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The Dependence of Waders and Waterfowl Migrating along the East Atlantic Flyway on their Coastal Food Supplies: what is the most Profitable Research Programme?

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ABSTRACT

Predicting the effects of human activities, like shell-fisheries, exploitation of gas, recreation, chemical pollution, land reclamation and man-induced sea-level rise, on the population dynamics and migratory behaviour of the waders and waterfowl using the Wadden Sea and other intertidal areas along the East Atlantic Flyway is a tall order. Mathematical models with a strong empirical basis are our only hope for achieving this aim. Though applied models almost always sacrifice generality to achieve precision and realism, it is important to develop unifying concepts that can guide empirical research. We should aim to understand the underlying processes at the level of the individual consumers and consumed. These processes include social competition among the waders and waterfowl (the consumers) for nesting territories and wintering sites, as well as seasonal changes in availability of the prey (the consumed). With regard to the former it can be remarked that ultimately social competition revolves around access to resources vital for reproduction and survival. With regard to the latter we suspect that changes in prey availability are often due to changes in risk-taking behaviour on the part of the prey. In all these cases behavioural ecology and life history theory provide the concepts that link the 'decisions' of individuals to the population processes we aim to predict. The research programme that we describe has proven very useful in investigations of prey choice, migratory behaviour and local distribution patterns. It is only very recently that attempts are made to put the programme to full use in predicting the effects of habitat changes on the population dynamics of the affected birds.

INTRODUCTION

A multitude of human activities threaten the waders and waterfowl that depend on the Wadden Sea for their reproduction in summer, their survival in winter, or their migration along the East Atlantic Flyway during spring and autumn. These activities include shell- and other fisheries, exploitation of gas, recreation, chemical pollution, land reclamation and man-induced sea-level rise or other global climate change. Despite much research effort during the past decades, our ability to come up with precise predictions of the effects of such human activities on the population dynamics and migratory behaviour of the waders and waterfowl using the Wadden Sea is limited in any particular case. The fundamental reason is that it is impossible to construct models that maximize simultaneously generality, realism, and precision (Levins, 1968). Models that can provide answers of sufficient precision and realism to the applied questions that we asked at the top of this paper must have sacrificed generality. For each new applied problem therefore, a new model will have to be built and new measurements must be taken.

However, though the models cannot be general, the concepts used in the construction of the models can and should be. Founding models on misguided concepts is a waste of human effort and money. Thus, it is important to develop unifying concepts that can guide empirical research and serve as a sound foundation of the desired models. To develop these concepts we must ask the right questions, one of which we will argue to be the following: 'How are animal societies linked to their food supply?' Replacing the word society for the more commonly used word population draws attention to the fact that animal populations consist of individuals differing from each other, while also being linked to each other via historically acquired, often site-dependent, social relationships. Thus, instead of simply contending with seeking statistical relationships between the numbers of birds and the size of the food supply we should aim to understand the underlying processes. These processes include social competition among the birds for nesting territories and wintering sites, as well as seasonal changes in prey availability.

When these concepts are put into practice with the use of a well-defined methodology they define a research programme. The research programme that we advocate has gradually developed during the past decades (see for instance Goss-Custard, 1977, 1980, 1985, 1993; Sutherland & Goss-Custard, 1991; Sutherland & Dolman, in press). Thus, we make no claim to an original suggestion. Instead, our aim is to review the underlying logic and discuss the practical and conceptual problems that are encountered when the programme is put to work. The following statements provide a brief description of the programme:

1. Population processes must be understood from the strategic decisions made by the individuals comprising the population, or 'society' as we called it.

2. Strategic decisions have been shaped by natural selection, i.e. animals are expected to choose those alternatives that yield the highest gains in terms of fitness, or a short-term goal expected to correlate with fitness.

3. The most likely short-term goal during the non-breeding season is maintaining energy balance. At the very least maintaining energy balance is an important constraint: no bird can maintain a negative energy balance indefinitely and a migrant without sufficient energy reserves will not reach its destination.

So far, we have not mentioned the fieldworkers whose empirical research was of paramount importance in shaping the research programme we describe, but some names will be mentioned as we go along. It is not our aim though, to provide an exhaustive review of the past research effort and how it relates to the research programme we describe. For such reviews we refer to Evans (1976), Goss-Custard (1980, 1984, 1985, 1993), Pienkowski & Evans (1985), Piersma (1987), Drent & Prins (1987), Goss-Custard & Durell (1990), Zwarts & Wanink (1993) and Meire (1993).

The paper is organized as follows: after a more thorough description of the conceptual foundation of the research programme, we start with a discussion of prey choice and prey availability, also referred to as prey harvestability (see later). We gradually work our way from these short-term and local decisions of a single individual to decisions of larger numbers of individuals that apply to larger areas and longer time scales. At the end of the paper we will show how the acquired knowledge is used to derive key population processes. Each section ends with a brief statement of the most important conclusions, often including topics in need of further study. We hope that this will increase the utility of the paper as a checklist for ecologists asked to conduct research on the applied problems that we addressed before.

ACKNOWLEDGEMENTS

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CONCEPTUAL FOUNDATION OF THE RESEARCH PROGRAMME

Not all population biologists will be convinced that to understand the dynamics of a population, it is necessary to understand the behaviour of the individuals comprising the population. An early plea for individually based concepts was made by Lomnicki (1978): 'the assumption that all individuals are equally affected by increasing population density disagrees with empirical evidence .. and leads theoretical population biology into a blind alley'. Thus, not all individuals are equally affected by an important population parameter, making it hard to understand and predict the response of the population with a model that does not differentiate between individuals. According to Murdoch et al. (1992) the enormous advantage of individual-based models is that they are 'by their nature preadapted to incorporate the mechanisms that determine a system's dynamics'. As a result, the individual-based models seem inherently better suited to predict the population consequences of drastically altered conditions than statistically derived population models that cannot be extrapolated beyond the range of observed population densities and food supplies (Goss-Custard, 1993). Finally, Schoener (1986) argues that by focusing on the individual, evolutionary theory can be brought to bear on the problem under investigation, since selection works mainly on individuals.

This brings us to the second element in the research programme, namely that strategic decisions are shaped by natural selection. Strategic decisions refer to the choice between alternative options available to the animal that have different consequences for immediate or future survival chances and possibilities for reproduction (McFarland, 1977). Examples include the decision to set up a territory or the decision to put on fat reserves. The idea that these decisions are shaped by natural selection is at the heart of the discipline called behavioural ecology (Krebs & Davies, 1991), which has shown that the mathematical cost-benefit approach developed by economists can also be applied to decision-making in animals. Optimization models can explain foraging behaviour, while game theory must be applied to situations where conflicts of interest occur. Since the models deal mostly with short-term problems, the currency has also mostly been short-term, like the maximization of energy gain. As a result, there is still a large gap between behavioural ecology and life history theory, which applies essentially the same mathematical tools to the study of fitness components, like clutch size and survival (Lessells, 1991; Stearns, 1992). From our population perspective, our primary interest is clearly in fitness components, not short-term goals. However, most life history theory deals with decisions made and evaluated on an annual basis and such time steps are much too coarse for our purposes. Though state-dependent life history theory (McNamara & Houston, 1992) is trying to bridge the gap between the short-term perspective of behavioural ecology and the long-term perspective of life history theory, there is still a long way to go. Thus, the conceptual side of the research programme has not yet fully crystallized. In the following we will therefore borrow our concepts from either behavioural ecology or life history theory, whichever is most appropriate or convenient.

There is clearly more to life during the non-breeding season than maintaining energy balance, like the avoidance of predation (e.g. Whitfield, 1985; Creswell, 1993) and parasitism (e.g. Booth et al., 1993). Yet, the assumption that maintaining energy balance is the most important short-term goal for the consumers, i.e. the waders and waterfowl, has proven to be of great heuristic value. In particular, the even more simplistic assumption that foraging animals seek to maximize the rate of

