Fitness, demographic rates and managing the coast for wader populations

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Apart from scientific interest, much of the research over the last 30 years on the ecology and behaviour of non-breeding (mainly coastal) waders has been motivated by the need to provide scientific advice on how best to manage their habitats in order to maintain or increase the size of their populations. I first discuss the limited usefulness and potentially serious drawbacks of two research paradigms (habitat association models and bird-days carrying capacity measured by depletion models) that have been proposed as the means by which we could provide that scientific advice. Instead, we need to predict whether, and by how much, a change in coastal management will increase or decrease the fitness of individuals and thus change the demographic rates, and therefore size, of the population, locally and globally. It is suggested that much more attention needs to be paid to individual variation in competitive abilities and to competitive process, such as interference, since these determine the form of the all-important density-dependent demographic functions.

INTRODUCTION

This article discusses the form that our scientific advice should take when we are advising policy-makers on how best to manage the coastal habitats of waders in order to conserve their populations. First I argue that we must be able to predict how a given management regime would affect the fitness of individuals during, and at the end of, the non-breeding season. I then detail the limitations, indeed potential dangers, of two research paradigms that cannot provide these predictions but which are still being proposed as suitable ways for advising policy-makers. I argue that rapid developments in new modelling techniques render these approaches obsolete except in some very prescribed and local situations. I conclude that we are now poised – and in many cases already able – to provide the predictions that are really required for wisely selecting between alternative coastal management options, and suggest a few research priorities that should enable us more quickly to reach this desirable state.

WHAT WE NEED TO BE ABLE TO PREDICT

The objective of people wanting to conserve non-breeding wader and wildfowl is to at least maintain present bird numbers, both locally in a given site and globally across a sub-species or sub-species range. It follows that the best measure of the effect of a human activity on birds is the predicted change in population size. Population size in waders, as in any other organism, is a function of the interaction between demographic rates. In waders, these are: (i) the mortality and reproductive rates in the breeding range and (ii) the mortality rate in the non-breeding range, including along the migratory routes (Goss-Custard 1993, Boyd & Piersma 2001).

We therefore need a method to predict the effect of any proposed change in coastal management on the two quantities that are believed to determine individual fitness, and thus demographic rates, in waders outside the breeding season. The first of these quantities is the size of the fat reserve to fuel migration and, in spring perhaps, also to breed successfully. The second is the probability of dying as a direct or indirect (e.g. by raptor predation) result of difficult feeding conditions. If one can show that the feeding conditions following a proposed change in coastal management regime would allow the present-day body condition and rates of overwinter survival at a given winter population size to continue, there would be no reason to be concerned for the birds. If, on the other hand, body condition and survival were predicted to decline, population size would be expected to decrease by an amount that depends on (i) the strength of any compensatory density-dependent reproduction on the breeding grounds (Goss-Custard & Durell 1990, Sutherland 1996a) and (ii) the availability of alternative wintering or passage sites (Pettifor *et al.* 2000). In evaluating a proposed change in coastal management on waders, decision-makers should therefore ask whether it would reduce bird fitness, either by increasing the numbers that die or by decreasing body condition (Goss-Custard *et al.* 2002).

