [W m^{-2}]

parameter	males		females	
population	European	Afro-Siberian	European	Afro-Siberian
K_u	0.0189 ± 0.0014	0.0197 ± 0.0014	0.0268 ± 0.0023	0.0274 ± 0.0024
exp	0.714 ± 0.032	0.714 ± 0.031	0.427 ± 0.040	0.427 ± 0.0404
K_r	0.00097 ± 0.00009	0.00101 ± 0.00009	0.00118 ± 0.00009	0.00120 ± 0.0009
r^2	0.821	0.821	0.792	0.792
n	381	381	387	387
K_{es}	0.0914 W °C^{-1}	0.0953 W °C^{-1}	0.1111 W °C^{-1}	0.1136 W °C^{-1}
BMR	2.27 W	2.07 W	2.76 W	2.46 W
body mass	274 g (March)	323 g (May)	333 g (March)	385 g (May)

The aim of this study was to investigate, how Afro-Siberian Bar-tailed Godwits manage to increase mass during stopover in the Wadden Sea at a much faster rate and end up with a higher mass than European birds do, although the former birds are smaller (Prokosch 1988). There exist two non mutually exclusive possibilities to increase fuel deposition. Birds can save energy by reducing energy consuming activities or they have to increase energy intake. To assess possible differences between the two populations, we looked for differences in energy intake, in energy expenditure in form of maintenance metabolism, and the time schedule of spring migration.

Methods

Study sites

Field observations were made at two sites in the northern part of the Wadden Sea (Königshafen/Sylt, 55°01'N, 8°26'E; Emmerlev, 54°59'N, 8°39'E) and at one site in the East-Friesian part (Neuharlingersiel, 53°43'N, 7°43'E, Fig. 7.1). In the area Königshafen Bar-tailed Godwits of the European population occurred, whereas at the other two sites birds of the Afro-Siberian population were present. This could be assumed since both populations have different phenologies (Fig. 7.1) and are spatially separated (Prokosch 1988, Meltofte et al. 1994). Additionally, morphometric data as well as ringing controls of birds from the Königshafen confirmed that birds in this area originated from the European population (Scheiffarth 2001a).

Metabolic rate

Standard metabolic rate (SMR) in relation to ambient temperature was measured in an standard open flow respirometry system (Hill 1972) as described in detail by Scheiffarth & Bairlein (1998b). Two birds of the European population were measured in winter after they had been in captivity for 2 ½ years. From the Afro-Siberian population four birds were measured in winter after eight months in captivity. During the entire period of captivity, birds were kept in outdoor aviaries in northern Germany.

Thermostatic costs

Maintenance metabolism was estimated by the use of 'heated taxidermic mounts' (Bakken et al. 1981, Wiersma & Piersma 1994) following the protocol as presented by Wiersma & Piersma (1994). After calibration with live birds in a standard laboratory environment, the power required under different weather conditions to keep mounts at the body temperature of Bar-tailed Godwits (41°C) could be calculated into maintenance metabolism. Parallel to the measurements with mounts, a weather station registered air temperature (T_a), wind speed (u), and global radiation (R_g, Lohse et al. 1993). All measured parameters were integrated in a model: $H_{sm} = (K_{es} + K_u u^{exp}) (T_m - T_a) - K_r R_g$ (Wiersma & Piersma 1994, for abbreviations s. Tab. 7.1). The coefficients K_u, and K_r, as well as, the exponent for wind speed (*exp*) were estimated by an iterative regression procedure. For each population and sex a separate model was derived (Tab. 7.1). With the help of the models and 10 years of continuous weather records from List (German Weather Service), a seasonal pattern of maintenance metabolism was calculated for each sex and population.

Energy intake

Calculation of energy intake was a two step procedure. First, energy intake rates (kJ min^{-1}) and foraging time were estimated independently. Second, by multiplying these two parameters and assuming an assimilation efficiency of 80 % (mean value of different sources: Kersten & Piersma 1987, Castro et al. 1989, Zwarts & Blomert 1990) assimilated energy intake per day was calculated. All observations were made during daylight hours and it was assumed that Bar-tailed Godwits were foraging at night with the same intensity. Radiotelemetric data confirmed that Bar-tailed Godwits were foraging for the same amount of time during the night as during the day (Scheiffarth own obs.).

Intake rates were estimated by the observation of individual foraging Bar-tailed Godwits (1992, 1993 on Sylt; 1993, 1994 in Emmerlev; 1995 in Neuharlingersiel). Birds were observed as long as possible and behaviour was recorded on a continuously running tape recorder ("focal animal sampling", "continuous recording"; Martin & Bateson 1986). Only observations with foraging behaviour lasting longer than 270 s were analysed. The size of each prey organism was determined in relation to bill length (for European birds: females 99.7 mm, males 80.5 mm, Scheiffarth 2001a; for Afro-Siberian birds: females 97 mm, males 78 mm, Prokosch 1988) or in relation to the height of colour leg rings (6 mm). Estimated prey sizes were calibrated with a stuffed bird (e.g. Goss-Custard et al. 1987, Zwarts & Esselink 1989) or by dropping analysis. All estimated prey sizes were converted into biomass on the basis of length-mass relationships. For any prey species, for which no own length-mass relationship was obtained, equations from Zwarts & Wanink (1993) were used. Biomass (AFDM) was converted into energy using energy densities given by Zwarts & Wanink (1993). Unidentified prey was corrected on the basis of a particular dropping analysis (Scheiffarth 2001b). For each bird the energy intake rate was calculated over the entire time the observed bird was foraging.

Foraging time was quantified by "scan sampling" in connection with "instantaneous recording" (Martin & Bateson 1986). Flocks of Bar-tailed Godwits were followed and either every 5 min the behaviour of 50 birds (Sylt in 1992 and 1993; Emmerlev in 1993 and 1994) or every 10 min the behaviour of 20 or 30 birds (Neuharlingersiel in 1994 and 1996) was recorded. For Sylt and Emmerlev, per month the mean proportion of foraging time over all observation days was calculated for each 5 min interval of the tidal cycle. From this, the proportion of foraging time was calculated as the mean of all 5 min intervals of a 12.5 h tidal cycle. The mean proportion of time spent foraging for the birds in Neuharlingersiel was calculated in the same way but on a tidal hour base instead of a 5 min base. To test for differences in foraging time, for both populations the mean percentage of time spent foraging per tidal hour was calculated and a sign test was performed.

Moult into breeding plumage

To follow the progress of moult of the population into breeding plumage, males in foraging flocks were scanned with telescopes. Extension of breeding plumage was recorded on a 7 point scale (Pienkowski 1980, s.a. Prokosch 1988, Piersma & Jukema 1993) for each male in the flock. Only samples with at least 20 males were included in the analysis. For each sample a mean plumage score was calculated.

Results

Thermostatic costs

Since thermostatic costs were analyzed in relation to basal metabolic rate (BMR), this parameter was measured for individuals from both populations in winter to obtain results from a comparable situation. European birds had a mass specific BMR of 0.0083 W g^{-1} (Fig. 7.2). Birds from the Afro-Siberian population showed a BMR of 0.00642 W g^{-1}. Conductances did not seem to differ between the two populations.

Based on BMR winter measurements thermostatic costs in the Wadden Sea varied between 1.37 * BMR and 3.41 * BMR (Fig. 7.3). Throughout the year Afro-Siberian males always would have incurred the highest thermostatic costs in the Wadden Sea fluctuating between 3.41 * BMR in February and 1.89 * BMR in August, whereas European females had the lowest thermostatic costs which varied between 2.41 * BMR in February and 1.37 * BMR in August. The seasonal pattern of maintenance metabolism showed consistently higher thermostatic costs for Afro-Siberian birds than for European birds of the same sex (three way ANOVA, $F_{1,892} = 1331.4$, $p < 0.01$). However, only in May Afro-Siberian birds experience the calculated high thermostatic costs for the Wadden Sea which are at the same level as for European birds in April.

Timing of moult into breeding plumage

European Bar-tailed Godwits went through a complete moult from winter plumage to breeding plumage dur-

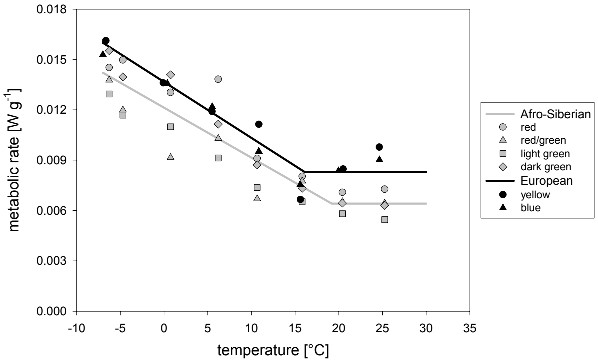

Fig. 7.2: Mass specific metabolic rate of European and Afro-Siberian Bar-tailed Godwits in relation to ambient temperature (Scholander model). All measurements were conducted in winter with birds kept in outdoor aviaries.

ing their stopover in the Wadden Sea (Fig. 7.4). They started moult in the middle of March and finished during the first half of May. On the contrary, Afro-Siberian Bar-tailed Godwits started to moult into breeding plumage already on West African wintering grounds in February (Zwarts et al. 1990). They left the Banc d'Arguin, Mauretania at the end of April with breeding plumage on average 3/4 completed. During their stopover in the Wadden Sea they only finished their moult into breeding plumage (Piersma & Jukema 1993).

Energy intake

When foraging on Wadden Sea tidal flats, Bar-tailed Godwits had an average net energy intake rate of 1.67 kJ min^{-1} (Fig. 7.5). There was no difference between the two populations (Kolmogorov-Smirnov, $D_{93,55} = 0.207$, $p > 0.1$). In European Bar-tailed Godwits during spring, time spent foraging was rather low with only 24 % of the tidal cycle in May. With 43 - 57 % of the tidal cycle, Afro-Siberian birds spent about twice as much time foraging (sign test, difference between means of April/May for European birds and Emmerlev/Neuharlingersiel for Afro-Siberian birds, p = 0.0063). Several additional observations indicate that Afro-Siberian birds were foraging the entire available time. Since in the Sylt-Rømø area 90 % of the intertidal flats are inundated for 33 % of the tidal cycle (Backhaus et al. 1998) and the upper 10 % of the intertidal are relatively unattractive for foraging, only 67 % of the tidal cycle were suitable for foraging. Together with a foraging activity of 57 % of the tidal cycle, only 10 % of the time were left for other activities. Furthermore, with a mean intake rate of 1.17 mg AFDM s^{-1} birds are likely to face a digestive bottleneck so that they are unable to forage non-stop during the entire emersion period (e.g. Diamond & Obst 1990, Kersten & Visser 1996, Zwarts et al. 1996).