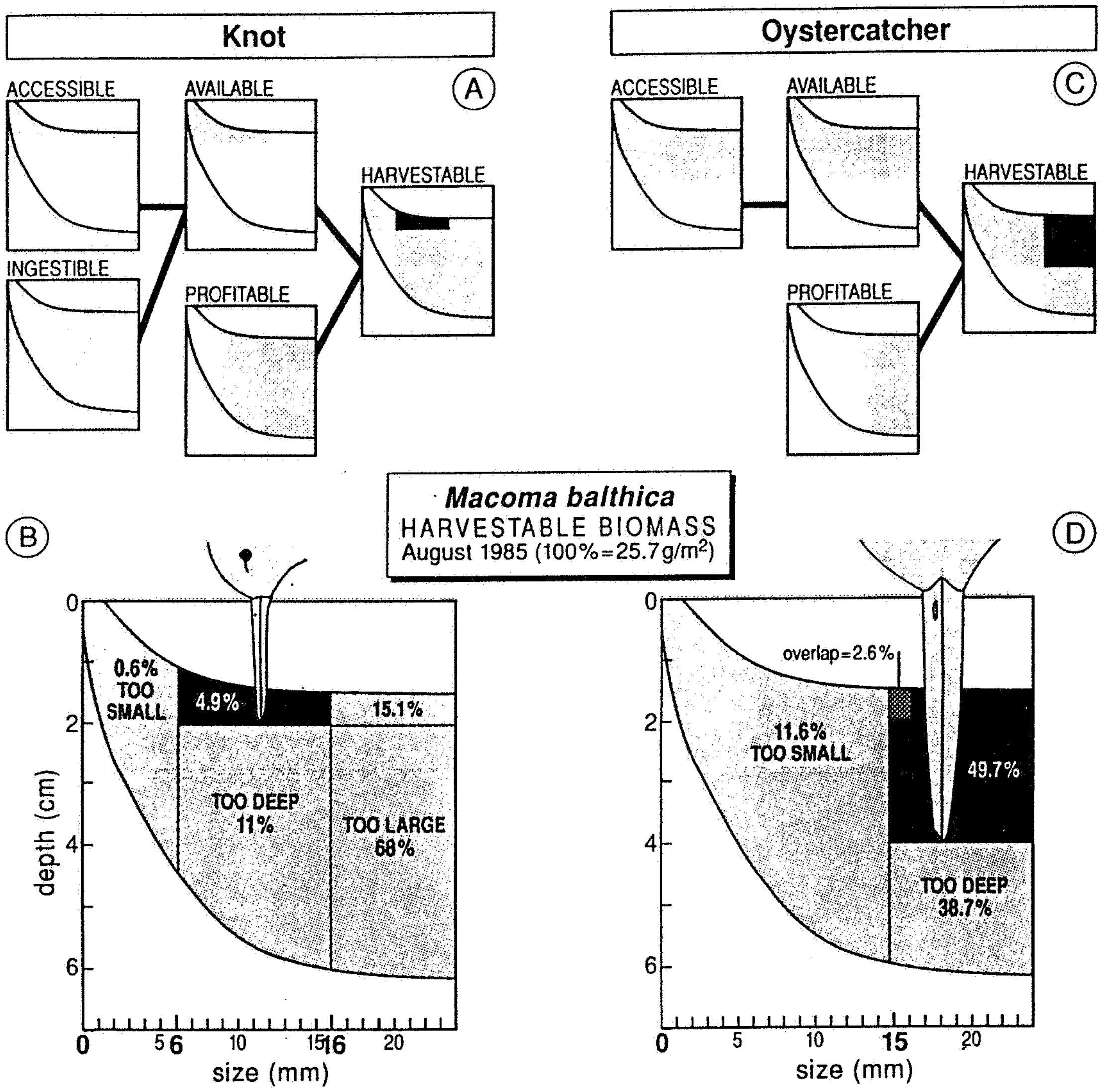

Fig. 1. Fraction of the bivalve *Macoma balthica* that is harvestable for knots and oystercatchers; depth at which *Macoma* occur is plotted against their size. In (a) and (c) it is shown how harvestability is a joint function of availability (itself a joint function of detectability, accessibility and ingestibility) and profitability, for knots and oystercatchers respectively (from Zwarts & Wanink, 1993). In (b) and (d) the fraction harvestable, for knots and oystercatchers respectively, is determined for a particular *Macoma* population along the Frisian coast (Zwarts, pers. comm.).

energy gain has yielded many valuable insights. An important cause of this success must be that the assumption specifies in great detail what measurements have to be taken. Furthermore, the methodology to take these measurements was available. Of course, we don't want to imply that measuring the energy balance of free-living birds is an easy task or that all problems have been solved.

WHICH PREY SHOULD BE TAKEN?

The cost-benefit approach and prey availability

The total amount of food that can be harvested by the birds in a given area is a product of the total density of food items times the availability of those food items. If prey availability is not taken into

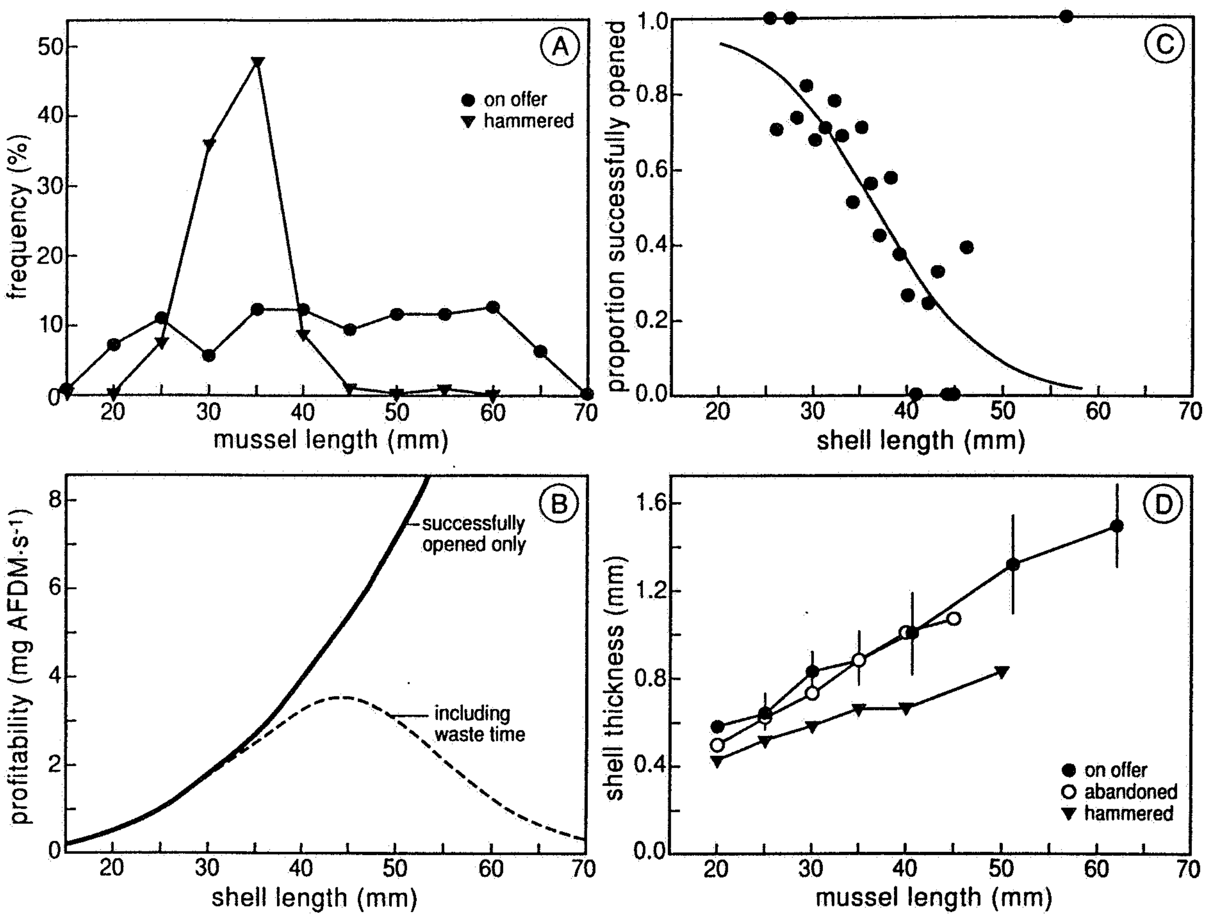

Fig. 2. Prey selection by oystercatchers hammering mussels from the ventral side. (a) Size distribution of mussels on offer compared to the size distribution of mussels abandoned or successfully opened. (b) Profitability (biomass gained per unit time spent handling) as a function of mussel size calculated for mussels that were successfully opened only and when the time wasted on abandoned mussels was included. (c) Probability that a mussel of a given size is successfully opened. (d) Shell thickness as a function of mussel size for mussels on offer, abandoned mussels and mussels that were successfully opened. Based on data in Ens & Alting (in press).

account it may be wrongly concluded that food supplies are much bigger than they actually are when the bird's point of view is taken. Zwarts et al. (1992) show how profitability, burying depth and ingestibility together delimit the fraction of the *Macoma* population that can actually be harvested by knots *Calidris canutus* and oystercatchers *Haematopus ostralegus* (Fig. 1). In fact, Zwarts et al. (1992) urge us to use the word harvestable for what we and many others have so far indicated with available. In the terminology of Zwarts et al. *available* prey are all prey that are both *accessible* (within reach of the bill), *ingestible* (small enough to be swallowed) and *detectable* (it is possible for the predator to discover the prey), while *harvestable* prey are all available prey, which are also of sufficient *profitability* (prey that yield a sufficient energy gain per unit time spent handling). In the following we will stick as much as possible to this terminology.

To show in some more detail how the cost-benefit approach has helped in identifying which prey are harvestable, we will spell out the example of oystercatchers hammering mussels *Mytilus edulis*. The optimal prey model (Charnov, 1976; see also Stephens & Krebs, 1986) assumes that predators maximize their intake rate during foraging. It follows that all prey whose profitability (the gain of energy per time unit spent handling the prey item) exceeds the average intake should be consumed if encountered. When Ens (1982) tested this for oystercatchers hammering mussels from the ventral side he found that large mussels were the most profitable, yet were clearly selected against (Fig. 2a). Instead of concluding that optimal foraging theory was a complete waste of time as suggested by Pierce & Ollason (1987), it seemed more logical to seek an additional selection criterion. Thus, the failure of the optimal prey model might be due to hammering birds selectively taking thin-shelled individuals within a size-class of mussels. Subsequent work proved this suggestion to be correct (Durell & Goss-Custard, 1984; Meire & Ervynck, 1986; Sutherland & Ens, 1987; Cayford & Goss-Custard, 1990; Ens & Alting, in press). When Meire & Ervynck (1986) modified the diet model to include the time wasted on mussels that were not opened they calculated that profitability first increased with size but then dropped off again (Fig. 2b). It was assumed that this was due to an increasing proportion of mussels being too thick-shelled, which was corroborated by Ens & Alting (in press); see also Fig. 2c&d. In a further refinement Meire (in press) determined the number of blows delivered by an experimental apparatus in a standard manner that were necessary to crack a shell of a given thickness and size. Relating the number of such standard blows to handling time Meire could then calculate the profitability for each combination of size and thickness: as expected profitability increased with size but decreased with shell thickness. The investigations have made it increasingly clear that a full understanding requires that we also attend to the mechanism of prey selection: Meire (pers. comm.) believes that hammerers assess shell thickness by listening to the sound of a few trial blows. If oystercatchers cannot judge shell thickness from the outside appearance of a mussel, some assessment time is necessarily wasted.