Whether birds starve or emigrate and, if the latter, whether they subsequently survive or not, may not be of immediate concern in the site in question but could have an important effect on that site in the long term through its effect on the size of the greater population to which the birds in the site belong. As Fig. 1 shows, and as Sandercock (this volume) also points out, this is because quite a small increase in mortality rate can greatly reduce population size in long-lived animals with the low annual mortality rates that are common in waders (Evans 1990, Goede 1993). For example, in oystercatchers, just a 2% increase from 6% to 8% in the adult annual mortality rate would reduce equilibrium population size to 30% or 62% of its previous level, depending whether the density dependence in recruitment in summer is, respectively, weak or strong (Goss-Custard *et al.* 1996). The increase of
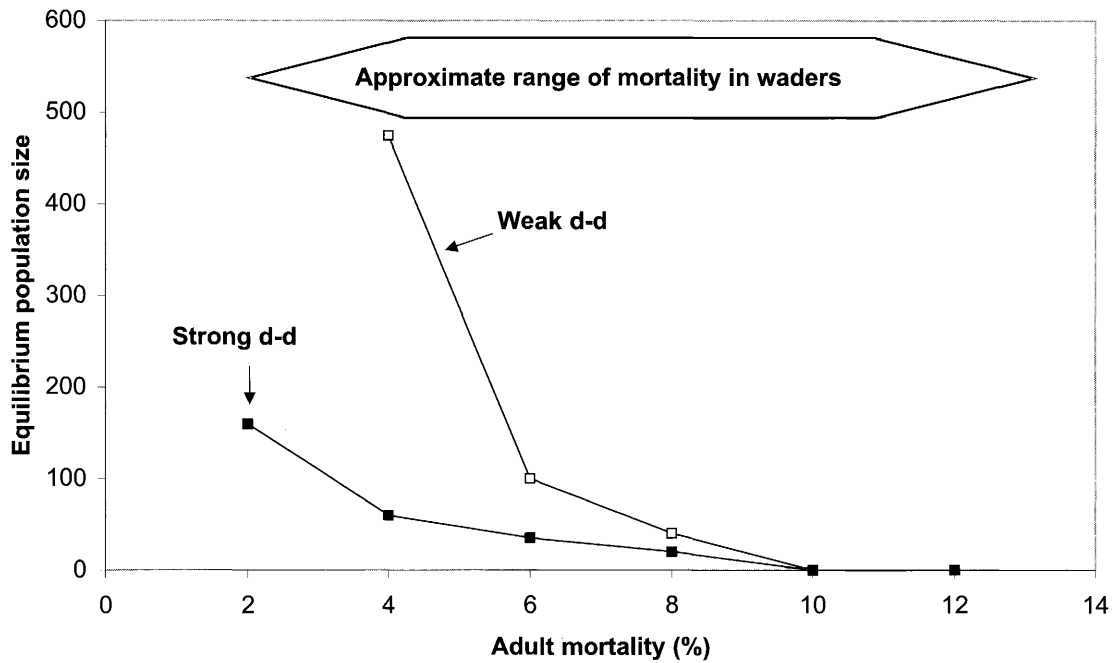
Fig. 1. The long-term equilibrium population size in long-lived animals, such as shorebirds, is very sensitive to the average annual mortality rate, whether the density dependence (d-d) during the breeding season is weak or strong. The typical range of annual mortality rates found in shorebirds is also shown. (Adapted from Goss-Custard 1980, 1981.)

2% may be small in absolute terms but it actually represents an increase of 33% in the mortality rate, and this has a consequentially large effect on the size of the population at equilibrium. The effect can be even larger if the increase in mortality occurs in juveniles, since these birds are the "seed-corn" of future generations (Goss-Custard & Durell 1984). Although the sensitivity of population size to the annual mortality rate in long-lived birds has been understood for many years (Sandercock, this volume), this extremely important point seems often to be overlooked. For wader biologists required to advise policy-makers on how to manage the coast in a wader-friendly way, it means that we must devise ways to predict quantitatively by how much a change in management will affect wader fitness and demographic rates. Since waders will often move from one site to another when a change in coastal management occurs, we have the extra challenge of making such predictions for a number of non-breeding sites, and not just the one for which a new management regime is being considered (Pettifor et al. 2000).