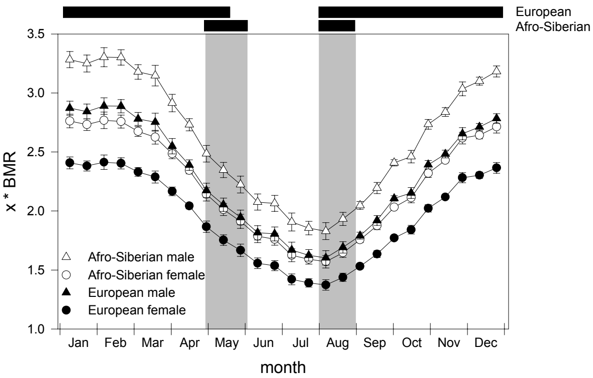

Fig. 7.3: Seasonal phenology of calculated maintenance metabolism in relation to BMR of Bar-tailed Godwits staging in the northern Wadden Sea. Data are based on measurements with heated taxidermic mounts. Maintenance metabolism was calculated with parameters for a solitary bird standing on an open mudflat in the northern part of the Wadden Sea (Tab. 7.1). Phenology is based on daily weather registrations of the German Weather Service of the station List near the Königshafen from the years 1988 - 1997. Calculated are fortnightly means (± SE) over 10 years. Black bars above the graph denote times when birds of either population are present in the Wadden Sea, shaded areas represent times when Afro-Siberian birds are present in the Wadden Sea.

Assuming the same amount of time spent foraging during day and night, assimilated energy intake was much higher for Afro-Siberian Bar-tailed Godwits (720 - 984 kJ day^{-1}) than for European Bar-tailed Godwits (526 - 660 kJ day^{-1}). If Afro-Siberian birds in May have a lower BMR than European birds, their energy intake in relation to BMR is even higher in comparison to European birds than absolute values suggest (3.7 -

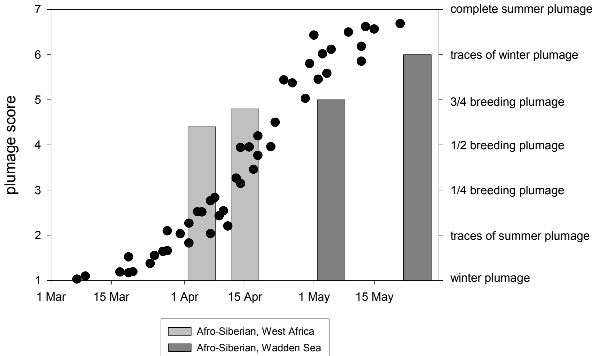

Fig. 7.4: Plumage score of male Bar-tailed Godwits in spring. For European birds mean score of at least 20 birds per sampling occasion was calculated. Data for Afro-Siberian birds originate from Piersma & Jukema (1993).

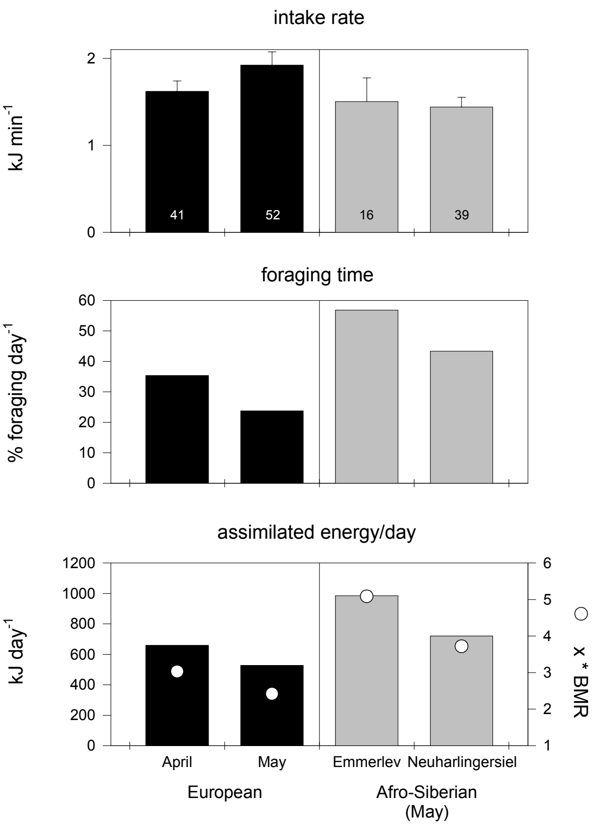

Fig. 7.5: Mean intake rates (+ SE), foraging time and energy intake of Bar-tailed Godwits in April/May foraging on tidal flats. Assimilated energy/day was calculated by multiplying foraging time with intake rate assuming an assimilation efficiency of 80 %. European birds were observed on Sylt, s. Fig. 7.1. Numbers in bars show sample size. ○ = energy intake in relation to basal metabolic rate (BMR).

5.1 * BMR for Afro-Siberian birds, 2.4 – 3 * BMR for European birds).

Discussion

Differences in BMR between Afro-Siberian and European Bar-tailed Godwits

Although birds of both populations were kept under the same outdoor winter conditions, mass specific BMR was higher for birds of the European population than of the Afro-Siberian population. As birds of the European population are larger (Prokosch 1988) it might be expected that they should have a lower mass specific BMR. In comparison to BMR calculated by allometric formulas, European birds appeared to have a higher BMR than predicted by any model (Tab. 7.2). BMR of Afro-Siberian birds, however, was in the same range as predicted.

A high BMR is considered to be a consequence of a large metabolic machinery (Kersten & Piersma 1987, Daan et al. 1990) which enables a high metabolic scope (Hammond & Diamond 1997). For waders wintering at temperate latitudes, as European Bar-tailed Godwits do, winter might be the season with highest metabolic demands (Piersma et al. 1996) and birds should adapt their metabolic machinery to these periods (Daan et al. 1990). As a consequence of the high BMR of European birds, thermostatic costs in relation to BMR are much lower than for Afro-Siberian birds (Fig. 7.3). This becomes particularly evident, when thermostatic costs in winter are considered. If Afro-Siberian males would stay in the Wadden Sea at this time of year, maintenance metabolism would reach a level close to 4 * BMR which is assumed not to be supported by the metabolism in the long-term without consequences for fitness (Drent & Daan 1980, Bryant 1997).

How do Afro-Siberian birds manage to increase in mass at a faster rate than European birds?

Afro-Siberian Bar-tailed Godwits show several marked differences to European birds during stopover on spring migration in the Wadden Sea. i) Afro-Siberian birds work harder by investing more time in foraging (s.a. Scheiffarth et al. 1993). When foraging on the tidal flats birds of both populations experience the same energy intake rates. Under the assumption that Bar-tailed Godwits forage at maximum intake rates (rate maximizers, Stephens & Krebs 1986), a higher absolute energy intake can only be achieved by elongation of the foraging time. ii) The tight time schedule of the Afro-Siberian birds supports the higher mass gain. They start moulting into breeding plumage already in February on their wintering grounds in West Africa (Zwarts et al. 1990) and only complete moult during their stopover in the Wadden Sea (Piersma & Jukema 1993). Thus, in contrast to European birds they have already spent most of the energy for moulting when they arrive in the Wadden Sea. Furthermore, despite their higher thermostatic costs, they do not spend more energy in relation to BMR for maintenance metabolism than European birds since they stay in the Wadden Sea at more favourable times. In May, they have a maintenance metabolism which is at the same level as for European Bar-tailed Godwits in April. In summary, Afro-Siberian Bar-tailed Godwits manage a tight time schedule and gain mass at a higher rate to end up with a higher takeoff mass than European birds by working harder, spending more time foraging per day, and a reduction of other energy consuming activities during stopover in the Wadden Sea.

Tab. 2: Comparison of BMR of Bar-tailed Godwits from the European and Afro-Siberian population measured during this study with predicted BMR from several equations scaling BMR to body mass. BMR values were calculated with the mean mass of the birds during measurements in the thermoneutral zone. When applicable, equations for non-passerine birds were taken.

Source	BMR [W] *European* (275 g)	ratio (measured BMR)/ (predicted BMR)	BMR [W] *Afro-Siberian* (341 g)	ratio (measured BMR)/ (predicted BMR)
measured values	**2.28**		**2.19**	
predictions based on:				
Prinzinger & Jackel 1986	2.05	1.11	2.39	0.92
Kersten & Piersma 1987	1.97	1.16	2.31	0.95
Daan et al. 1990	1.77	1.29	2.06	1.06
Reynolds & Lee 1996	1.72	1.33	1.98	1.11
Kendeigh et al. 1977	1.57	1.45	1.84	1.19
Lasiewski & Dawson 1967	1.49	1.53	1.74	1.26
Aschoff & Pohl 1970b	1.38	1.65	1.62	1.36
Bennett & Harvey 1987	1.17	1.95	1.36	1.61
mean of predictions	1.64	1.43	1.91	1.18
SD	0.30	0.28	0.35	0.23

Time vs. energy minimized migration in Bar-tailed Godwits?

Bar-tailed Godwits seem to follow two different strategies during spring migration. Afro-Siberian birds were foraging the entire time feeding grounds were available and most probably at maximum rate. Furthermore, due to their tight time schedule they try to save as much energy for fuel deposition as possible. In contrast, European birds were not foraging the entire available time and spent more energy on other activities like moulting. If the former population would perform a time minimized migration, optimal bird migration theory predicts that their departure fuel load should be sensitive to the fuel deposition rate (Alerstam & Lindström 1990, Lindström 1995). During this study mass changes could not be measured, but this prediction of the optimal bird migration theory must have several consequences on foraging behaviour. If the overall aim is to minimize migration time (Alerstam & Lindström 1990), birds should forage at maximum rate and use all the time that feeding areas are available. This is what Afro-Siberian birds did and these birds store fuel at the upper limit of their energy metabolism (Lindström 1991). In consequence, if birds with such a tight time schedule stay for a rather fixed short time at a stopover site and forage the entire available time at maximum rate, departure fuel load must be dependent on the actual food stock and therefore must be sensitive to the fuel deposition rate. In years with a low spring biomass or production, this population might be food limited. As was shown for Brent Geese, a low mass gain in spring can affect the reproductive success (Ebbinge & Spaans 1995).