This example demonstrates two points, which we consider to be general:

1. The cost-benefit approach will often initially fail to account for the prey choice of the birds under investigation. However, these failures help draw attention to aspects of the problem that hitherto have been ignored and will suggest ways to refine the model.
2. A complete assessment of the harvestability of the prey is only possible if the mechanics and psychology of prey selection and prey handling are also taken into account.

Elusive encounter rates

In the above we ignored for simplicity the density at which the prey occur. This cannot be done, since the rate at which different prey are encountered must be known before the optimal prey model can be solved (Stephens & Krebs, 1986). Under poor feeding conditions prey of low profitability may be included in the diet that should be ignored under better feeding conditions, e.g. when density of very profitable prey is high. In the extreme case potentially harvestable prey may not be harvestable, because the density at which they occur is too low. Thus, it is of vital importance to determine encounter rates. Two methods have been used to measure encounter rates.

The first method is to determine search speed and assume that the probability of detection does not depend on prey type (Thompson, 1983). From search speed and density of a prey type, the relative encounter rate with that prey type can then be calculated. This was the method employed by Meire & Ervynck (1986). The second method to determine encounter rates is to start from first principles. For knots and oystercatchers hunting by touch for bivalves buried in the mud, this means starting from the mechanics of prey detection (Hulscher, 1976, 1982; Wanink & Zwarts, 1985; Zwarts & Blomert, 1992). The crucial parameter is the effective touch area of the bivalves, which is the maximal surface area of the shell in a horizontal plane, enlarged by the surface of the bill tip (Fig. 3). In combination with the density of the prey this effective touch area yields the probability that a random probe of the bill will hit a prey. In combination with the probe rate this probability gives us the encounter rate. Deeper probes take longer and deeper prey require more time for handling. Applying the optimal prey model Wanink & Zwarts (1985) therefore predicted that an oystercatcher feeding on the bivalve *Scrobicularia plana* buried at different depths and densities should select increasingly shallower prey when prey densities were increased. This happened, but

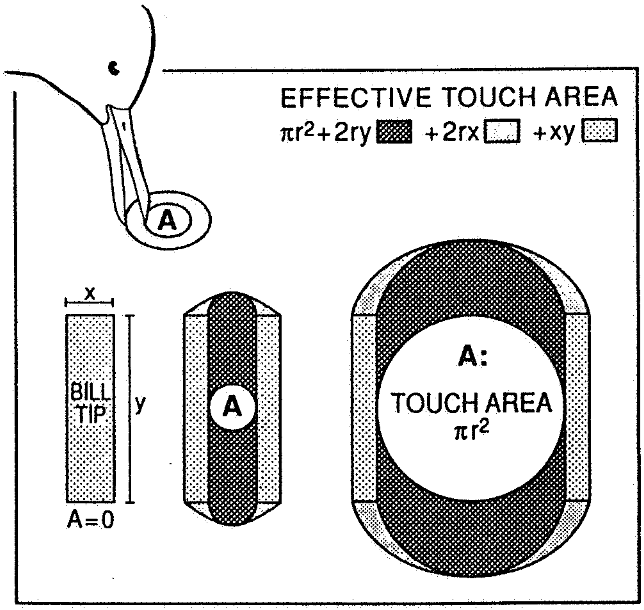

Fig. 3. Diagram showing how the effective touch area (sensu Wanink & Zwarts, 1985) depends on the surface of the projection in a horizontal plane of both the shell and the tip of the bill.

at high prey densities the observed intake rates were even higher than predicted. Wanink & Zwarts suggested that the bird started to ignore closed bivalves associated with long handling times.

It is only partly true that the second method allows us to determine encounter rate from first principles, since probe rate has to be measured. It seems likely that probe rate, or more generally search speed, is under the control of the animal. Suggestive evidence is the observation of Swennen et al. (1989) that oystercatchers could increase the rate at which they captured cockles *Cerastoderma edule* when feeding time was experimentally reduced. Thus, what determines search speed? According to Gendron & Staddon (1983) there is a trade-off between speed and probability of detecting cryptic prey: when speed is increased the probability of detection declines. As a consequence there is an optimal search speed, which is lower when prey is more cryptic. There is evidence that curlews *Numenius arquata* and oystercatchers hunt more slowly when feeding on cryptic species of prey (Zwarts & Esselink, 1989; Ens et al., in press). In fact, Ens et al. go so far as to suggest that for oystercatchers hunting for the bivalve *Macoma* is incompatible with hunting for the worm *Nereis*. As a result, individuals tend to specialize on either *Nereis* or *Macoma* during a given feeding bout. Another reason for specialization is that bill morphology makes an individual more efficient at feeding on certain prey. For example, female curlews have longer bills than males and feed more often on deep-buried prey (Ens & Zwarts, 1980). This is also true for oystercatchers, but in addition the shape of the bill tip adapts to the feeding technique (Swennen et al., 1983; Hulscher, 1985). In turnstones *Arenaria interpres*, feeding specializations can be linked to social status (Whitfield, 1990). Since specialization invalidates a basic assumption of the optimal prey model, namely that the decision to consume or reject a prey item is made after the item has been encountered, it highlights the importance of studying marked individuals.

The following conclusions can be drawn:

1. It is hard to determine optimal prey choice with great precision, since optimal prey choice depends on encounter rate, which is partly under the control of the bird through search speed and hunting method.

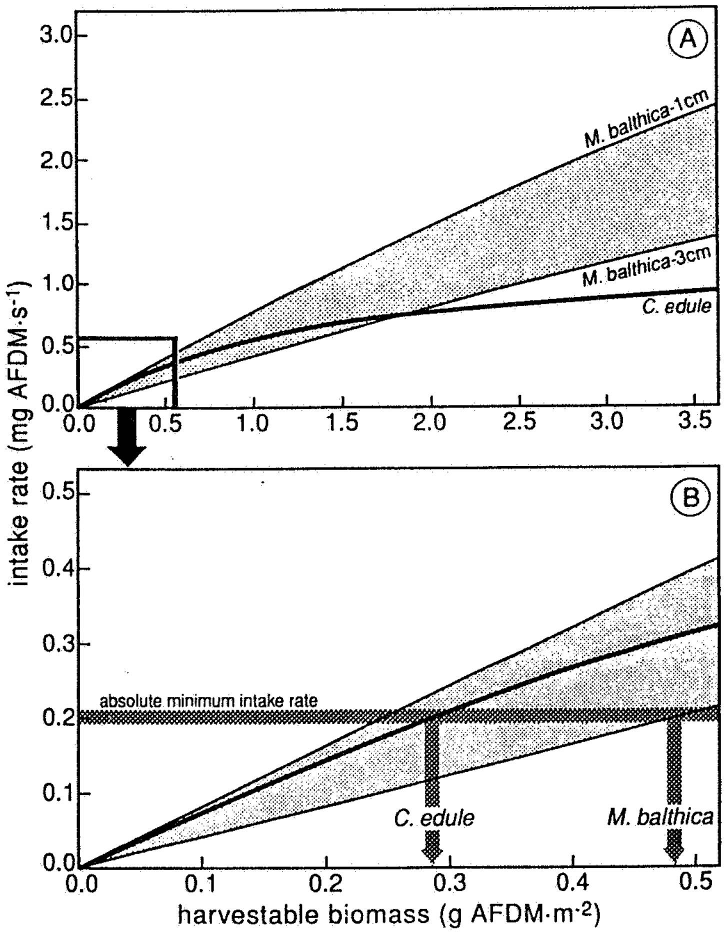

Fig. 4. Relationship between intake rate and density of harvestable biomass of *Macoma* and cockles determined in cage experiments. The minimum densities at which the prey are still harvestable for knots are found from the intersection of the absolute minimum intake rate with these relationships. Based on Piersma et al. (1993).

2. Detailed investigations are called for on optimal search speeds, incompatibility of hunting methods and feeding specializations, as they may allow a more fundamental understanding of encounter rates, and therefore optimal prey choice.

WHERE TO FEED?

Apart from deciding what prey to feed on, the bird should also decide where to feed. The optimal patch choice model seeks to answer the question after how much feeding time the predator should move to a new patch (Stephens & Krebs, 1986). It works from the assumptions that food is distributed in clear patches and that the presence of a predator in a patch reduces the availability of food. Whereas the optimal prey choice model has stimulated much research on the feeding behaviour of waders, the optimal patch choice model has not. There are two reasons for this. First, though mudflats are full of gradients, there are no well-defined patches. Second, waders and waterfowl can rarely be considered solitary foragers. Usually, the birds feed day after day in the same general area, surrounded by conspecifics. Therefore, attention has focused on linking the distribution of the

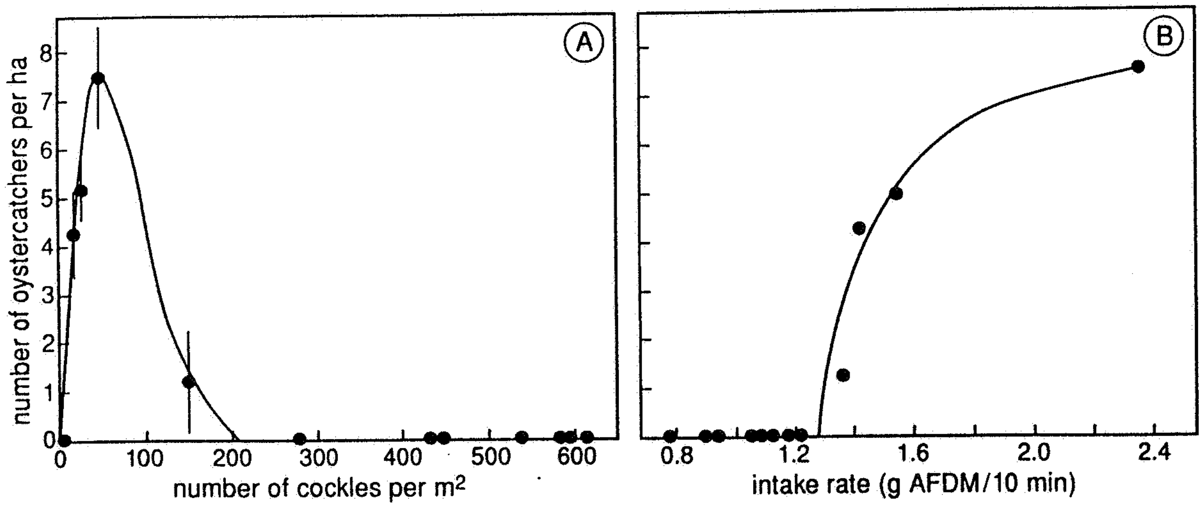

Fig. 5. Density of feeding oystercatchers plotted against (a) the density of cockles, their main prey, (b) their intake rate. From Sutherland (1982b).

birds to the distribution of the food. The leading assumption has been that the birds prefer to feed in the area where they can achieve the highest intake rate of food. If it is known how intake rate depends on the density of food and on the density of conspecifics, we can then predict the distribution of the birds from the distribution of the food (Kacelnik et al., 1992). Below, we consider these two relationships.