HABITAT ASSOCIATION MODELS

Habitat association models are widely used in ecology and were proposed as a provisional approach to predicting the effects on waders of various estuary management regimes by Goss-Custard (1995). In such models, empirical relationships are established between an environmental predictor variable and (i) the bird species community or (ii) the density of particular species on the wintering areas. The predictor variable can be food density itself (e.g. Goss-Custard et al. 1991) or habitat (e.g. area of mud) and physical (e.g. estuary shape) variables that are themselves predictors of food density (Goss-Custard & Yates 1992, Yates et al. 1993, Rehfisch et al. 1997, Yates & Goss-Custard 1997). Other factors, such as risk of attack from birds of prey, can be incorporated, perhaps by using a proxy measure of risk, such as estuary width (Rehfisch

et al. 2000). Such models are attractive because of their simplicity and because the values of the predictor variables (e.g. estuary width, tidal range) in new scenarios for which predictions are required can usually be predicted with confidence.

A serious limitation of these models is that their predictions are likely to be pessimistic. This is because their empirical relationship may not be fixed in parameter-space so that the intercept or slope, or both, may change in the new scenario for which predictions are required (Goss-Custard et al. 1994). Fig. 2 shows an hypothetical function that one might use to predict the effect of habitat loss on waders. If the relationship was fixed in space – for example, because it is situated at the maximum limit (or "carrying capacity") all along its length – the equation might apply following a change in coastal management. But if not, bird density could increase and the present-day equation would give a pessimistic prediction for local bird numbers because the "compaction" of birds would allow the same number to live in a reduced area. Since the supply of birds to estuaries may seldom reach the numbers needed to compact the birds to the point at which the maximum possible density on the wintering grounds is reached (Goss-Custard 1993, Sutherland 1996b), such a present-day empirical relationship is likely to overestimate the effect of a loss of habitat on the birds. This unreliability would be reinforced if the change in coastal management also changed estuary productivity and thus food density.

There is a second and more fundamental problem with applying this attractively simple approach. From Fig. 2, it might be predicted that a change in estuary management (*A* to *B*) would reduce bird numbers from *a* to *b*: let us say, by 1000 birds. But this would not mean that the population size, either locally on the estuary or more widely in the greater population to which the birds belong, would thereby be reduced by 1000. Not only might compaction of birds enable more birds to remain and survive in good condition than predicted by this method, but compensatory behavioural and population-
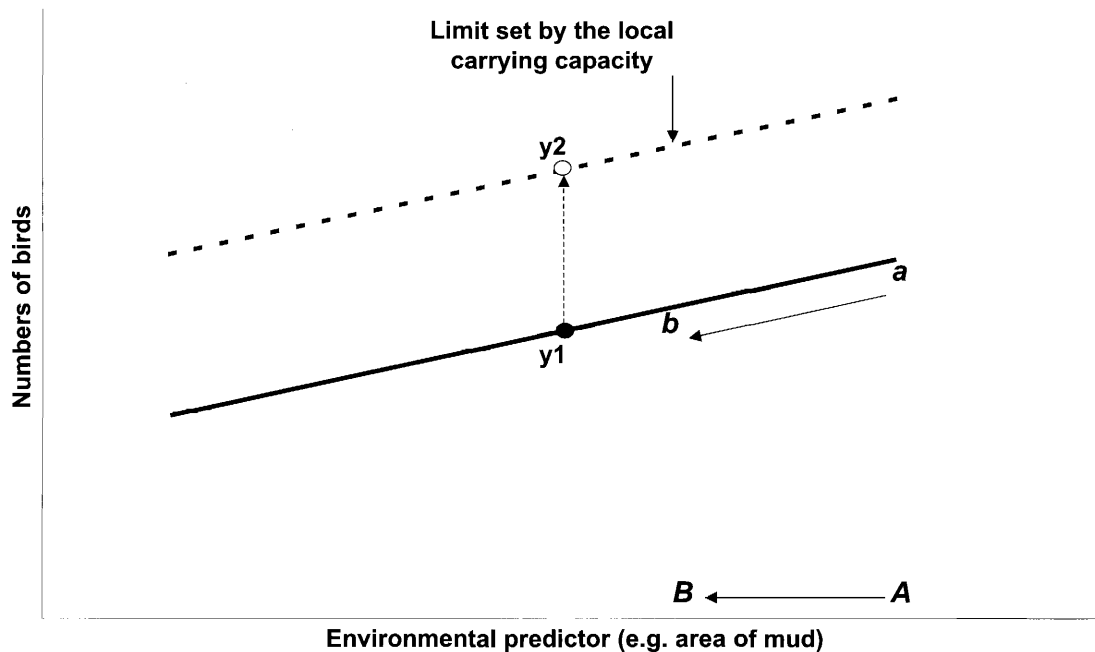
Fig. 2. An hypothetical relationship between an environmental predictor variable and shorebird abundance. If the present-day function is fixed in parameter space (solid line) we would predict that a reduction in the area of the feeding grounds from **A** to **B** would lead to a reduction in bird numbers from **a** to **b**. However, if bird abundance at a particular value of the predictor variable could increase from y1 to y2 so that bird density is not already at some maximum limit, no reduction in numbers would occur. (Adapted from Goss-Custard *et al.* 1994.)