In contrast, European Bar-tailed Godwits might follow a strategy of energy minimized migration (cf. Alerstam & Lindström 1990). For this migration strategy optimal bird migration theory predicts that departure fuel load is independent of the fat deposition rate (Alerstam & Lindström 1990, Lindström 1995). Consequences for the foraging strategy are that in years with average prey availability birds should forage either below maximum rate or for less time than potentially available. European Bar-tailed Godwits, however, increased their intake rate from March to April, and foraged with the same intake rate as Afro-Siberian birds did. Instead of reducing intake rate, they foraged for less time than potentially available by reducing foraging activity around low tide (own obs.). Additionally, their energy intake, as well as, energy turn-over amounts to only 2 - 3 * BMR, so that a higher energy intake should have been possible on the basis of their energy metabolism (own obs.). Furthermore, with 1.6 g d^{-1} for males and 2.2 g d^{-1} for females (Prokosch 1988) they were storing fuel far below the maximum theoretical rate which is 8 - 10 g d^{-1} for a bird of their size (cf. Lindström 1991). Apart from following an energy minimized migration strategy, it is a safer stopover strategy not to depend on a high food stock every year. As these birds deposit fuel earlier in the year (March and April) than Afro-Siberian birds (May), food availability is lower (Piersma et al. 1994) with large variation between years in early spring (Zwarts & Wanink 1993). With an energy intake below the long term average carrying capacity, a sufficient safety margin should exist so that no food limitation may occur during spring migration for European Bar-tailed Godwits in the Wadden Sea.

If in Afro-Siberian birds selection has been directed to minimize time for migration, costs must exist for late arrival in the Siberian breeding area. This might include the chance of getting a mate and/or getting a suitable breeding territory and therefore can cause differences in reproductive success. For most cases in long-distance migrants, for which optimal bird migration theory has been tested so far, time minimized migration was confirmed (Ellegren 1991, Gudmundsson et al. 1991, Lindström & Alerstam 1992, Lindström 1995, Klaassen & Lindström 1996) and might be the 'standard' migration strategy. A consequence of time minimized migration could be a higher predation risk, since birds have to forage at maximum rate at the expense of vigilance (Metcalfe & Furness 1984). The selection pressure on European birds to minimize energy for migration may relate to birds trying not to arrive exhausted on the breeding grounds so that they are able to direct more energy to reproduction. Additionally, the low energy expenditure on migration may reflect a trade-off with the high energetic costs resulting from wintering in temperate areas demanding high energetic expenditures (Piersma et al. 1996). Although differences in the annual energy budget between the two populations are only small (Drent & Piersma 1990), they might be large enough to cause differences in reproductive output or survival as has been suggested for two populations of Red Knot (*Calidris canutus*, Piersma 1994).

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It is not a matter of politeness and formal procedure, that the first person to mention is my supervisor, Franz Bairlein. We got known to each other already at the University of Cologne when I was a student in biology and he was just on the way to become professor. There he had the faith in me that in some near (or distant) future I would manage to finish a PhD thesis after having written my 'Diplomarbeit' which was also supervised by him. After some years working on breeding Oystercatchers I managed to convince him that switching to stopover ecology of Bar-tailed Godwits was the right thing to do for a PhD thesis. Since I was away from the Institute of Avian Research where he had become director in the meantime, doing fieldwork for most time of the year, it must not have been an easy task for him keeping track of the things I was doing. I never forget the encouraging and constructive atmosphere when we met on Friday afternoons for several hours in his office discussing all the things which had happened during my work for the last half a year. Even when I started to work on other things than stopover ecology of Bar-tailed Godwits, he kept on encouraging me to finish the thesis. Fortunately, he was right in the end.

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9. Summary

Migratory birds have to take several life history decisions during the annual cycle. Among others, they have to find a migratory strategy connected to stopover and wintering sites which allows the maximization of lifetime reproductive success. Depending on the migratory strategy followed, birds have different demands concerning a stopover site. The leap-frog migration system found in Bar-tailed Godwits offers an excellent study system to investigate the constraints and choices acting on different migratory strategies within one species. In the European Wadden Sea the Afro-Siberian population stops over on migration between African wintering and Siberian breeding areas. For the European population the Wadden Sea acts either as a stopover site between Western European wintering and Scandinavian breeding areas or as a wintering area itself. In the Sylt-Rømø Wadden Sea, located in the northern part of the European Wadden Sea, consequences of different migratory strategies on stopover ecology, as well as interactions with soft sediment intertidal systems were investigated.

Although more than 10 – 12 Mio. waterbirds spend at least a part of their life cycle in the Wadden Sea, their general impact on the benthic community is small in terms of biomass consumption. As in other temperate intertidal areas, carnivorous birds in the Wadden Sea consume 10 – 25 % of the annual secondary production. For the Sylt-Rømø Wadden Sea annual consumption of intertidal secondary production was estimated at 8.7 g AFDM m^{-2} a^{-1}, which should be representative for the entire Wadden Sea in the 1990ies. In a small, adjacent bay to the Sylt-Rømø Wadden Sea, the Königshafen, mean annual consumption by carnivorous birds was elevated due to an elongated tideline in the bay in relation to intertidal area. Consumption was dominated by the Common Eider with 37 and 60 % of the total consumption, respectively. Because of the high proportion of sandy intertidal area, Bar-tailed Godwits took a share of 11 % of the total consumption by birds in the Königshafen as opposed to 3 % in the entire Sylt-Rømø Wadden Sea.

Bar-tailed Godwits occurring in the Königshafen belonged to the European population as morphometric and ringing data confirmed. In contrast to Afro-Siberian Bar-tailed Godwits which stopover for approximately one month in the Wadden Sea, individually marked birds in the Königshafen stayed for 30 – 40 days in spring. Furthermore, between years Bar-tailed Godwits turned out to be highly site-faithful. Moult from winter into breeding plumage took 43 days in spring and moult from ¾ breeding plumage back to winter plumage took 28 days. Sex ratio was always 1:1 apart from late May and winter. In winter the smaller males left for milder areas in the western Wadden Sea and Great Britain. Even when assuming 100 % site faithfulness, annual mortality rates for adult birds were as low as 17 – 26 %.

Diet of Bar-tailed Godwits in the Königshafen area was estimated by a combination of faeces analysis and visual observations. Overall, 17 prey species were found in droppings but only four polychaetes, *Arenicola marina*, *Nereis diversicolor*, *Nephtys hombergii*, *Scoloplos armiger*, and one crustacean, *Carcinus maenas*, were taken regularly. The diet showed strong seasonal variations, as well as differences between the sexes which were more pronounced in spring and summer than in winter. At this time of year small and easily accessible polychaetes dominated the diet.

The seasonal phenology of birds wintering in the Wadden Sea must depend on local conditions. By means of an energy budget, for the European population of Bar-tailed Godwits was investigated whether birds are constrained by energy intake on spring migration and in how far thermostatic costs influence winter distribution in Europe. The seasonal pattern of energy intake and basic energetic costs (without e.g. activity costs) were closely correlated. During spring migration birds regulated energy intake to a low level by reducing foraging time as soon as intake rates increased. Therefore, a much higher energy gain and should have been possible. The low body mass increase was interpreted as a part of an energy minimizing migratory strategy. During winter thermostatic costs in the northern Wadden Sea increased to 2.4 and 2.9 * BMR for females and males, respectively. Males left the area earlier than females as a consequence of higher thermostatic cost. Although the relation between thermostatic costs and energy intake is much better in the main wintering areas, some birds take the choice of wintering as far north as possible.

Migration can be optimized by minimizing time, energy expenditure or predation risk. Behaviour of the two Bar-tailed Godwit populations occurring in the Wadden Sea indicated that birds from the European population followed an energy minimizing migratory strategy whereas birds from the Afro-Siberian population followed a time minimizing strategy with much higher energy demands. The latter birds achieved the higher energy intake in relation to European birds by an elongation of foraging time, start of moult into breeding plumage already the wintering quarters and arriving in the Wadden Sea at times with lower thermostatic costs.

10. References

Alerstam, T. 1990. Bird Migration. - Cambridge University Press, Cambridge.

Alerstam, T. and Hedenström, A. 1998. The development of bird migration theory. - J. Avian Biol. 29: 343-369.

Alerstam, T. and Högstedt, G. 1980. Spring predictability and leap-frog migration. - Ornis Scand. 11: 196-200.

Alerstam, T. and Högstedt, G. 1985. Leap-frog arguments: reply to Pienkowski, Evans and Townshend. - Ornis Scand. 16: 71-74.

Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: The relative importance of time, energy and safety. - In: Gwinner, E. (ed.) Bird migration, physiology and ecophysiology. Springer-Verlag, Berlin, Heidelberg, pp. 331-351.

Altenburg, W., Engelmoer, M., Mes, R. and Piersma, T. 1982. Wintering waders on the Banc d'Arguin. - Stichting Veth tot steun aan Waddenonderzoek, Leiden.

Aschoff, J. and Pohl, H. 1970a. Rhythmic variations in energy metabolism. - Federation Proceedings 29: 1541-1552.

Aschoff, J. and Pohl, H. 1970b. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. - J. Ornithol. 111: 38-47.

Asmus, H. 1982. Field measurements on repiration and secondary production of a benthic community in the northern Wadden Sea. - Neth. J. Sea Res. 16: 403-413.

Asmus, H. 1987. Secondary production of an intertidal Mussel bed community related to its storage and turnover compartments. - Mar. Ecol. Prog. Ser. 39: 251-266.

Asmus, R., Jensen, M. H., Murphy, D. and Doerffer, R. 1998. Primärporduktion von Microphytobenthos, Phytoplankton und jährlicher Biomasseertrag des Makrophytobenthos im Sylt-Rømø Wattenmeer. - In: Gätje, C. and Reise, K. (eds.): Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, Heidelberg, pp. 367-391.

Atkinson, P. W. 1996. The origins, moult, movements and changes in numbers of Bar-tailed Godwits *Limosa lapponica* on the Wash, England. - Bird Study 43: 60-72.

Austen, I. 1994. The surficial sediments of Königshafen - variations over 50 years. - Helgoländer Meeresunters. 48: 163-171.

Backhaus, J., Hartke, D. and Hübner, U. 1995. Hydrodynamisches und thermodynamisches Modell des Sylter Wattenmeeres. - SWAP Teilprojekt 4.1a. Abschlußbericht, Hamburg.

Backhaus, J., Hartke, D., Hübner, U., Lohse, H. and Müller, A. 1998. Hydrographie und Klima im Lister Tidebecken. - In: Gätje, C. and Reise, K. (eds.): Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, Heidelberg, pp. 39-54.

Backhaus, K., Erichson, B., Plinke, W. and Weiber, R. 1990. Multivariate Analysemethoden. – Springer-Verlag, Berlin, Heidelberg.