The functional response

The functional response describes the relationship between the intake rate of an individual predator and the density of the prey. In the well-known type-2 functional response described by Holling (1959), better known as the 'disc equation', the intake rate of the predator increases with prey density but reaches an asymptote at very high prey densities because the predator will spend nearly all its time handling prey and very little time searching for prey. The disc equation can only describe the relationship between intake rate and prey density when prey density is the only variable that changes; other variables should be held constant. Though experimental studies have generally produced positive relationships between prey density and intake rate, these relationships generally do not fit the disc equation. It turns out that nearly always encounter rates and/or handling times vary with prey density, instead of being constant as assumed in the model (Wanink & Zwarts, 1985). As we have seen when we discussed encounter rates, this was due to the birds becoming increasingly selective at high prey densities. If variability among prey is so important under laboratory conditions, it must be even more important under field conditions. One solution is to measure the biomass density of harvestable prey (assuming a fixed lower threshold for profitability) and investigate how it affects intake rate. In combination with knowledge on the absolute minimum intake rate that must be achieved to survive, such a plot allows us to estimate the minimum densities at which the prey are still harvestable (Fig. 4).

Conclusion: In the absence of a fundamental understanding of encounter rates and the large scope under natural conditions for changes in selectivity with changing prey density, there is currently no other option than to be rather pragmatic in the study of the functional response in the field.

The numerical response

If intake rates are highest where the density of harvestable prey is highest, we also expect the density of feeding birds to be highest where the density of harvestable prey is highest. An example is the study of Sutherland (1982b) on oystercatchers feeding on cockles. In his study area there was a negative correlation between the size of the cockles and their density, comparing sites. Intake rate correlated positively with both the size and the density of the cockles. This explained why feeding densities were highest at intermediate densities of prey (Fig. 5a). Indeed, when feeding density was plotted against the average intake rate in the site, it was clear that the highest densities were in sites where the intake rate was highest (Fig. 5b). However, as is clear from Fig. 5b, it was not true that all birds were feeding in the best site. This seems to be the rule in studies of the numerical response. Though the highest densities of birds are indeed generally found in the best feeding areas, more often than not, a substantial number of birds is also found to be feeding in areas of lower quality.

COMPETITION FOR FOOD

Interference and dominance behaviour

A likely mechanism to explain the phenomenon that not all birds are feeding in the best site is *interference*, whereby an increase in feeding density leads to an immediate decrease in the intake rate of food (Goss-Custard, 1980). So far, the study of interference has concentrated nearly exclusively on the oystercatcher, following up the pioneering studies of Vines (1980), Zwarts & Drent (1981) and Sutherland & Koene (1982). Hence, there are no alternatives to taking oystercatchers as an example. The study of marked individuals proved of paramount importance, as it was shown that dominant individuals suffered less from an increase in the density of conspecifics than subdominant individuals (Ens & Goss-Custard, 1984; Goss-Custard et al., 1984; Goss-Custard & Durell, 1988); see Fig. 6a. This difference between individuals rules out the possibility that interference is due to prey depression, i.e. prey making themselves less available in response to the presence of predators, as this would affect all birds equally. When feeding density increases, the rate at which the birds attack each other, including many attempts to steal mussels, also increases (Fig. 6b&c). Thus, a simple explanation for interference is that when the birds are feeding close together dominant birds have more opportunities to steal food from subdominant birds. However, the decrease in intake rate of the subdominant individuals results only in part from an increase in the loss of mussels to more dominant individuals. Even more important is a decrease in the rate at which mussels are captured. This decrease may be due to an increase in the avoidance behaviour of the subdominant individuals, or to the subdominants being increasingly often displaced from good feeding spots. The available evidence does not favour either of these hypotheses (Ens & Cayford, in press).

Though subdominant birds suffer much from interference it does not necessarily follow that their chances of surviving the winter are impaired. However, without exception those bits of evidence that are available do suggest that subdominant birds are at a disadvantage (Ens & Cayford, in press). Therefore, the life history perspective forces us to ask why subdominant birds do not choose to engage in escalated fighting to climb the social ladder. One possibility is that subdominants are poor fighters, so that they cannot win from fighting. Dominance tends to increase with age and the data of Caldow & Goss-Custard (in press) suggest that it takes many years to become a top-dominant bird on the mussel bed. However, subdominant birds are not only younger, but also have much larger home ranges than the dominant and old birds (Ens & Goss-Custard, 1986), which occupy very small patches on the mussel bed to which they return year after year. Thus, young birds are less committed to their site-dependent social status. The sudden influx of a large number of immature oystercatchers following a massive spatfall of cockles *Cerastoderma edule*

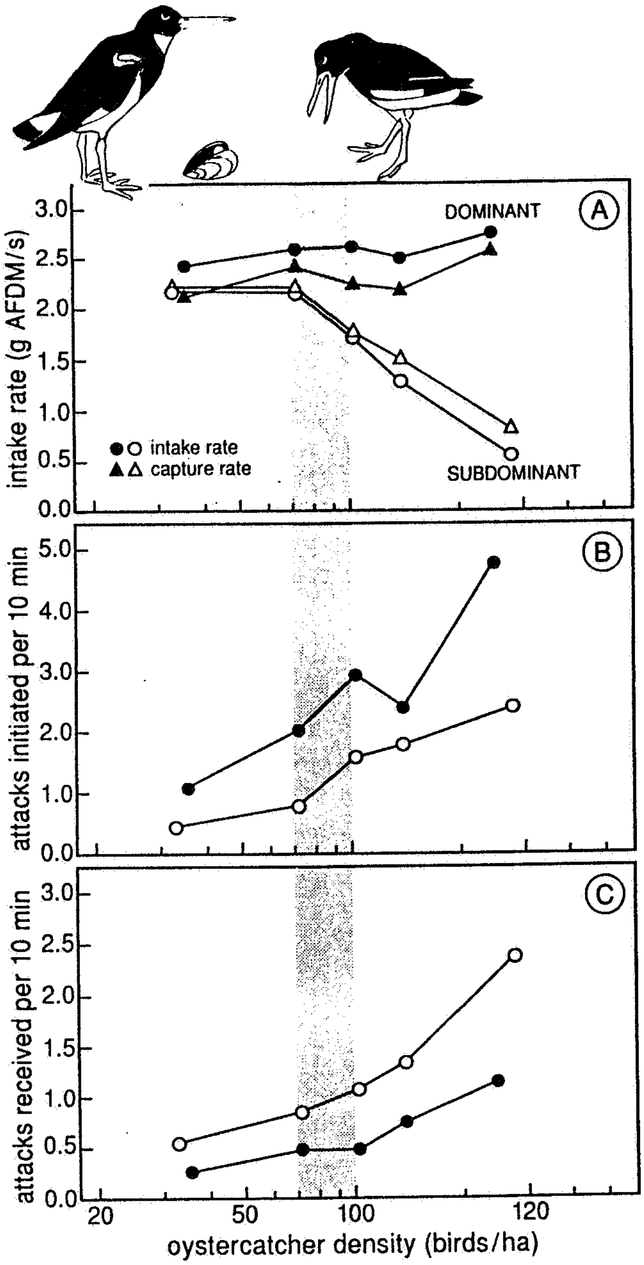

Fig. 6. Effects of changes in the feeding density caused by changes in the area of the mussel bed that was exposed due to the changing tide; the grey bar indicates the modal density of oystercatchers; based on data in Ens & Goss-Custard (1984). (a) Capture rate and intake rate (expressed in mg AFDM per sec foraging) of dominant and subdominant oystercatchers; the difference between capture rate and intake rate is due to the gain or loss of mussels to conspecifics. (b) Rate at which dominant and subdominant oystercatchers attack conspecifics. (c) Rate at which dominant and subdominant oystercatchers are attacked by conspecifics.

testifies to this lack of commitment (Sutherland, 1982a). These observations have led Ens & Cayford (in press) to suggest that the queue model proposed for breeding oystercatchers (Ens et al., MS) may also apply to oystercatchers during the non-breeding season. There could be a trade-off between many years of low status (before high status is reached) on a high quality mussel bed, or few years of low status (before high status is reached) on a low quality mussel bed. Thus, it could be that fighting ability does not increase much with age, but that for young birds queuing maximizes the chances of reaching high status later in life.

Though the study of interference in oystercatchers is certainly a success story, we should be aware that few waders allow such an intensive study of the social system in winter. A notable exception is the turnstone studied by Whitfield (1988, 1990) which exhibits a very similar pattern. In both species individuals show a strong site fidelity, but dominant birds do not exclude other individuals from their home range. In many other wader species some individuals are territorial while other individuals roam around in flocks of non-territorial birds (review: see Myers, 1984). In the most extreme case, huge flocks may build up that roam over vast areas: knots apparently use an area of no less than 800 square kilometres in the western part of the Wadden Sea (Piersma et al., 1993).