level processes would further reduce the impact on population size.

At the individual behavioural level, birds may compensate, for example, by feeding more at night or over high tide in salt pans or fields, or by moving to other estuaries. At the population level, any change in mortality rate outside the breeding season will generally be compensated by a *per capita* increase in the reproductive rate, causing the reduction in population size to be less than would otherwise be the case (Goss-Custard & Durell 1990, Sutherland 1996a).

Models that predict bird numbers or density from habitat characteristics not only give "worst case" predictions but are also unable to predict the effects of environmental change on fitness and demographic rates, and thus population size, at either local or global scales. Nor can they predict body condition at the time of spring migration. Yet these are the very components of fitness that decision-makers should consider when evaluating the impact on waders of a change in coastal management (Goss-Custard *et al.* 2002). The limitations of this approach have been appreciated for many years but were provisionally accepted before methods were devised to predict bird fitness (Goss-Custard 1995). But the development – and much earlier than expected – of models for doing this (see below) have removed much of the original need for developing habitat association models.

This is not to say that there are no circumstances in which habitat association models are useful. For example, regression models that relate species density on the feeding grounds to easily measured and predictable environmental variables (e.g. shore level, shore width and distance from the estuary mouth) can predict whether mudflats created as a mitigating measure are likely to provide the same quality and quantity of food supplies as the areas they are designed to replace. If they succeed in doing this, the feeding conditions as a whole should remain the same and so bird fitness, demo-

graphic rates and population size should be unaffected. Such predictions are probably reliable because they are essentially interpolations, rather than extrapolations to new scenarios, since the values of the predictor variables in the new scenario lie within the present-day empirical range.

Furthermore, in some well-studied cases, it may be possible to produce habitat association models in which the dependent variable is a demographic rate, or some other component of fitness, rather than bird numbers or density on a shore. As Atkinson *et al.* (2003) demonstrate, statistical models which relate mortality rate in oystercatchers *Haematopus ostralegus* on the Wash to the abundance of shellfish (cockles *Cerastoderma edule* and mussels *Mytilus edulis*) can be useful in selecting wader-friendly ways in which to manage the shellfishery from amongst those that have been already tried. The difficulty with these models arises when – as is often the case – (i) mortality and body condition have not been measured sufficiently well even to evaluate present policies, or, (ii) the new management scenario for which predictions are required has never been tried. In the latter case, one could only hazard a guess as to what might happen to bird fitness were a new shellfishery management regime to be implemented because one would have to extrapolate beyond the present-day empirical range. One could, of course, get round this problem by trying a variety of shellfishery management regimes and monitoring the resulting mortality rate and body condition of the birds. But as this would have to be done in a number of sites over a number of years for each of the bird species that might be affected, it is only rarely a realistic option.