Baird, D. and Milne, H. 1981. Energy flow in the Ythan estuary, Aberdeenshire, Scotland. - Estuar. Coast. Shelf Sci. 13: 455-472.

Baird, D. and Ulanowicz, R. E. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. - Mar. Ecol. Prog. Ser. 99: 221-237.

Baird, D., Evans, P. R., Milne, H. and Pienkowski, M. W. 1985. Utilization by shorebirds of benthic invertebrate production in intertidal areas. - Oceanogr. Mar. Biol. Ann. Rev. 23: 573-597.

Baird, D., McGlade, J. M. and Ulanowicz, R. E. 1991. The comparative ecology of six marine ecosystems. - Phil. Trans. R. Soc. Lond. B 333: 15-29.

Bairlein, F. 1985. Efficiency of food utilization during fat deposition in the long-distance migratory garden warbler, *Sylvia borin*. - Oecologia 68: 118-125.

Bairlein, F. 2001. Results of bird ringing in the study of migration routes. - Ardea 89: 7-19.

Bakken, G. S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. - J. theor. Biol. 60: 337-384.

Bakken, G. S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. - Auk 107: 587-594.

Bakken, G. S. 1992. Measurement and application of operative and standard operative temperatures in ecology. - Amer. Zool. 32: 194-216.

Bakken, G. S., Buttemer, W. A., Dawson, W. R. and Gates, D. M. 1981. Heated taxidermic mounts: a means of measuring the standard operative temperature affecting small animals. - Ecology 62: 311-318.

Bakken, G. S., Santee, W. R. and Erskine, D. J. 1985. Operative and standard operative temperature: tools for thermal energetics studies. - Amer. Zool. 25: 933-943.

Banse, K. 1995. Antarctic marine top predators revisited - homeotherms do not leak much CO_2 to the air. - Polar Biol. 15: 93-104.

Begon, M. and Mortimer, M. 1986. Population ecology. A unified study of animals and plants. - Blackwell Scientific Publications, Oxford.

Bell, C. P. 1996. Seasonality and time allocation as causes of leap-frog migration in the Yellow Wagtail *Motacilla flava*. - J. Avian Biol. 27: 334-342.

Bell, C. P. 1997. Leap-frog migration in the Fox Sparrow: minimizing the cost of spring migration. - Condor 99: 470-477.

Bennett, P. M. and Harvey, P. H. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. - J. Zool. 213: 327-363.

Berthold, P. 1998. Bird migration: Genetic programs with high adaptability. - Zoology 101: 235-245.

Berthold, P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. - Ostrich 70: 1-11.

Berthold, P. 2000. Vogelzug. Eine aktuelle Gesamtübersicht. - Wissenschaftliche Buchgesellschaft, Darmstadt.

Beukema, J. J. 1981. Quantitative data on the benthos of the Wadden Sea proper. - In: Dankers, N., Kühl, H. and Wolff, W. J. (eds.): Invertebrates of the Wadden Sea. A. A. Balkema, Rotterdam, pp. 134-142.

Beukema, J. J. 1987. Influence of the predatory polychaete *Nephtys hombergii* on the abundance of other polychaetes. - Mar. Ecol. Prog. Ser. 40: 95-101.

Beukema, J. J. 1989. Long-term changes in macrozoobenthic abundance on the tidal flats of the western part of the Dutch Wadden Sea. - Helgoländer Meeresunters. 43: 405-415.

Beukema, J. J. 1991. The abundance of Shore Crabs *Carcinus maenas* (L.) on a tidal flat in the Wadden Sea after cold and mild winters. - J. exp. mar. Biol. Ecol. 153: 91-113.

Beukema, J. J. 1992. Dynamics of juvenile Shrimp *Crangon crangon* in a atidal flat nursery of the Wadden Sea after mild and cold winters. - Mar. Ecol. Prog. Ser. 83: 157-165.

Beukema, J. J., Essink, K., Michaelis, H. and Zwarts, L. 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? - Neth. J. Sea Res. 31: 319-330.

Biebach, H. 1978. Regulationsmechanismen zur Reduktion der Wärmeverluste bei Amseln (*Turdus merula*). - Verh. Dtsch. Zool. Ges. 71: 203.

Biebach, H. 1996. Energetics of winter and migratory fattening. - In: Carey, C. (ed.) Avian energetics and nutritional ecology. Chapman & Hall, New York, pp. 280-323.

Bligh, J. and Johnson, K. G. 1973. Glossary of terms for thermal physiology. - J. Appl. Physiol. 35: 941-961.

Boddeke, R. 1976. The seasonal migration of the Brown Shrimp *Crangon crangon*. - Neth. J. Sea Res. 10: 103-130.

Boland, J. M. 1990. Leapfrog migration in North American shorebirds: intra- and interspecific examples. - Condor 92: 284-290.

Boyd, H. 1962. Mortality and fertility of European *Charadrii*. - Ibis 104: 368-387.

Boyd, H. and Piersma, T. 2001. Changing balance between survival and recruitment explains population trends in Red Knots *Calidris canutus* islandica wintering in Britain, 1969-1995. - Ardea 89: 301-317.

Bruinzeel, L. W. and Piersma, T. 1998. Cost reduction in the cold: heat generated by terrestrial locomotion partly substitutes for thermoregulation costs in Knot *Calidris canutus*. - Ibis 140: 323-328.

Bryant, D. M. 1991. Constraints on energy expenditure by birds. - Acta XX Congressus Internationalis Ornithologici: 1989-2001.

Bryant, D. M. 1997. Energy expenditure in wild birds. - Proceedings of the Nutrition Society 56: 1025-1039.

Byrkjedal, I., Larsen, T. and Moldsvor, J. 1989. Sexual and antagonistic behaviour of Bar-tailed Godwits on the breeding grounds. - Ornis Scand. 20: 169-175.

Calder, W. A. 1974. Consequences of body size for avian energetics. - In: Paynter, R. A. (ed.) Avian energetics. Publications of the Nuttall Ornithological Club, No. 15, Cambridge, pp. 86-144.

Carss, D. N. and Parkinson, S. G. 1996. Errors associated with otter *Lutra lutra* faecal analysis .1. Assessing general diet from spraints. - J. Zool., Lond. 238: 301-317.

Cartar, R. V. and Morrison, R. I. G. 1997. Estimating metabolic costs for homeotherms from weather data and morphology: An example using calidridine sandpipers. - Can. J. Zool. 75: 94-101.

Castro, G., Stoyan, N. and Myers, J. P. 1989. Assimilation efficiency in birds: a function of taxon or food type? - Comp. Biochem. Physiol. 92A: 271-278.

Castro, G., Myers, J. P. and Ricklefs, R. E. 1992. Ecology and energetics of Sanderlings migrating to four latitudes. - Ecology 73: 833-844.

Chappell, M. A., Bachman, G. C. and Hammond, K. A. 1997. The heat increment of feeding in house wren chicks: Magnitude, duration, and substitution for thermostatic costs. - J. Comp. Physiol. B 167: 313-318.

Cramp, S. and Simmons, K. E. L. 1983. Handbook of the birds of Europe, the Middle East, and North Africa. - Vol. 3. Oxford University Press, Oxford.

Cranswick, P. A., Kirby, J. S. and Waters, R. J. 1992. Wildfowl and Wader counts 1991 - 92. - The Wildfowl & Wetlands Trust, Slimbridge.

Cresswell, W. 1996. Surprise as a winter hunting strategy in Sparrowhawks *Accipiter nisus* Peregrines *Falco peregrinus* and Merlins *F. columbarius*. - Ibis 138: 684-692.

Cresswell, W. and Whitfield, D. P. 1994. The effects of raptor predation on wintering wader populations at the Tyninghame estuary, southeast Scotland. - Ibis 136: 223-232.

CWSS without date. The Wadden Sea. A shared nature area. - Common Wadden Sea Secretariat, Wilhelmshaven.

Daan, S. and Tinbergen, J. M. 1997. Adaptation of Life Histories. - In: Krebs, J. R. and Davies, N. B. (eds.): Behavioural ecology. An evolutionary approach. Blackwell Science, Oxford, pp. 311-333.

Daan, S., Deerenberg, C. and Dijkstra, C. 1996. Increased daily work precipitates natural death in the kestrel. - J. Anim. Ecol. 65: 539-544.

Daan, S., Masman, D. and Groenewold, A. 1990. Avian metabolic rates: their associaton with body composition and energy expenditure in nature. - Am. J. Physiol. 259: R333-R340.

Dawson, W. R. and Marsh, R. L. 1989. Metabolic acclimatization to cold and season in birds. - In: Bech, C. and Reinertsen, R. E. (eds.): Physiology of cold adaptation in birds. Plenum Press, New York, pp. 83-94.

Dawson, W. R. and O'Connor, T. P. 1996. Energetic features of avian thermoregulatory responses. - In: Carey, C. (ed.) Avian energetics and nutritional ecology. Chapman & Hall, New York, pp. 85-124.

de Goeij, P. 2001. Burying depth as a trade-off in the bivalve *Macoma balthica*. - Ph.D. Thesis, University of Groningen.

de Jong, F., Bakker, J. F., Dahl, K., Dankers, N., Farke, H., Jäppelt, W., Koßmagk-Stephan, K. and Madsen, P. B. (eds.): 1993. Quality Status Report of the North Sea. Subregion 10. The Wadden Sea. - The Common Wadden Sea Secretariat, Wilhelmshaven.

Dekinga, A. and Piersma, T. 1993. Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the Knot *Calidris canutus*. - Bird Study 40: 144-156.

Dernedde, T. 1993. Vergleichende Untersuchungen zur Nahrungszusammnesetzung von Silbermöwe (*Larus argentatus*), Sturmmöwe (*L. canus*) und Lachmöwe (*L. ridibundus*) im Königshafen/Sylt. - Corax 15: 222-240.

Diamond, J. and Obst, B. 1990. Constraints that digestive physiology imposes on behavioural ecology and development. - Proc. Int. 100. DO-G Meeting, Current Topics Avian Biol., Bonn 1988: 97-101.

Dingle, H. 1996. Migration: the biology of life on the move. - Oxford University Press, New York, Oxford.

dit Durell, S. E. A. le V. and Kelly, C. P. 1990. Diets of Dunlin *Calidris alpina* and Grey Plover *Pluvialis squatarola* on the Wash as determined by dropping analysis. - Bird Study 37: 44-47.

Dittmann, S. (ed.) 1999. The Wadden Sea ecosystem - Stability properties and mechanisms. - Springer-Verlag, Berlin, Heidelberg.