The following conclusions can be drawn:

1. It is currently not possible to derive interference from more fundamental relationships, as even in oystercatchers the precise mechanism of interference is not fully known.
2. Interference as a short-term process is a component of the social organization of the birds. This social organization can only be understood from a long-term life history perspective.
3. There is an urgent need to study interference in species with a social organization different from that of the oystercatcher (e.g. redshank *Tringa totanus*: Goss-Custard, 1970).

Depletion of the harvestable prey

Interference is a major component of competition. As we have seen, large differences in intake rate arise through interference, and access to rich feeding areas may be denied to birds low in the social hierarchy. When the excluded birds cannot sustain themselves in the poor areas, interference effects will translate into survival penalties. Whenever food supply in the prime areas suffers depletion during the phase of exploitation by the birds, these effects will become noticeable even within the best sites. Our next question is therefore: how commonly do birds deplete their food supplies?

Contrary to the reasoning of arm-chair biologists (e.g. Hairston et al., 1960), intensive research on herbivore animals has thrust upon us the reality of local depletion of a harvestable food supply. For example, in a study of the african buffalo *Syncerus caffer*, Prins (1987) was able to demonstrate the cyclic nature of the grazing regime, the herds following a well-timed movement pattern characterized by grazing plots to threshold biomass and returning on time to harvest nutritious regrowth. This recurring grazing cycle has also been observed on a much smaller scale involving brent geese, *Branta bernicla*, during spring exploitation of saltmarsh vegetations (reviewed by Drent & Prins, 1987), where preferred plants are rapidly depleted during grazing bouts.

Local depletion of food stocks is not restricted to herbivorous animals. It has been demonstrated in flock-feeding ducks (Suter, 1989), and in 27 prey species taken by waders in 13 studies summarized by Székely & Bamberger (1992), the average value of depletion amounted to 49 %. In their own meticulous work on a community of waders feeding on chironomid larvae on the Hortobágy mudflats of Hungary, they established a reduction in prey density of 87% in only 13 days. Such catastrophic losses of the prey population generally hold only over short periods of heavy exploitation during migration. In situations where waders are present throughout the whole winter, prey are generally reduced by 25-45% (Goss-Custard, 1984). It would be wrong to conclude, however, that this means that the birds do not suffer from depletion since what matters to the birds is the harvestable fraction. We can use our example of hammering oystercatchers mentioned earlier to demonstrate the difference. The estimated overwinter consumption of hammering oystercatchers is only a small portion of all mussels present at the start of the winter (Fig. 7). However, expressed

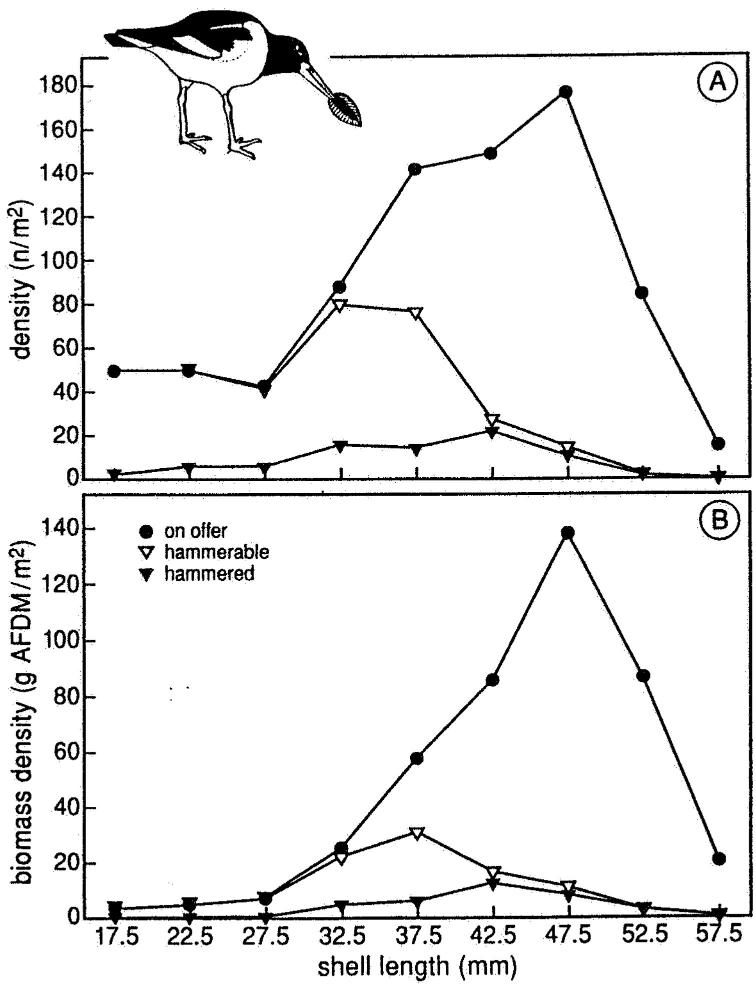

Fig. 7. (a) Size distribution of mussels in the study of Meire (in press), the fraction available to hammerers, and the fraction estimated to be taken by hammering oystercatchers over the winter. (b) Same as (a), except that density is expressed in biomass per m^2, instead of numbers per m^2.

as a fraction of the hammerable mussels the consumption is quite considerable, especially when density is represented in terms of biomass instead of numbers. Meire (in press) calculated for his study population that the available thin-shelled mussels of the largest size classes were nearly completely depleted in the course of winter (Fig. 7). Since the larger mussels contain the most biomass, it turned out that no less than 70% of the annual production of biomass available to hammerers was consumed.

Conclusions:

1. Waders and waterfowl can deplete their local food supply.

2. When prey depletion is not immediately obvious from crude measurements on prey density, it is nonetheless dangerous to conclude that depletion plays no role, since harvestable prey can still be severely depleted.

Interspecific competition

In some of the above examples on depletion, more than one species of predator or herbivore contributed to the decline of a particular food stock, but very few studies have specifically addressed the problem of interspecific competition for food. With the notable exception of Zwarts (1980), the question whether different species also compete for space, i.e. whether interference between species occurs, has received even less attention. This fits with the prediction of Schoener (1986) that individual-based concepts will draw attention away from community processes. We hope that it is a temporary lapse in interest. In fact, the new insights that are emerging from consistent application of individual-based concepts may stimulate the study of this important topic from a fresh perspective.

MIGRATION

One response to local depletion of the harvestable prey in the best feeding areas is a redistribution within the area. Another option is to migrate to a completely new area. Especially in waterfowl the birds may deplete a series of staging sites in this way. For example, van Eerden (1984) and Madsen (1988) were able to relate seasonal movements of herbivorous waterfowl to depletion effects on seed stocks in the fall, these finite supplies not being replenished until the next season. Another nice illustration is the interaction between Bewick's swan *Cygnus columbianus bewickii* and *Potamogeton pectinatus* nodules during autumn (Beekman et al., 1991). It is unlikely, though, that such successive depletion can be a general and full explanation for migration patterns.

Migration offers new possibilities, but also creates new problems for the birds. Before we discuss the possibilities (moving to sites where feeding conditions are good or where maintenance costs are low) it is useful to pay attention to those decisions and problems that are special to a migratory bird.

According to the idealized decision scheme in Fig. 8 (from Ens et al., 1994), the migratory journey of an individual bird can be broken down into four major decisions: (1) the decision to start preparations necessary for migration, like building up fuel reserves, (2) the decision to depart on the migratory flight, (3) the decision to interrupt the migratory flight for refuelling and (4) the decision to end migration altogether and search for a good site to breed or survive the non-breeding season. These decisions lead to one of three phases: the fuelling phase, the flight phase or the resident phase.

The most important parameter during the flight phase is the flight cost, as it determines which staging sites can be reached with a given fuel load. In actual fact, life is not so simple. To calculate how far a bird can fly with a given fuel load, it must not only be known at what rate energy is expended (which must be estimated from theoretical equations), but the magnitude of head- or tailwinds *en route* must also be known for the entire journey (see for instance Piersma & Jukema, 1990). Furthermore, water loss instead of energy expenditure may potentially limit flight range (Carmi et al., 1992). Thus, flight costs will be an important topic for study for some time to come.

The length of the fuelling phase depends on the speed with which the necessary amount of fuel can be deposited. It has only recently been realized that during such periods of hyperphagia the rate of mass gain may be limited, not by the rate at which food can be collected, but by the rate at which it can be digested (e.g. Zwarts & Dirksen, 1990). Limitation of the rate of mass gain through a digestive bottleneck will increase the number of days that the bird has high mass, which may, perhaps, increase the risk of predation (Hedenström, 1992; Witter & Cuthill, 1993). This is but one of the many possible fitness costs of migration. Though such costs are important in models that seek to explain the distribution of the birds over wintering grounds at different distances from the breeding grounds (Sutherland & Dolman, in press), our knowledge on their nature and magnitude is largely speculative (Ens et al., 1994).

Conclusion:

1. Whereas the benefits of migration are obvious (movement to areas with better feeding condi-

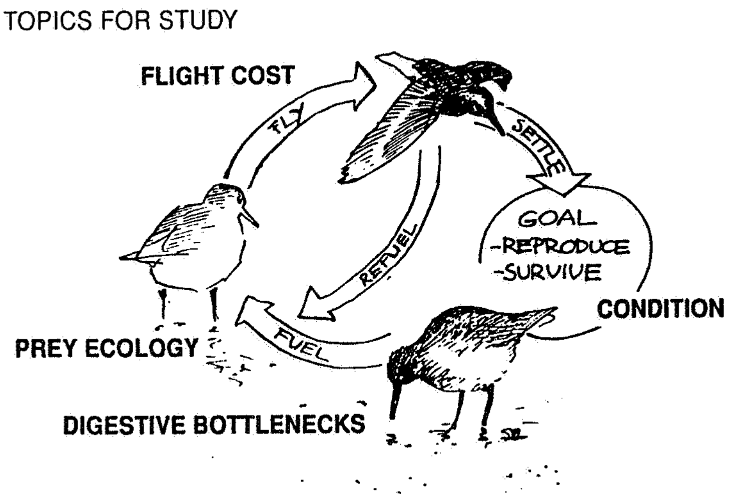

Fig. 8. Idealized decision scheme of a bird during migration. Also indicated some important topics for study as they apply to particular phases of the migratory cycle. Adapted from Ens et al. (1994).

tions and/or lower costs of maintenance), the costs are much harder to assess.