BIRD-DAYS CARRYING CAPACITY

Another approach is to measure the effect of a proposed change in coastal management on the number of bird-days
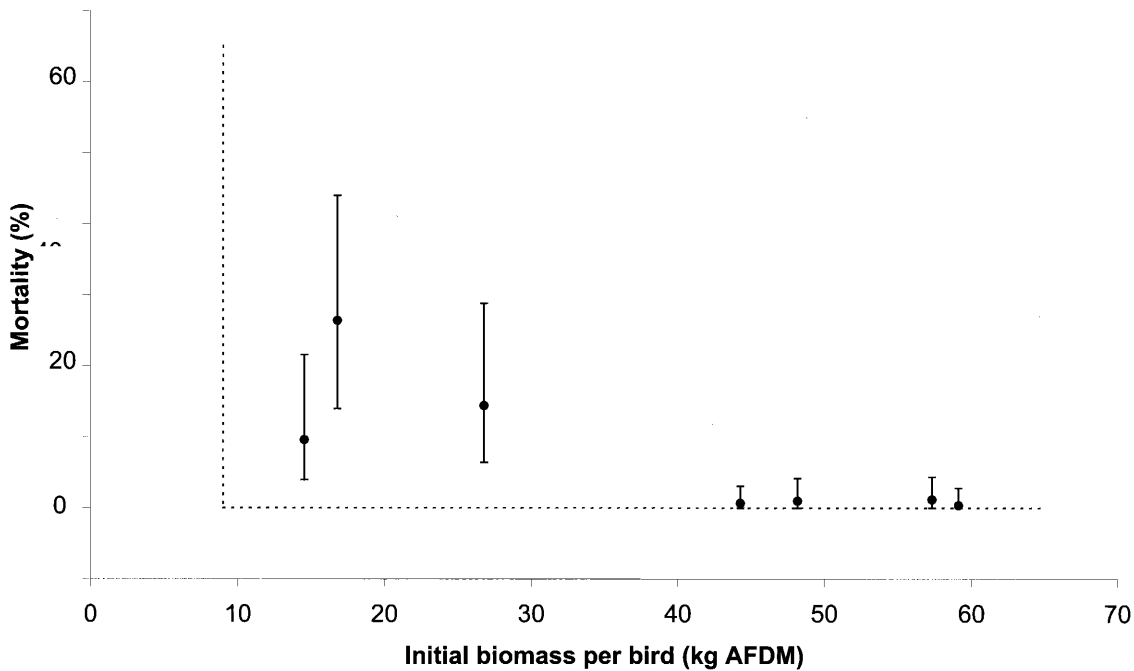
Fig. 3. The data points show the observed mortality rate during seven non-breeding seasons of adult oystercatchers on the Wash from September to March in relation to the quantity of shellfish biomass available per bird (measured as kg ash-free dry mass) in September, excluding the subsequent reduction in shellfish biomass due to shellfishing. The dotted line shows how a depletion model, without individual variation in competitive ability, would predict (i) that no mortality would occur during any of the non-breeding seasons for which data were available, and (ii) all birds would starve were the food supply per bird in September fall to just below 10 kgAFDM, the total quantity consumed by an individual oystercatcher on the Wash over the whole of the non-breeding season. (Adapted from Stillman *et al.* submitted.)

that the food supply can support; i.e. the "bird-days carrying capacity". With this approach, the daily energy requirement of the average bird is divided into the predicted total stock of energy contained within the accessible part of the food supply that occurs at densities above the "giving up" density below which the average bird cannot collect its daily energy requirements in the time available. This approach has been applied may times to overwintering wildfowl (references in Goss-Custard *et al.* 2003) and, more recently to waders, using spatial depletion models (Gill *et al.* 2001a).

The fundamental problem with this approach is again that it cannot predict the effect of a change in coastal management on fitness or demographic rates because all birds are assumed to be identical and not to compete for food (Goss-Custard *et al.* 2002, 2003). This difficulty is not so immediately apparent as it is with habitat association models because of the superficial similarity between two concepts: "bird-days carrying capacity" and "population size". But predicting the bird-days carrying capacity of a site is not the same as predicting the effect on population size. Bird-days carrying capacity is simply the maximum numbers of birds that the food supply, in principle, could support. It is not equivalent to demographic rates, which are the parameters that actually determine population size in the long-term.