Dittmann, S. and Scheiffarth, G. in press. Die Bedeutung von Arten für das Ökosystem Wattenmeer. Schriftenreihe des FZ Terramare 11a.

Dittmann, S., Marencic, H. and Roy, M. 1997. Ökosystemforschung im Niedersächsischen Wattenmeer. - In: Fränzle, O., Müller, F. and Schröder, W. (eds.): Handbuch der Umweltwissenschaften. ecomed Verlagsgesellschaft, Landsberg, pp. V-4.1.2 1-17.

Drent, R. H. and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. - Ardea 68: 225-252.

Drent, R. and Piersma, T. 1990. An exploration of the energetics of Leap-Frog migration in arctic breeding Waders. - In: Gwinner, E. (ed.) Bird migration, physiology and ecophysiology. Springer-Verlag, Berlin, Heidelberg, pp. 399-412.

Droste-Hülshoff, F. 1869. Die Vogelwelt der Nordseeinsel Borkum. - Selbstverlag des Verfassers, Münster.

Duffy, D. C. and Jackson, S. 1986. Diet studies of seabirds: a review of methods. - Col. Waterbirds 9: 1-17.

Ebbinge, B. S. and Spaans, B. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b bernicla* in the high Arctic. - J. Avian Biol. 26: 105-113.

Ehlers, J. 1994. Geomorphologie und Hydrologie des Wattenmeeres. - In: Lozán, J. L., Rachor, E., Reise, K., von Westernhagen, H. and Lenz, W. (eds.): Warnsignale aus dem Wattenmeer. Blackwell Wissenschafts-Verlag, Berlin, pp. 1-11.

Eisma, D. 1980. Natural forces. - In: Dijkema, K. S., Reineck, H.-E. and Wolff, W. J. (eds.): Geomorphology of the Wadden Sea. Report No. 1 of the Wadden Sea Working Group. A. A. Balkema, Rotterdam, pp. 20-31.

Ellegren, H. 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. - Ornis Scand. 22: 340-348.

Engelmoer, M. and Roselaar, C. S. 1998. Geographical variation in waders. - Kluwer Academic Publishers, Dordrecht, Boston, London.

Ens, B. J., Piersma, T. and Tinbergen, J. M. 1994. Towards predictive models of bird migration schedules: theoretical and empirical bottlenecks. - NIOZ-rapport 1995-5, Den Burg, Texel.

Ens, B. J., Piersma, T., Wolff, W. J. and Zwarts, L. 1990. Homeward bound: problems waders face when migrating from the Banc d'Arguin, Mauretania, to their northern breeding grounds in spring. - Ardea 78: 1-16.

Esselink, P. and Zwarts, L. 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. - Mar. Ecol. Prog. Ser. 56: 243-254.

Evans, A. 1987. Relative availability of the prey of wading birds by day and by night. - Mar. Ecol. Prog. Ser. 37: 103-107.

Evans, P. R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertevrate prey. - In: Naylor, E. and Hartnoll, R. G. (eds.): Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford, New York, pp. 357-366.

Evans, P. R. and Dugan, P. J. 1984. Coastal birds: numbers in relation to food resources. - In: Evans, P. R., Goss-Custard, J. D. and Hale, W. G. (eds.): Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, London, New York, pp. 8-28.

Evans, P. R., Herdson, D. M., Knights, P. J. and Pienkowski, M. W. 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. I. Shorebird diets, invertebrate densities, and impact of predation on the invertebrates. - Oecologia 41: 183-206.

Exo, K.-M. 1994. Bedeutung des Wattenmeeres für Vögel. - In: Lozán, J. L., Rachor, E., Reise, K., von Westernhagen, H. and Lenz, W. (eds.): Warnsignale aus dem Wattenmeer. Blackwell Wissenschafts-Verlag, Berlin, pp. 261-270.

Flemming, B. W. and Davis, R. A. 1994. Holocene evolution, morphodynamics and sedimentology of the Spiekeroog barrier island system (Southern North Sea). - Senckenbergiana marit. 24: 117-155.

Flemming, B. W. and Nyandwi, N. 1994. Land reclamation as a cause of fine-grained sediment depletion in backbarrier tidal flats (Southern North Sea). - Neth. J. aquat. Ecol. 28: 299-307.

Forstmeier, W. 2002. Benefits of early arrival at breeding grounds vary between males. – J. Anim. Ecol. 71: 1 – 9.

Friedrich, H. 1938. *Polychaeta*. - In: Grimpe, G. and Wagler, E. (eds.): Tierwelt der Nord- und Ostsee. Teil VI. b. Akademische Verlagsgesellschaft, Leipzig, pp. 1-201.

Galbraith, H. 1989. The diet of Lapwing *Vanellus vanellus* chicks on Scottish farmland. - Ibis 131: 80-84.

Gätje, C. and Reise, K. (eds.) 1998. Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. - Springer-Verlag, Berlin, Heidelberg.

Glutz von Blotzheim, U. N, Bauer, K. M. and Bezzel, E. 1986. Handbuch der Vögel Mitteleuropas. - Vol. 7. Aula Verlag, Wiesbaden.

Goss-Custard, J. D. 1973. Current problems in studying the feeding ecology of estuarine birds. - Coastal Ecology Research Paper 4: 1-33.

Goss-Custard, J. D. and Jones, R. E. 1976. The diets of Redshank and Curlew. - Bird Study 23: 233-243.

Goss-Custard, J. D., Jenyon, R. A., Jones, R. E., Newbery, P. E. and Williams, R. L. B. 1977. The ecology of the Wash. II. Seasonal variation in the feeding conditions of wading birds (*Charadrii*). - J. Appl. Ecol. 14: 701-719.

Goss-Custard, J. D., Cayford, J. T., Boates, J. S. and dit Durell, S. E. A. le. V. 1987. Field tests of accuracy of estimating prey size from bill length in Oystercatchers, *Haematopus ostralegus*, eating Mussels, *Mytilus edulis*. - Anim. Behav. 35: 1078-1083.

Green, M., Piersma, T., Jukema, J., de Goeij, P., Spaans, B. and van Gils, J. 2002. Radio-telemetry observations of the first 650 km of te migration of Bar-tailed Godwits from the Wadden Sea to the Russian arctic. - Ardea 90: 71-80.

Green, R. E. 1978. Factors affecting the diet of farmland Skylarks, *Alauda arvensis*. - J. Anim. Ecol. 47: 913-928.

Green, R. E. 1984. The feeding ecology and survival of Partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in East Anglia. - J. Appl. Ecol. 21: 817-830.

Greenberg, R. 1986. Competition in migrant birds in the nonbreeding season. - Current Ornithology 3: 281-307.

Greenwood, J. J. D. and Goss-Custard, J. D. 1970. The relative digestibility of the prey of Redshank *Tringa totanus*. - Ibis 112: 543-544.

Gudmundsson, G. A., Lindström, Å. and Alerstam, T. 1991. Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sanderlings *C. alba* and Turnstones *Arenaria interpres*. - Ibis 133: 140-152.

Hammond, K. A. and Diamond, J. 1997. Maximal sustained energy budgets in humans and animals. - Nature 386: 457-462.

Hartley, P. H. T. 1948. The assessment of the food of birds. - Ibis 90: 361-381.

Hartmann-Schröder, G. 1971. Die Tierwelt Deutschlands und der angrenzenden Meeresteile. 58. Teil: *Annelida*, Borstenwürmer, *Polychaeta*. - Gustav Fischer Verlag, Jena.

Hayes, M. O. 1979. Barrier island morphology as a function of tidal wave regime. - In: Leatherman, S. P. (ed.) Barrier islands. From the Gulf of St. Lawrence to the Gulf of Mexico. Academic Press, New York, pp. 1-27.

Hedenström, A. and Alerstam, T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. - J. theor. Biol. 189: 227-234.

Herrmann, J.-P., Jansen, S. and Temming, A. 1998. Saisonale, diurnale und tidale Wanderungen von Fischen und der Sandgarnele (*Crangon crangon*) im Wattenmeer bei Sylt. - In: Gätje, C. and Reise, K. (eds.): Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, Heidelberg, pp. 499-514.

Hild, A. 1999. Description of the Spiekeroog backbarrier system. - In: Dittmann, S. (ed.) Stability properties and mechanisms of the Wadden Sea ecosystem. Springer-Verlag, Berlin, Heidelberg, pp. 15-18.

Hill, R. W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. - J. Appl. Physiol. 33: 261-263.

Hilton, G. M., Ruxton, G. D. and Cresswell, W. 1999. Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. - Oikos 87: 295-302.

Hockey, P. A. R., Navarro, R. A., Kalejta, B. and Velasquez, C. R. 1992. The riddle of the sands: Why are shorebird densities so high in southern estuaries? - Am. Nat. 140: 961-979.

Homeyer, E. F. 1880. Reise nach Helgoland, den Nordseeinseln Sylt, Lyst etc. - Mahlau & Waldschmidt/Frankfurt a. M.,

Hulings, N. C. and Gray, J. S. 1971. A manual for the study of meiofauna. - Smithsonian Contr. Zool. 78: 1-84.

Hulscher, J. B., Exo, K.-M. and Clark, N. A. 1996. Why do oystercatchers migrate? - In: Goss-Custard, J. D. (ed.) The Oystercatcher - From individuals to populations. Oxford University Press, Oxford, pp. 155-185.

Humphreys, W. F. 1979. Production and respiration in animal populations. - J. Anim. Ecol. 48: 427-453.

Ireland, P. L., Lessels, C. M., McMeeking, J. M. and Minton, C. D. T. 1991. Cannon netting. - In: Bub, H. (ed.) Bird trapping and banding. A handbook for trapping methods all over the world. Cornell University Press, Ithaca, New York, pp. 288-308.

Jenni, L., Reutimann, P. and Jenni-Eiermann, S. 1990. Recognizability of different food types in faeces and in alimentary flushes of Sylvia warblers. - Ibis 132: 445-453.

Jensen, K. T. 1992. Macrozoobenthos on an intertidal mudflat in the Danish Wadden Sea: comparisons of surveys made in the 1930s, 1940s and 1980s. - Helgoländer Meeresunters. 46: 363-376.

Kalejta, B. 1993. Diets of shorebirds at the Berg River estuary, South Africa: spatial and temporal variation. - Ostrich 64: 123-133.

Karasov, W. H. 1996. Digestive plasticity in avian energetics and feeding ecology. - In: Carey, C. (ed.) Avian energetics and nutritional ecology. Chapman & Hall, New York, pp. 61-84.