2. Although considerable progress has been made in measuring the costs in terms of energy, it is not yet possible to translate these into fitness costs.

Climate and habitat effects on energy expenditure

Until now we have implicitly assumed that low intake rates of food are bad. However, what matters is the net rate of energy gain and low intakes may be offset by low needs. Especially for the smaller waterbird species, the maintenance costs (the costs of keeping up a stable body temperature of ca. 41°C) make up more than half of the total energy expenditure in the field (Piersma & Morrison, in press; Poot & Piersma, 1994). One part of the maintenance costs is fixed (the costs of maintaining the body, the *basal metabolic rate*), while the other part is determined by habitat and weather. The latter are called *thermoregulation costs*. Weather, habitat and flocking behaviour strongly interact in determining the microclimate, and thereby the maintenance costs, of waterbirds, especially through the effect on the wind speeds experienced by the bird. Fig. 9 shows that knots in sheltered environments, such as when sitting among saltmarsh vegetation or in a dense flock, incur much smaller maintenance requirements than knots standing open and exposed on a mudflat. To obtain these measurements, Wiersma et al. (1993) and Wiersma & Piersma (1994) applied the underused technique of Bakken and co-workers (1981, 1983) to measure heat loss under different environmental conditions with the use of heated taxidermic mounts. The resulting knot-specific equations to predict the maintenance requirements in different microhabitats (Wiersma & Piersma, 1994) can be generalized to other wader species. For the knots the equations were applied to examine differences in maintenance requirement as a function of wintering latitude. Where knots wintering in the Dutch Wadden Sea would incur an average maintenance requirement of 2.51 Watt (J/s), knots on the West African Banc d'Arguin would expend only 1.38 W, a saving of 45% relative to the costs in the north (Fig. 10). Wintering in the tropics is thus much cheaper for medium-sized and small waders such as knots than wintering at temperate latitudes, and these reductions more than compensate for the cost of travelling (Piersma et al., 1991, Wiersma & Piersma, 1994). It is estimated that knots in west Africa incur at least 40% lower costs during the non-breeding season as a whole compared to their more northerly wintering conspecifics.

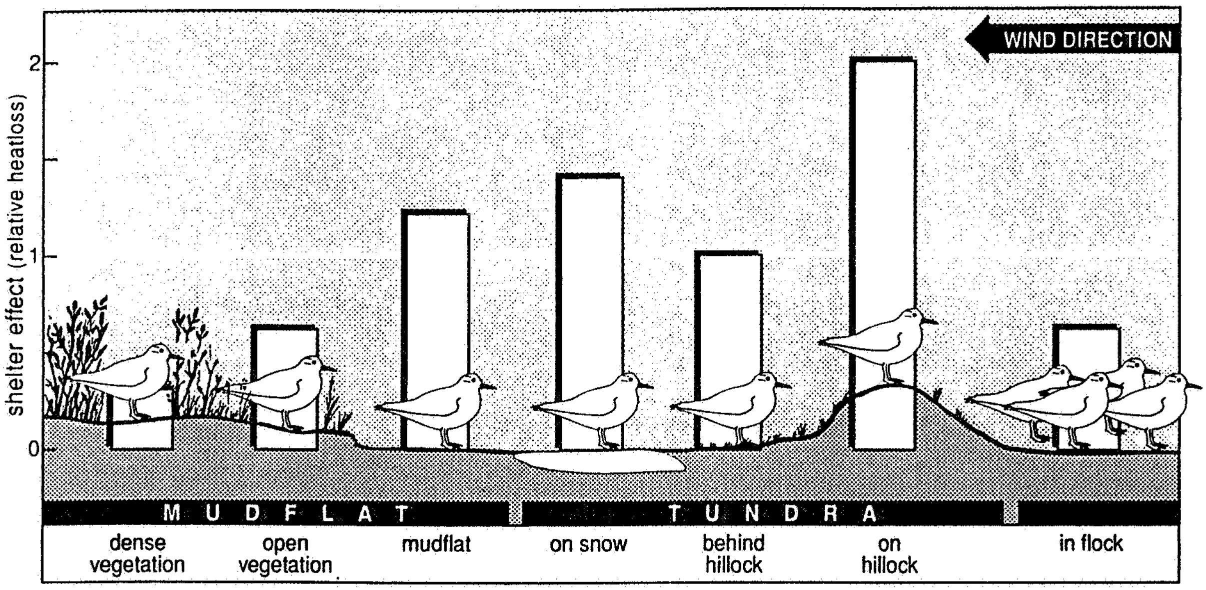

Fig. 9. Relative thermostatic costs of knots in various natural habitats, in a flock (nearest neighbour distance 0.5-1 bird lengths) and with the flank in the wind. Radiation set at 0 W/m^2 (night). The white line is the mean of all values. Adapted from Wiersma et al. (1993).

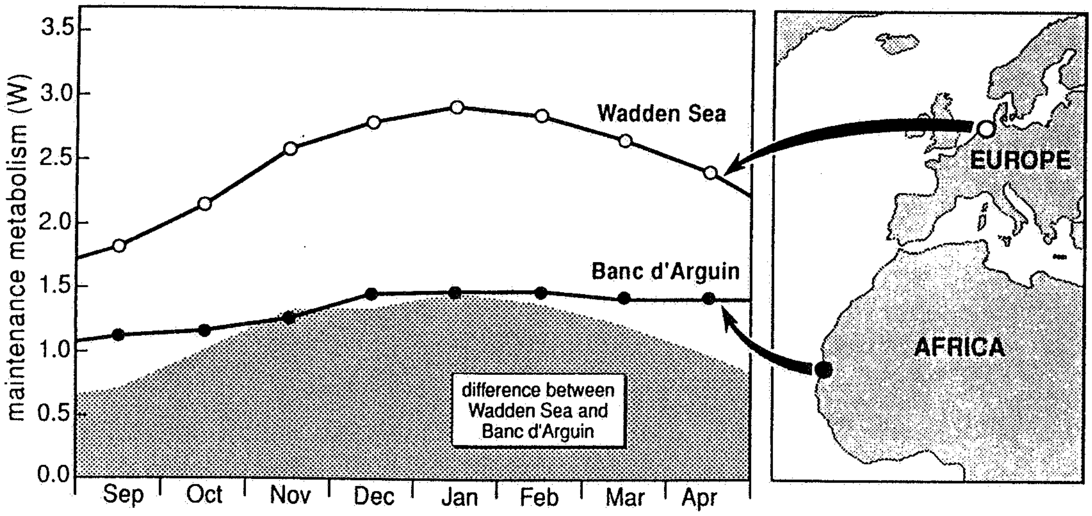

Fig. 10. Maintenance metabolism in the temperate Dutch Wadden Sea and on the tropical Banc d'Arguin, West Africa predicted for *C.c. islandica* knots on the basis of meteorological data and microhabitat specific equations. These equations were calibrated with the use of heated taxidermic mounts. From Wiersma & Piersma (1994).

This example suggests that:

1. The energy savings of migration to a warmer climate can be considerable, despite the high flight costs.

2. The methodology to make detailed and comprehensive assessments of the maintenance requirement of waterbirds in relation to habitat and weather characteristics has matured sufficiently to warrant a wider application than knots or the energetics of migration.

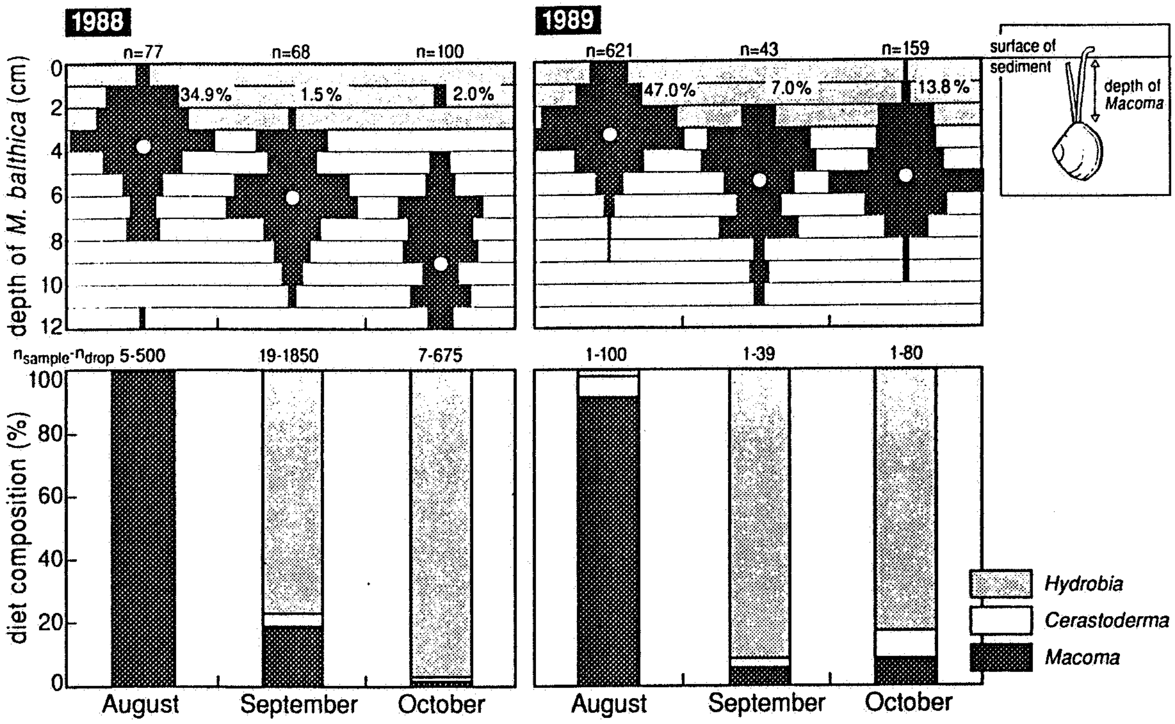

Fig. 11. The diet of knots on Griend compared to the changing depth distribution of *Macoma balthica* during the autumns of 1988 and 1989. Adapted from Piersma et al. (1993).