An empirical example that illustrates the dangers of using the bird-days carrying capacity approach comes from oystercatchers on the Wash where, during the 1990s, high winter mortality rates (and low body condition) were recorded in three winters of low shellfish abundance (Atkinson *et al.* 2003). Fig. 3 shows how, even in those three years, the bird-days carrying capacity was not fully utilised. Even excluding the stocks of supplementary prey, such as *Nereis diversicolor*, *Scrobicularia plana* and *Macoma balthica*, the birds

did not eat all the food supply available to them, yet up to 20% of adults starved (Stillman *et al.* submitted). Had the bird-days carrying capacity of the Wash each winter been used to decide how many shellfish should be harvested, very many oystercatchers would have starved or lost condition every year, and not just during the years of extreme shortage. The resulting high mortality rates repeated annually would have slashed the population by even more than actually occurred. It is therefore not safe to argue that, because spare carrying capacity would remain after a change in coastal management regime had been implemented, the birds would be unaffected. In fact, the change in regime might substantially reduce their fitness.

The bird-days carrying capacity approach cannot predict realistic demographic rates because it assumes that all individuals are identical. As Fig. 3 illustrates, this means that either all birds survive or all birds starve. In fact, as other empirical studies on oystercatchers (Goss-Custard *et al.* 2001) and theoretical studies (Goss-Custard *et al.* 2002) demonstrate, some birds die a long way before the carrying capacity is exceeded because they are poor competitors, and cannot collect their daily energy requirements in the time available even though plenty of food – in principle – remains. Food acquisition is not simply a question of picking up a packaged daily ration of food, as if in a super-market. It is a rate process and factors that affect the rate of feeding, such as the presence of competitors and individual differences in foraging efficiency, have an important influence on fitness.

This point is further highlighted by the predictions of a behaviour-based model (with individual differences) of the oystercatchers on the Wash (see below). The model was used to predict by how much winter survival rate would be improved in years of general shellfish shortage if artificial

mussel beds were laid in the intertidal zone. The reduction in mortality varied enormously according to the level of the shore at which the mussels were placed and the area over which they were spread (Stillman et al. submitted). Putting a tonne of mussels at high shore-levels reduced the mortality rate by a great deal more than did putting the same amount downshore: this is because mussels upshore extended the amount of time for which birds could feed over each tidal cycle. Spreading a tonne of mussels at a particular shore-level over a large area rather than a small one was also more effective at reducing the mortality rate because this reduced the amount of interference between birds as sub-dominant birds could more easily avoid being attacked by dominants. These model results show that, because consumption is time-constrained rate process, a tonne of mussels can have very different value in terms of bird fitness depending on its location and how it is provided. In contrast, the bird-days carrying capacity approach attributes the same value to a tonne of food, wherever and however it is provided (Goss-Custard et al. 2003).

This is not to say that measuring bird-days carrying capacity has no useful application as a guide to policy. A number of useful examples have been provided in studies of geese; e.g. predicting the stage in the winter when brent geese Branta bernicla bernicla switch from intertidal food to fields (Sutherland 1996b). The approach is safe here because there is almost certainly no mortality in these wintering brent geese and so one can be quite certain that there are no fitness and demographic consequences of the diet switch; the only issue is when the switch occurs, and how one might manage it.

But in many other cases, there are likely to be fitness consequences, even if their magnitude is currently unknown. The black-tailed godwits Limosa limosa studied by Gill et al. (2001a) is a good example. When godwits have eaten out their main intertidal foods (i.e. reached the bird-days carrying capacity of the coast), they switch increasingly to other intertidal invertebrates and, particularly, to earthworms in coastal meadows, and this switch is important for survival and probably body condition (Gill et al. 2001b). The bird-days carrying capacity approach cannot predict the fitness and demographic consequences of such a switch either before the switch is made and as the carrying capacity on the coast is approached or afterwards, when birds have changed diet. One might forecast that a change in coastal management policy might have no effect on the birds because (i) it would not cause the bird-days carrying capacity to be exceeded on the coast, and (ii) there are plenty of worms in the fields anyway. But, in fact, it could reduce fitness and survival, which, in such long-lived birds, could lead to a reduction in population size.