Kendeigh, S. C., Dol'nik, V. R. and Gravilov, V. M. 1977. Avian energetics. - In: Pinowski, J. and Kendeigh, S. C. (eds.): Granivorous birds in ecosystems. Their evolution, populations, energetics, adaptations, impact and control. Cambridge University Press, Cambridge, pp. 127-204.

Kersten, M. and Piersma, T. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. - Ardea 75: 175-187.

Kersten, M. and Visser, M. 1996. The rate of food processing in the Oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. - Funct. Ecol. 10: 440-448.

Ketterson, E. D. and Nolan Jr., V. 1983. The evolution of differential bird migration. - In: Johnston, R. F. (ed.) Current Ornithology. Vol. 1. Plenum Press, New York, pp. 357-402.

Kirkwood, J. K. 1983. A limit to metabolisable energy intake in mammals and birds. - Comp. Biochem. Physiol. 75A: 1-3.

Klaassen, M. and Lindström, Å. 1996. Departure fuel loads in time-minimizing migrating birds can be explained by the energy costs of being heavy. - J. theor. Biol. 183: 29-34.

Klaassen, M., Lindström, Å., Meltofte, H. and Piersma, T. 2001. Arctic waders are not capital breeders. - Nature 413: 794.

Kokko, H. 1999. Competition for early arrival in migratory birds. - J. Anim. Ecol. 68: 940-950.

Koslowski, G. 1990. Der Eiswinter 1989/90 im deutschen Küstengebiet zwischen Ems und Trave. - Dt. hydrogr. Z. 43: 89-90.

Koslowski, G. 1991/92. Der Eiswinter 1990/91 im deutschen Küstengebiet zwischen Ems und Oder. - Dt. hydrogr. Z. 44: 51-56.

Koslowski, G. 1991/92. Der Eiswinter 1991/92 im deutschen Küstengebiet zwischen Ems und Oder. - Dt. hydrogr. Z. 44: 153-155.

Koslowski, G. 1993. Der Eiswinter 1992/93 im deutschen Küstengebiet zwischen Ems und Oder. - Dt. Hydrogr. Z. 45: 211-214.

Köster, R. 1991. Entstehung und künftige Entwicklung des deutschen Wattenmeeres. - In: Prokosch, P., Mielke, S. and Fleet, D. M. (eds.): The common future of the Wadden Sea. Technical Report. World Wide Fund for Nature, Husum, pp. 53-59.

Krebs, C. J. 1985. Ecology. The experimental analysis of distribution and abundance. - Harper & Row, New York, Cambridge.

Kuipers, B. R., de Wilde, P. A. W. and Creutzberg, F. 1981. Energy flow in a tidal flat ecosystem. - Mar. Ecol. Prog. Ser. 5: 215-221.

Küster, H. 1999. Geschichte der Landschaft in Mitteleuropa. Von der Eiszeit bis zur Gegenwart. - Verlag C. H. Beck, München.

Lackschewitz, D. 1995. Besiedlungsmuster des Macrozoobenthos im Sylt-Römö-Wattenmeer. - SWAP Teilprojekt 2.2/2.3/3.2. Abschlußbericht, List.

Lasiewski, R. C. and Dawson, W. R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. - Condor 69: 13-23.

Lindström, Å. 1991. Maximum fat deposition rates in migrating birds. - Ornis Scand. 22: 12-19.

Lindström, Å. 1995. Stopover ecology of migrating birds: Some unsolved questions. - Israel J. Zool. 41: 407-416.

Lindström, Å. and Alerstam, T. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. - Am. Nat. 140: 477-491.

Lindström, Å. and Kvist, A. 1995. Maximum energy intake is proportional to basal metabolic rate in passerine birds. - Proc. R. Soc. Lond. B 261: 337-343.

Lindström, Å. and Piersma, T. 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. - Ibis 135: 70-78.

Lindström, Å., Visser, G. H. and Daan, S. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. - Physiol. Zool. 66: 490-510.

Lohse, H., Müller, A. and Siewers, H. 1993. Mikrometeorologische Messungen im Wattenmeer. - Annalen der Meteorologie 27: 143.

Marsh, R. L. and Dawson, W. R. 1989. Avian adjustments to the cold. - In: Wang, L. C. H. (ed.) Advances in comparative and environmental physiology. Vol. 4. Springer-Verlag, Berlin, Heidelberg, pp. 205-253.

Martin, P. and Bateson, P. 1986. Measuring behaviour. - Cambridge University Press, Cambridge London, New York.

Masman, D., Daan, S. and Dietz, M. 1989. Heat increment of feeding in the Kestrel, Falco tinnunculus, and its natural seasonal variation. - In: Bech, C. and Reinertsen, R. E. (eds.): Physiology of cold adaptation in birds. Plenum Press, New York, pp. 123-135.

Matthews, S. L., Boates, J. S. and Walde, S. J. 1992. Shorebird predation may cause discrete generations in an amphipod prey. - Ecography 15: 393-400.

McNamara, J. M., Welham, R. K. and Houston, A. I. 1998. The timing of migration within the context of an annual routine. - J. Avian Biol. 29: 416-423.

Meier, D. 1994. Geschichte der Besiedlung und Bedeichung im Nordseeküstenraum. - In: Lozán, J. L., Rachor, E., Reise, K., von Westernhagen, H. and Lenz, W. (eds.): Warnsignale aus dem Wattenmeer. Blackwell Wissenschafts-Verlag, Berlin, pp. 11-17.

Meininger, P. L., Berrevoets, C. M. and Strucker, R. C. W. 1994. Watervogeltellingen in het zuidelijk Deltagebiet, 1987-91. - Rijksinstituut voor Kust en Zee rapport RIKZ-94.005, NIOO-CEMO, Middelburg/Yerseke.

Meininger, P. L., Berrevoets, C. M. and Strucker, R. C. W. 1995. Watervogels in de Zoute Delta 1991-94. - Rijksinstituut voor Kust en Zee rapport RIKZ-95.025, Middelburg/Yerseke.

Meininger, P. L., Berrevoets, C. M. and Strucker, R. C. W. 1996. Watervogels in de Zoute Delta 1994/95. - Rijksinstituut voor Kust en Zee rapport RIKZ-96.009, Middelburg/Yerseke.

Meire, P. M., Schekkermann, H. and Meininger, P. L. 1994. Consumption of benthic invertebrates by waterbirds in the Oosterschelde estuary, SW Netherlands. - Hydrobiologia 282/283: 525-546.

Meltofte, H. 1996. Are african wintering waders really forced south by competition from northerly wintering conspecifics? Benefits and constraints of northern versus southern wintering and breeding in waders. - Ardea 84: 31-44.

Meltofte, H., Blew, J., Frikke, J., Rösner, H.-U. and Smit, C. J. 1994. Numbers and distribution of waterbirds in the Wadden Sea. Results and evaluation of 36 simultaneous counts in the Dutch-German-Danish Wadden Sea 1980 - 1991. - IWRB Publication 34/Wader Study Group Bull. 74, Special issue.

Metcalfe, N. B. and Furness, R. W. 1984. Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. - Behav. Ecol. Sociobiol. 15: 203-206.

Moreau, R. E. 1954. The main vicissitudes of the European avifauna since the Pliocene. - Ibis 96: 411-431.

Moreira, F. 1995. The winter feeding ecology of Avocets *Recurvirostra avosetta* on intertidal areas. II. Diet and feeding mechanism. - Ibis 137: 99-108.

Mouritsen, K. N. 1994. Day and night feeding in Dunlins *Calidris alpina*: choice of habitat, foraging technique and prey. - J. Avian Biol. 25: 55-62.

Nehls, G. 1989. Occurence and food consumption of the Common Eider, *Somateria mollissima*, in the Wadden Sea of Schleswig-Holstein. - Helgoländer Meeresunters. 43: 385-393.

Nehls, G. 1991. Bestand, Jahresrhythmus und Nahrungsökologie der Eiderente, *Somateria mollissima*, L. 1758, im Schleswig-Holsteinischen Wattenmeer. - Corax 14: 146-209.

Nehls, G. 1995. Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente (*Somateria mollissima* (L. 1758)). - Berichte, Forsch.- u. Technologiezentrum Westküste d. Univ. Kiel 10: 1-177.

Nehls, G. and Scheiffarth, G. 1998. Rastvogelbestände im Sylt-Rømø Wattenmeer. - In: Gätje, C. and Reise, K. (eds.): Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, Heidelberg, pp. 89-94.

Nehls, G. and Tiedemann, R. 1993. What determines the densities of feeding birds on tidal flats? A case study on Dunlin, *Calidris alpina*, in the Wadden Sea. - Neth. J. Sea Res. 31: 375-384.

Newton, I. 1995. The contribution of some recent research on birds to ecological understanding. - J. Anim. Ecol. 64: 675-696.

Niesel, V. 1999. Hydrographic conditions in the Spiekeroog backbarrier system. - In: Dittmann, S. (ed.) Stability properties and mechanisms of the Wadden Sea ecosystem. Springer-Verlag, Berlin, Heidelberg, pp. 26-30.

Norusis, M. J. 1986. SPSS/PC+ advanced statistics. - SPSS Inc., Chicago.

O'Connor, M. P. and Spotila, J. R. 1992. Consider a spherical Lizard: animals, models, and approximations. - Amer. Zool. 32: 179-193.

Parker, G. A. 1984. Evolutionary stable strategies. - In: Krebs, J. R. and Davies, N. B. (eds.): Behavioural ecology. An evolutionary approach. Blackwell Scientific Publications, Oxford, pp. 31-61.

Peréz-Hurtado, A., Goss-Custard, J. D. and Garcia, F. 1997. The diet of wintering waders in Cádiz Bay, southwest Spain. - Bird Study 44: 45-52.

Petersen, B. and Exo, K.-M. 1999. Predation of waders and gulls on *Lanice conchilega* tidal flats in the Wadden Sea. - Mar. Ecol. Prog. Ser. 178: 229-240.

Pienkowski, M. W. 1980. A new WSG data form and prospects for analysis. - Wader Study Group Bull. 28: 11-14.

Pienkowski, M. W. 1983. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. - Mar. Ecol. Prog. Ser. 11: 141-150.

Pienkowski, M. W., Ferns, P. N., Davidson, N. C. and Worrall, D. H. 1984. Balancing the budget: measuring the energy intake and requirements of shorebirds in the field. - In: Evans, P. R., Goss-Custard, J. D. and Hale, W. G. (eds.): Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, London, New York, pp. 29-56.

Pienkowski, M. W., Evans, P. R. and Townshend, D. J. 1985. Leap-frog and other migration patterns of waders: a critique of the Alerstam and Högsted hypothesis, and some alternatives. - Ornis Scand. 16: 61-70.