Seasonal changes in harvestability of the prey

Our previous calculation on depletion of the harvestable food supplies make sense only if no production occurs and if harvestability is constant during the period of interest. Reality, of course, is much more complex. In autumn, and especially in spring, when many migratory birds pass through the Wadden Sea, a considerable amount of production and other changes in the harvestability of the food may occur.

An example where (re)growth of food is important is spring staging of the brent goose *Branta bernicla* on the saltmarshes of the Wadden Sea. Prop & Deerenberg (1991) have shown that the successful accumulation of fuel reserves depends critically on the growth of food plants. There is considerable variation between years in the phenology of this growth, and hence, in the amount of fuel accumulated at the time of spring departure. Ebbinge (1989) has clearly shown that departing with large reserves is certainly a *necessary* condition for high reproductive success, though, on account of highly variable conditions on the breeding grounds, this is not a *sufficient* condition.

Recently, Zwarts & Wanink (1993) have produced an impressive compilation of the seasonal changes in harvestability of several tidal-flat invertebrates that serve as prey for waders in the Wadden Sea. One example is the bivalve *Macoma balthica* hunted by knot, which we discussed earlier (Fig. 1). It is well known that this species buries at greater depths in winter (Reading & McGrorty, 1978; Zwarts & Wanink, 1993). For the relatively short-billed knot this sinking down of *Macoma* means a dramatic decline in the accessible food supply (Fig. 11), especially since *Macoma* is the 'preferred' prey (Zwarts & Blomert, 1992, Piersma et al., 1993). No wonder that the 'disappearance' of *Macoma* was accompanied by a diet switch of the knot (Fig. 11).

The best way to come to an understanding of such changes in prey availability is to study the prey. Benthic prey seem to have three main defenses against predation: growing a thick shell (only possible for molluscs), burying to great depths and remaining inactive. However, a thick-shelled, deep-

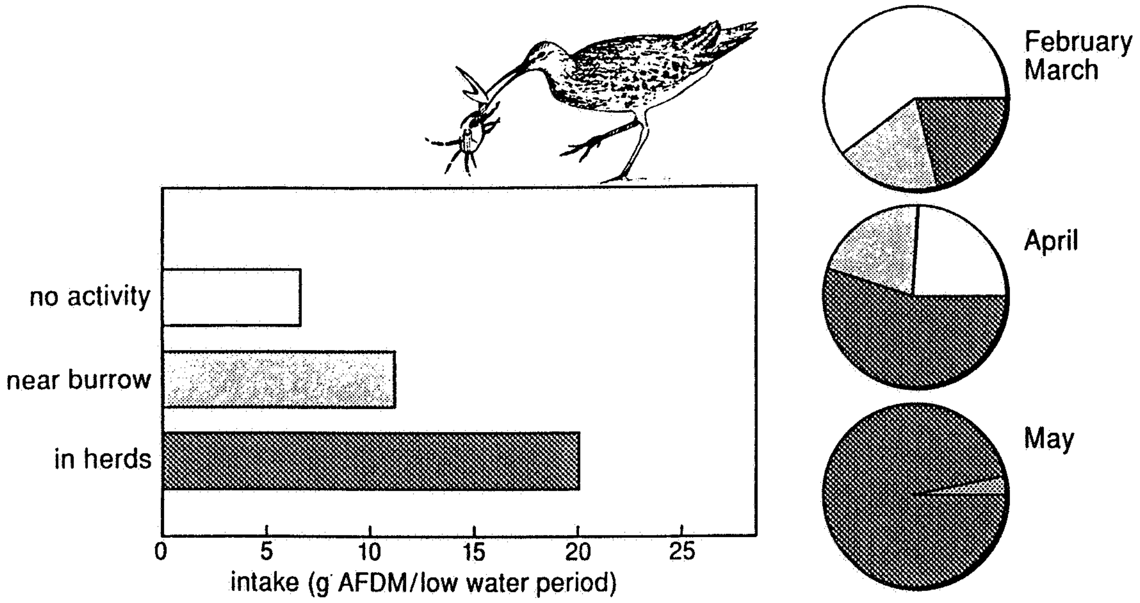

Fig. 12. The intake rate of whimbrels defending a feeding territory on the Banc d'Arguin in West Africa as a function of the surface behaviour of the fiddler crabs, their main prey. The pie charts at the right show for each month in spring the frequency of a specific type of surface behaviour of the crabs. Calculated from Zwarts (1990).

buried inactive bivalve will not eat much food. Thus, in most cases the need to feed, grow and reproduce will force the benthic animals to reduce the effectiveness of their defenses. We can now specify the aim of our study of the prey more precisely: we must enquire into the costs and benefits of taking a certain amount of risk at a given moment in the season. We will take fiddler crabs *Uca tangeri* being preyed upon by whimbrels *Numenius phaeopus* as our example. Fiddler crabs have three feeding options of increasing risk, as well as increasing energy gains: (1) stay in the burrow, (2) feed on the substrate near the burrow which then serves as a safe haven, or (3) move in a flock to feeding areas of high quality (Ens et al., 1993; Klaassen & Ens, 1993). Zwarts (1990) has shown that the whimbrels achieved the highest intake rate when they could feed on flocking crabs (Fig. 12). The likelihood that the crabs will form flocks during a tide not only increases in the course of spring (Fig. 12), but also fluctuates with the lunar cycle (Zwarts, 1990). Zwarts (1990) provided suggestive evidence that spring departure of the whimbrel from the Banc d'Arguin is delayed in years when the timing of crab flocks is relatively late. Probably, availability of diatoms drives the seasonal and perhaps even the two-weekly changes in the flocking behaviour, but decisive measurements are lacking. What we do know is that only the largest crabs feed in flocks and that this may be due to the fact that they derive increasingly less safety from feeding close to a burrow due to their increased demands for food (Ens et al., 1993; Klaassen & Ens, 1993). This suggests that the benefits of growing big are not related to an increased defence against predation. Such a defence works for burying bivalves and worms, where the largest individuals live at depths where even the longest-billed birds cannot reach them (Zwarts & Wanink, 1993). In these species an increase in size probably also leads to an increase in reproductive success, but this must be the only advantage of large size for fiddler crabs: large females can lay more eggs (Greenspan, 1980; Salmon, 1987) and large males attract larger females (Greenspan, 1980) and are more successful in competing for burrows with which to attract females (Christy & Salmon, 1984).

The following conclusions can be drawn:

1. Benthic prey are available to waders because they face a trade-off between feeding themselves and risking being fed upon.

2. The costs and benefits for the prey of performing risky behaviour are likely to vary during the course of the season.

3. A full understanding of prey availability requires nothing less than a detailed study of the entire life history of the prey species, but this is obviously a rewarding line to follow.

DERIVING KEY POPULATION PROCESSES

In the introduction we argued that to understand and predict the population dynamics of the birds using the Wadden Sea, we should study the costs and benefits of strategic decisions made by the individual consumers and the individuals risking being consumed. Now that we have described the kind of knowledge and the way it is obtained we should show how it helps us to understand the dynamics of bird populations. There can be little doubt that an interaction of processes on both the wintering and the breeding grounds regulate its size (Fretwell, 1972; Goss-Custard, 1980). At equilibrium, mortality during the non-breeding season is balanced by reproduction during the breeding season, assuming mortality during the breeding season is negligible. For a stable equilibrium it is necessary that either non-breeding mortality, and/or reproduction are negatively affected by an increase in bird density. The precise location of the equilibrium will depend on the intersection of the two curves. In this paper, we are not concerned with density dependent processes during the breeding season, but have focused on the non-breeding season.

How can we derive the density-dependence of mortality during the non-breeding season from our knowledge on the behaviour of individuals? Goss-Custard & Durell (1990) have described the argument with the diagram depicted in Fig 13. Our knowledge on prey harvestability allows us to determine the areas that contain the highest densities of harvestable prey. If there is no interference we expect all birds to feed there. If there is interference, it may pay some birds to feed in areas with lower densities of harvestable prey. Exactly how many depends on the strength and the mechanism of interference. To arrive at a precise prediction, the distribution models of Fretwell & Lucas (1970), in which each individual seeks to achieve a maximum gain, have to be adapted to fit the specific situation (Kacelnik et al., 1992). Since individuals suffer to a different degree from interference and since areas with different densities of harvestable prey are occupied simultaneously, it should be possible to calculate for each population size the distribution in intake rates (Fig. 13). The next assumption is that there exists a lower critical intake rate. Birds whose intake rate falls below this will die (or leave the estuary). This is a rather simplistic assumption. Many bird species build up fat reserves to last them through cold spells during which they cannot feed (e.g. Hulscher, 1989). Thus, the critical intake rate may be the intake rate at which it is impossible to build up reserves and birds with low intake rates will only die if cold spells do occur. For each equilibrium distribution we can calculate how many birds do not achieve the critical intake rate and therefore face an increased mortality risk. The procedure can be repeated for different initial population sizes and this yields the desired relationship between initial population size and overwinter mortality.