Piersma, T. 1982. Foraging of Bar-tailed Godwits. - In: Altenburg, W., Engelmoer, M., Mes, R. and Piersma, T. (eds.): Wintering waders on the Banc d'Arguin. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp. 136-148.

Piersma, T. 1987a. Hink, stap of sprong? Reisbeperkingen van arctische steltlopers door voedselzoeken, vetopbouw en vliegsnelheid. - Limosa 60: 185-194.

Piersma, T. 1987b. Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. - Mar. Ecol. Prog. Ser. 38: 187-196.

Piersma, T. 1994. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. - Uitgeverij Het Open Boek, Den Burg, Texel.

Piersma, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. - Integ. and Comp. Biol. 42: 51-67.

Piersma, T. and Gill, J. R. E. 1998. Guts don't fly: small digestive organs in obese Bar-tailed Godwits. - Auk 115: 196-203.

Piersma, T. and Jukema, J. 1990. Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of Bar-tailed Godwits at successive spring staging sites. - Ardea 78: 315-337.

Piersma, T. and Jukema, J. 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the Bar-tailed Godwit. - Condor 95: 163-177.

Piersma, T. and Lindström, Å. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. - Trends Ecol. Evol. 12: 134-138.

Piersma, T. and van de Sant, S. 1992. Pattern and predictability of potential wind assistance for waders and geese migrating from West Africa and the Wadden Sea to Siberia. - Ornis Sve. 2: 55-66.

Piersma, T., Drent, R. and Wiersma, P. 1991. Temperate versus tropical wintering in the world's northernmost breeder, the Knot: metabolic scope and resource levels restrict subspecific options. - Acta XX Congressus Internationalis Ornithologici: 761-772.

Piersma, T., Verkuil, Y. and Tulp, I. 1994. Resources for long-distance migration of Knots *Calidris canutus islandica* and *C. c. canutus*: how broad is the temporal exploitation window of benthic prey in the western and eastern Wadden Sea? - Oikos 71: 393-407.

Piersma, T., Cadée, N. and Daan, S. 1995. Seasonality in basal metabolic rate and thermal conductance in a long-distance migrant shorebird, the Knot (*Calidris canutus*). - J. Comp. Physiol. B 165: 37-45.

Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., van der Meer, J. and Wiersma, P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. - Physiol. Zool. 69: 191-217.

Pihl, S. and Frikke, J. 1992. Counting birds from aeroplane. - In: Komdeur, J., Bertelsen, J. and Cracknell, G. (eds.): Manual for aeroplane and ship surveys of waterfowl and seabirds. IWRB Spec. Publ. 19, Slimbridge, pp. 37 pp.

Porter, W. P. 1969. Thermal radiation in metabolic chambers. - Science 166: 115-117.

Porter, W. P. and Gates, D. M. 1969. Thermodynamic equilibria of animals with environment. - Ecological Monographs 39: 227-244.

Postma, H. 1983. Hydrography of the Wadden Sea: Movements and properties of water and particulate matter. - In: Wolff, W. J. (ed.) Ecology of the Wadden Sea. A. A. Balkema, Rotterdam, pp. 2/1-2/75.

Prater, A. J. 1981. Estuary birds of Britain and Ireland. - T & A D Poyser, Calton.

Prater, A. J., Marchant, J. H. and Vuorinen, J. 1977. Guide to the identification and ageing of holoarctic waders. - British Trust for Ornithology, Tring.

Prinzinger, R. 1996. Das Geheimnis des Alterns. Die programmierte Lebenszeit bei Mensch, Tier und Pflanze. - Campus Verlag, Frankfurt.

Prinzinger, R. and Jackel, S. 1986. Energy metabolism, respiration frequency and O_2-consumption per breathing act in 11 different sunbird species during day and night. - Experientia 42: 1002-1003.

Prokosch, P. 1988. Das Schleswig-Holsteinische Wattenmeer als Frühjahrs-Aufenthaltsgebiet arktischer Watvogelpopulationen am Beispiel von Kiebitzregenpfeifer (*Pluvialis squatarola*, L. 1758), Knutt (*Calidris canutus*, L. 1758) und Pfuhlschnepfe (*Limosa lapponica*, L. 1758). - Corax 12: 273-442.

Reading, C. J. and McGrorty, S. 1978. Seasonal variations in burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. - Estuar. coast. mar. Sci. 6: 135-144.

Reise, K. 1985. Tidal flat ecology. - Springer-Verlag, Berlin.

Reise, K. and Riethmüller, R. 1998. Die Sylt-Rømø Wattenmeerbucht: Ein Überblick. - In: Gätje, C. and Reise, K. (eds.): Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, Heidelberg, pp. 21-23.

Reise, K., Herre, E. and Sturm, M. 1994. Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the norhtern Wadden Sea. - Helgoländer Meeresunters. 48: 201-215.

Reise, K., Köster, R., Müller, A., Armonies, W., Asmus, H., Asmus, R., Hickel, W. and Riethmüller, R. 1998. Austauschprozesse im Sylt-Rømø Wattenmeer: Zusammenschau und Ausblick. - In: Gätje, C. and Reise, K. (eds.): Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, Heidelberg, pp. 529-558.

Reynolds, P. S. and Lee, R. M. 1996. Phylogenetic analysis of avian energetics: Passerines and nonpasserines do not differ. - Am. Nat. 147: 735-759.

Ricklefs, R. E. 1996. Avian energetics, ecology, and evolution. - In: Carey, C. (ed.) Avian energetics and nutritional ecology. Chapman & Hall, New York, pp. 1-30.

Robinson, M. F. and Stebbings, R. E. 1993. Food of the serotine bat, *Eptesicus serotinus* - is faecal analysis a valid qualitative and quantitative technique? - J. Zool., Lond. 231: 239-248.

Root, T. 1988. Energy constraints on avian distributions and abundances. - Ecology 69: 330-339.

Rosenberg, K. V. and Cooper, R. J. 1990. Approaches to avian diet analysis. - Studies in Avian Biology 13: 80-90.

Rösner, H.-U. 1994. Population indices for migratory birds in the Schleswig-Holstein Wadden Sea from 1987 to 1993. - Ophelia Suppl. 6: 171-186.

Rösner, H.-U. and Prokosch, P. 1992. Coastal birds counted in a spring-tide rhythm - a project to determine seasonal and long-term trends of numbers in the Wadden Sea. - Neth. Inst. Sea Res. Publ. Ser. 20: 275-279.

Rösner, H.-U., Roomen, M., Südbeck, P. and Rasmussen, L. M. 1994. Migratory waterbirds in the Wadden Sea 1992/1993. - Wadden Sea Ecosystem No. 2, Common Wadden Sea Secretariat & Trilateral Monitoring and Assessment Group, Wilhelmshaven.

Rumohr, H., Brey, T. and Ankar, S. 1987. A compilation of biometric conversion factors for benthic invertebrates of the Baltic Sea. - BMB (The Baltic Marine Biologists) 9: 1-56.

Sachs, L. 1984. Angewandte Statistik. - Springer-Verlag, Berlin, Heidelberg.

Safriel, U. N. 1995. The evolution of Palearctic migration - The case for southern ancestry. - Isr. J. Zool. 41: 417-431.

Salmonsen, F. 1955. Evolution and Bird-Migration. - Acta XI Congr. Int. Ornithol. 337-339.

Scheiffarth, G. 1995. Energiehaushalt und Nahrungsökologie der Pfuhlschnepfe. - In: Bohlken, H. and Hötker, H. (eds.): Trophischer und regulierender Stellenwert der Vögel im Ökosystem Wattenmeer. SWAP Teilprojekt 1.7a/2.5a/4.5b. Abschlußbericht, Büsum, pp. 77-94.

Scheiffarth, G. 1996. How expensive is wintering in the Wadden Sea? Thermostatic costs of Bar-tailed Godwits (*Limosa lapponica*) in the northern part of the Wadden Sea. - Verh. Dtsch. Zool. Ges. 89.1: 178.

Scheiffarth, G. 1998. Das Rätsel der Sandbank: Wo gehen Pfuhlschnepfen (*Limosa lapponica*) auf Nahrungssuche? - Seevögel 19, Sonderheft: 86.

Scheiffarth, G. 2001a. Bar-tailed Godwits (*Limosa lapponica*) in the Sylt-Rømø Wadden Sea: which birds, when, from where, and where to? - Vogelwarte 41: 53-69.

Scheiffarth, G. 2001b. The diet of Bar-tailed Godwits *Limosa lapponica* in the Wadden Sea: combining visual observations and faeces analysis. - Ardea 89: 481-494.

Scheiffarth, G. and Bairlein, F. 1998a. Spring migration strategies of two populations of Bar-tailed Godwits *Limosa lapponica* in the Wadden Sea. - In: Adams, N. J. and Slotow, R. H. (eds.): Proc. 22 Int. Ornithol. Congr., Durban. Ostrich 69., pp. 365.

Scheiffarth, G. and Bairlein, F. 1998b. Wann frieren Pfuhlschnepfen? - BIOforum 21/10: 572-574.

Scheiffarth, G. and Nehls, G. 1995. Nutzung unterschiedlicher Wattflächen im Königshafen. - In: Bohlken, H. and Hötker, H. (eds.): Trophischer und regulierender Stellenwert der Vögel im Ökosystem Wattenmeer. SWAP Teilprojekt 1.7a/2.5a/4.5b. Abschlußbericht, Büsum, pp. 107-137.

Scheiffarth, G. and Nehls, G. 1997. Consumption of benthic macrofauna by carnivorous birds in the Wadden Sea. - Helgoländer Meeresunters. 51: 373-387.

Scheiffarth, G. and Nehls, G. 1998. Saisonale und tidale Wanderungen von Watvögeln im Sylt-Rømø Wattenmeer. - In: Gätje, C. and Reise, K. (eds.): Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, Heidelberg, pp. 515-528.

Scheiffarth, G., Ketzenberg, C. and Exo, K.-M. 1993. Utilization of the Wadden Sea by waders: differences in time budgets between two populations of Bar-tailed Godwits (*Limosa lapponica*) on spring migration. - Verh. Dtsch. Zool. Ges. 86.1: 287.

Scheiffarth, G., Nehls, G. and Austen, I. 1996. Modelling distribution of shorebirds in the Wadden Sea and visualisation of results with the GIS IDIRSI. - In: Lorup, E. and Strobl, J. (eds.): IDRISI GIS 96 = Salzburger Geographische Materialien. Vol. 25. Selbstverlag des Instituts für Geographie der Universität Salzburg, Salzburg, http://www.edvz.sbg.at/geo/idrisi/idrgis96/scheiff/idrisicd.htm.

Scheiffarth, G., Wahls. S., Ketzenberg, C. and Exo, K.-M. 2002. Spring migration strategies of two populations of bar-tailed godwits, *Limosa lapponica*, in the Wadden Sea: time minimizers or energy minimizers? - Oikos 96: 346-354.

Schmidt-Nielsen, K. 1983. Animal physiology: adaptation and environment. - Cambridge University Press, Cambridge, London.

Scholander, P. F., Hock, R., Walters, V. and Irving, L. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biol. Bull. 99: 237-258.

Schubert, A. and Reise, K. 1986. Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. - Mar. Ecol. Prog. Ser. 34: 117-124.

Smit, C. J. 1981a. Production of biomass by invertebrates and consumption by birds in the Dutch Wadden Sea area. - In: Smit, C. J. and Wolff, W. J. (eds.): Birds of the Wadden Sea. Report No. 6 of the Wadden Sea Working Group. Stichting Veth tot Steun aan Waddenonderzoek, Leiden, pp. 290-301.

Smit, C. J. 1981b. The importance of the Wadden Sea for estuarine birds. - In: Smit, C. J. and Wolff, W. J. (eds.): Birds of the Wadden Sea. Report No. 6 of the Wadden Sea Working Group. Stichting Veth tot Steun aan Waddenonderzoek, Leiden, pp. 280-289.

Smit, C. J. and Piersma, T. 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. - In: Boyd, H. and Pirot, J.-Y. (eds.): Flyway and reserve networks for water birds. Vol. 9. IWRB Special Publication, Slimbridge, pp. 24-63.

Smit, C. J. and Wolff, W. J. 1981. Birds of the Wadden Sea, Report 6 of the Wadden Sea Working Group. - Stichting Veth tot Steun aan Waddenonderzoek, Leiden.

Smit, C. J. and Zegers, P. M. 1994. Shorebird counts in the Dutch Wadden Sea, 1980-91: a comparison with the 1965-77 period. - Ophelia Suppl. 6: 163-170.

Smith, P. C. 1975. A study of the winter feeding ecology and behaviour of the Bar-tailed Godwit (*Limosa lapponica*). – Ph.D. Thesis, University of Durham, Durham.

Smith, P. C. and Evans, P. R. 1973. Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit. - Wildfowl 24: 135-139.

Stearns, S. C. 1992. The evolution of life histories. - Oxford University Press, Oxford.

Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. - Princeton University Press, Princeton.

Stibor, H. and Lampert, W. 2000. Components of additive variance in life-history traits of *Daphnia hyalina*: seasonal differences in response to predator signals. - Oikos 88: 129-138.

Stock, M., Schrey, E., Kellermann, A., Gätje, C., Eskilden, K., Feige, M., Fischer, G., Hartmann, F., Knoke, V. and Vorberg, R. 1996. Ökosystemforschung Wattenmeer - Synthesebericht: Grundlagen für einen Nationalparkplan. - Schriftenreihe des Nationalparks Schleswig-Holsteinisches Wattenmeer, Heft 8.

Strübing, K. 1994. Der Eiswinter 1993/94 im deutschen Küstengebiet zwischen Ems und Oder. - Dt. Hydrogr. Z. 46: 177-182.

Strübing, K. 1995. Der Eiswinter 1994/95 im deutschen Küstengebiet zwischen Ems und Oder mit einer Übersicht für den gesamten Ostseeraum. - Dt. Hydrogr. Z. 47: 153-160.

Strübing, K. 1996. The ice winter of 1995/96 on the German coasts between Ems and Oder, with a survey of the entire Baltic area. - Dt. Hydrogr. Z. 48: 73-87.

Swennen, C. 1984. Differences in quality of roosting flocks of Oystercatchers. - In: Evans, P. R., Goss-Custard, J. D. and Hale, W. G. (eds.): Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, London, pp. 177-189.

Székely, T. 2002. Putting all eggs into one basket: Review of Klaassen, Lindström, Meltofte & Piersma (2001) "Arctic waders are not capital breeders". - Wader Study Group Bull. 97: 4-5.

Tomkovich, P. S. and Serra, L. 1999. Morphometrics and prediction of breeding origin in some holoarctic waders. - Ardea 87: 289-300.

Veenstra, H. 1976. Struktur und Dynamik des Gezeitenraumes. - In: Abrahamse, J., Joenje, W. and van Leeuwen-Stelt, N. (eds.): Wattenmeer. Ein Naturraum der Niederlande, Deutschlands und Dänemarks. Karl Wachholtz Verlag, Neumünster, pp. 19-45.

Veenstra, H. 1983. Introduction to the geomorphology of the Wadden Sea area. - In: Wolff, W. J. (ed.) Ecology of the Wadden Sea. A. A. Balkema, Rotterdam, pp. 1/8-1/19.

Verboven, N. and Piersma, T. 1995. Is the evaporative water loss of Knot *Calidris canutus* higher in tropical than in temperate climates? - Ibis 137: 308-316.

Verkuil, Y. 1996. Stomach pumping of waders does not necessarily provide more information on diet than faecal analysis. - Wader Study Group Bull. 79: 60-63.

Walsberg, G. E. and Wolf, B. O. 1996. An appraisal of operative temperature mounts as tools for studies of ecological energetics. - Physiol. Zool. 69: 658-681.

Weathers, W. W. 1980. Seasonal and geographic variation in avian standard metabolic rate. - Acta XVII Congressus internationalis Ornithologici: 283-286.

Weathers, W. W., Weathers, D. L. and van Riper III, C. 1983. Basal metabolism of the Apapane: Comparison of freshly caught birds with long-term captives. - Auk 100: 977-978.

Weber, T. P. and Piersma, T. 1996. Basal metabolic rate and the mass of tissues differing in metabolic scope: Migration-related covariation between individual knots *Calidris canutus*. - J. Avian Biol. 27: 215-224.

Wiersma, P. and Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. - Condor 96: 257-279.

Wiersma, P., Bruinzeel, L. and Piersma, T. 1993. Energiebesparing bij wadvogels: over de kieren van de Kanoet. - Limosa 66: 41-52.

Wilson, W. H. 1991. Competition and predation in marine soft-sediment communities. - Annu. Rev. Ecol. Syst. 21: 221-241.

Withers, P. C. 1977. Measurement of VO_2, VCO_2, and evaporative water loss with a flow-through mask. - J. Appl. Physiol.: Respirat. Environ. Excercise Physiol. 42: 120-123.

Wolff, W. J. 1991a. Ecology of the Wadden Sea. - In: Prokosch, P., Mielke, S. and Fleet, D. M. (eds.): The common future of the Wadden Sea. Technical Report. World Wide Fund for Nature, Husum, pp. 13-22.

Wolff, W. J. 1991b. The interaction of benthic macrofauna and birds in tidal flat estuaries: a comparison of the Banc d'Arguin, Mauretania, and some estuaries in the Netherlands. - In: Elliot, M. and Ducrotoy, J.-P. (eds.): Estuaries and Coasts: Spatial and Temporal Intercomparisons. Olsen & Olsen, Fredensborg, pp. 299-306.

Wolff, W. J. 1992. The end of a tradition: 1000 years of embankment and reclamation of wetlands in the Netherlands. - Ambio 21: 287-291.

Wolff, W. J. 1993. Netherlands-Wetlands. - Hydrobiologia 265: 1-14.

Wolff, W. J. and Smit, C. J. 1990. The Banc d'Arguin, Mauretania, as am environment for costal birds. - Ardea 78: 17-38.

Worrall, D. H. 1984. Diet of the Dunlin *Calidris alpina* in the Severn Estuary. - Bird Study 31: 203-212.

Wymenga, E., Engelmoer, M., Smit, C. J. and Spanje, T. M. 1990. Geographical breeding origin and migration of waders wintering in West Africa. - Ardea 78: 83-112.

Zerba, E. and Walsberg, G. E. 1992. Excercise-generated heat contributes to thermoregulation by Gambel's Quail in the cold. - J. Exp. Biol. 171: 409-422.

Zwarts, L. 1988. Numbers and distributions of coastal waders in Guinea-Bissau. - Ardea 76: 42-55.

Zwarts, L. 1991. Seasonal variation in body weight of the Bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. - Neth. J. Sea Res. 28: 231-245.

Zwarts, L. and Blomert, A.-M. 1990. Selectivity of Whimbrels feeding on Fiddler Crabs explained by component specific digestibilities. - Ardea 78: 193-208.

Zwarts, L. and Blomert, A.-M. 1992. Why Knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. - Mar. Ecol. Prog. Ser. 83: 113-128.

Zwarts, L. and Esselink, P. 1989. Versatility of male Curlews *Numenius arquata* preying upon *Nereis diversicolor*: deploying contrasting capture modes dependent on prey availability. - Mar. Ecol. Prog. Ser. 56: 255-269.

Zwarts, L. and Wanink, J. H. 1991. The macrobenthos fraction accessible to waders may represent marginal prey. - Oecologia 87: 581-587.

Zwarts, L. and Wanink, J. H. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. - Neth. J. Sea Res. 31: 441-476.

Zwarts, L., Blomert, A.-M., Ens, B. J., Hupkes, R. and van Spanje, T. M. 1990. Why do waders reach high freeding densities on the intertidal flats of the Banc d'Arguin, Mauretania? - Ardea 78: 39-52.

Zwarts, L., Ens, B. J., Kersten, M. and Piersma, T. 1990. Moult, mass and flight range of waders ready to take off for long-distance migrations. - Ardea 78: 339-364.

Zwarts, L., Ens, B. J., Goss-Custard, J. D., Hulscher, J. B. and Kersten, M. 1996. Why Oystercatchers *Haematopus ostralegus* cannot meet their daily energy requirements in a single low water period. - Ardea 84A: 269-290.

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01.04.99 – 31.10.99	Anstellung als wissenschaftlicher Mitarbeiter bei BioConsult SH im Rahmen des Miesmuschelmonitorings im Schleswig-Holsteinischen Wattenmeer
01.02.00 – 31.12.00	Anstellung als wissenschaftlicher Mitarbeiter am Institut für Vogelforschung in Wilhelmshaven zur Konzeption, Organisation und Durchführung des Untervorhabens „Animal Tracking – Neue Wege der Tierbeobachtung“ auf der EXPO am Meer, Wilhelmshavens Beitrag zur EXPO 2000
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Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig verfasst und nur die angegeben Hilfsmittel benutzt habe.

Wilhelmshaven, den