Using their extensive database, Goss-Custard and co-workers calculated in this way that at maximum 2000-2500 oystercatchers can winter on the mussel beds of the Exe estuary (a preview of this work is provided in Goss-Custard et al., in press). Interestingly, the number of oystercatchers wintering on the mussel beds has steadily increased from 1000 to 2000 over the past two decades. This may be evidence of the fact that the dynamics of local populations cannot be understood without reference to the metapopulation, i.e. the sum of all local populations (Goss-Custard, 1993). Since the population models of Fretwell (1972) and Goss-Custard (1980) do not incorporate the possibility of immigration or emigration they must be models of the metapopulation.

We are inclined to draw the following conclusions:

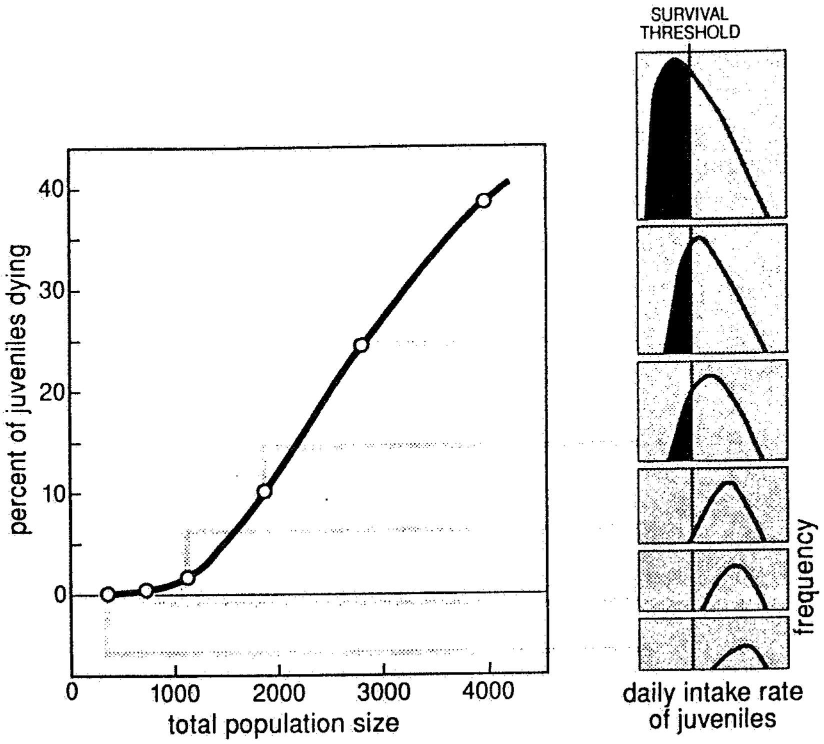

Fig. 13. Scheme depicting how density-dependence in winter mortality can be derived from knowledge on the behaviour of individuals. With increasing numbers of birds settling in an estuary, the distribution of intake rates becomes increasingly skewed to low values; an increasing proportion of intake rates being in fact so low that the chances for the individual of surviving the winter are slim. Modified from Goss-Custard & Durell (1990).

1. From knowledge on the distribution of harvestable prey, the feeding behaviour of the birds and the mechanism(s) of food competition, it is possible to derive the relationship between mortality during the non-breeding season and bird density. Many improvements can be made though.
2. For instance, the assumption that individuals must achieve a minimum intake is rather simplistic.
3. Also, if the assumption that birds that do not achieve the minimum intake will die is replaced with the assumption that they leave the estuary it must be known how much their mortality is increased by emigration.

Carrying capacity

So far, we have not used the word carrying capacity. Yet, this concept is invariably invoked in studies that seek to predict the effect of habitat loss (e.g. Meire, 1993). According to Dhondt (1988) the concept is used in so many ways that it should be abandoned. Against this, Goss-Custard (1985), Sutherland & Goss-Custard (1991) and Goss-Custard (1993) have argued that the concept has a strong intuitive appeal, because it contains the useful general idea: 'that animals cannot be squeezed in ever increasing densities into an area: resources are always limited so that some upper threshold to density must exist'. Furthermore, Goss-Custard (1985) has proposed that a useful working definition of carrying capacity is the density at which for every new bird that arrives another must either leave or otherwise will die. This definition excludes studies that fail to identify individuals and rely exclusively on counts to compare the changes in numbers in a particular estuary to those in the population at large. If the numbers using an estuary level off whereas the population at large continues to increase, it is concluded that the numbers in the estuary have reached carrying capacity (e.g. Moser, 1988; Goss-Custard & Moser, 1988). Though suggestive, such counts provide no definitive proof that additional birds would not be able to survive in the estuary. It is possible that the numbers in an estuary do not increase due to a lack of potential settlers, not because new settlers have no chance of surviving.

What other methods are available if carrying capacity cannot be determined from counts? It is important to realize that the method depends on the mechanism of food competition (Goss-Custard & Charman, 1976). If depletion of harvestable prey occurs, we can estimate how many prey can be taken before unharvestable densities are reached. This amount corresponds to a certain number of bird-days: a few birds can reside a long time in the estuary, or many birds can reside a short period. A particularly nice illustration is the study of Madsen (1988) on brent geese and wigeon *Anas penelope* depleting a *Zostera* bed in the Danish Wadden Sea in autumn. Depletion of the food was delayed in a year when hunting was intensified. When shooting ceased the remaining brent geese could capitalize on the unharvested food stocks. The lost feeding opportunity could not be completely recovered though, since unharvested stocks also lost biomass due to leaves dying off or breaking off and consumption by invertebrates.

If overwinter depletion of the food is negligible, it is still possible that interference sets a limit to the number of birds that can feed in an area. In that case there is simply a maximum number of birds, which might be called the carrying capacity. Under these circumstances compensation is not possible: if birds are disturbed from a feeding area at the beginning of the season, it is not possible to feed in higher densities during the remainder of the season.

Finally, we must ask ourselves how the concept of carrying capacity relates to our belief that the population at large will fluctuate around a level where reproduction during summer equals mortality during winter. If all estuaries are at carrying capacity it is clear that the population cannot increase. However, even if many estuaries are below carrying capacity it would seem possible that mortality in the population at large equals reproduction so that a population increase is impossible. In such cases taking away winter habitat may still lead to a decrease in the total population. This speculation suggests that the condition that all estuaries are at carrying capacity is *sufficient*, but not *necessary*, for a negative effect of habitat loss in winter on the size of the metapopulation.

We draw the following conclusions:

1. Carrying capacity can only be measured if the mechanism of food competition is known.
2. Theoretical work is needed to check the suggestion that a population decline due to loss of winter habitat seems possible, even if the habitat was taken from an estuary that was not at carrying capacity.
3. Finally, it seems important to 'measure' the relationship between the mortality rate and the density of potential settlers for different estuaries. The density-dependence in mortality for the metapopulation is then the aggregate of the relationships established for single estuaries.

CONCLUSIONS

In this paper we have described what we think to be the most profitable research programme to allow predictions on the effects of various human activities on the populations of waders and waterfowl using the Wadden Sea. So far, it has yielded many insights on the harvestable food supply and the feeding and migratory behaviour of the birds, as well as the mechanisms by which the birds compete for food. The translation to population models is still in its infancy, but especially the work of Goss-Custard and co-workers suggests that it can be done. Nonetheless, it is a sobering thought that it took Goss-Custard and his team 15 years of intensive field studies before they felt sufficiently confident to estimate the carrying capacity of the mussel beds in the Exe estuary for oystercatchers.

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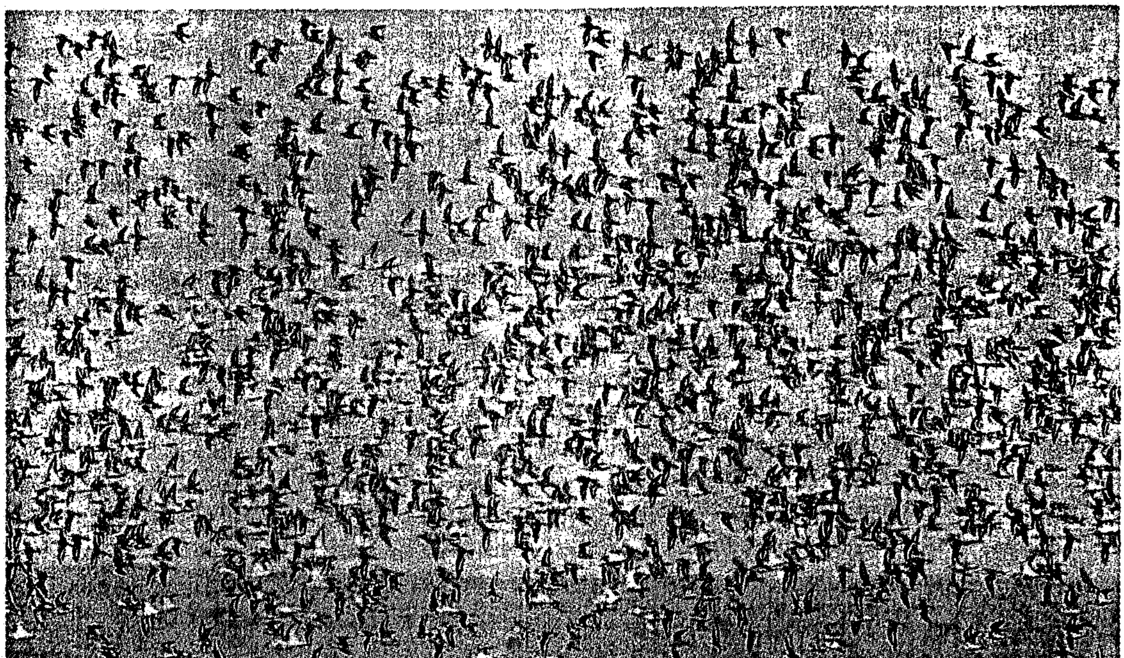

A flock of dunlins *Calidris alpina.* Photo: John Frikke.