FITNESS, DEMOGRAPHIC RATES AND DENSITY-DEPENDENT FUNCTIONS

In most cases where predictions are required, we need to predict how a change in the quality, quantity and accessibility of the food supply (the "feeding conditions") will "affect" the birds; i.e. affect their fitness. This usually means predicting the effect on fitness of a change in the intensity of competition (Goss-Custard 1977, Goss-Custard & Durell 1990). A reduced food density (e.g. arising from changed nutrient status) causes food to be depleted sooner in the winter, with the result that more of the least efficient foragers would suffer reduced fitness. A reduced area of food (e.g. arising either permanently from habitat loss or temporarily from disturbance) causes birds to feed at higher densities, so depletion and interference competition intensify, again with the result that poor competitors suffer reduced fitness. Reduced foraging time (e.g. by preventing birds feeding at the top of the shore as the tide ebbs and flows, draining coastal meadows or removing salt pans) reduces the chances that inferior competitors will be able to compensate for their failure to obtain sufficient food supplies over the main low water feeding period.

As the feeding conditions deteriorate and competition intensifies, there will come a point when fitness starts to decrease and the mortality rate and the proportion of birds in poor condition starts to increase: it is therefore a "density-dependent function" (Fig. 4). Without variation between birds, this will be an "all-or-nothing" step function, with a slope of infinity which, in classical ecology, represents extreme scramble competition. However, if there is individual variation in competitive ability, so that contest competition plays a greater role, the slope will be less steep because the poorer competitors starve first as feeding conditions deteriorate and thus reduce the pressure on the remaining birds (Goss-Custard & Sutherland 1997).

The "step-function scramble competition" scenario is, in fact, the assumption made when the bird-days carrying capacity approach is adopted. It seems unlikely to occur widely in over-wintering waders. First, to my knowledge, there is no case where a partial change in the feeding conditions in a coastal site has caused the mortality rate to flip suddenly from a very low to a high value (e.g. 0% to 100%), so that birds became locally extinct. At Teesmouth, for example, a partial reduction in the food supply led only to partial reductions in bird numbers and not to a total (step-function) collapse of the population (Evans 1981, Evans et al. 1979). Second, the only density-dependent function yet published for waders has a gradual slope (Durell et al. 2000, 2001, 2003). Finally, where studies have been carried out, individual birds have often been shown to vary in competitive ability (e.g. Whitfield 1988). Given the potentially serious consequences for the conservation of waders of assuming that only scramble competition occurs, we would be wise to assume that gradual density-dependent functions are more likely to occur in nature than are step-functions. Certainly, this assumption is consistent with the precautionary principle.

To advise policy-makers, we really need to know where present-day populations are along these density-dependent functions (Goss-Custard & Durell 1990). It is likely that bird numbers are sometimes so low relative to the feeding conditions that competition between birds – even if it does occur – has no effect on fitness. But, at some point as bird numbers rise, or the food supply per bird diminishes, the intensifying competition will start to reduce fitness (the "inflexion point"), as the data for oystercatchers on the Wash illustrate (Fig. 3). Further deterioration in the feeding conditions will reduce fitness further, reducing overwinter survival and body condition in spring, and thus reducing population size.

When advising policy-makers, we need not be concerned about the effect of a proposed reduction in the feeding conditions if the population currently lies well to the right of this inflexion point. Even a series of habitat losses will have no effect on the birds until the inflexion point is reached. It is therefore no more appropriate to argue (as is sometimes done) that a series of piecemeal reductions "must cumulatively have an effect the birds" than it is to say that summing a number of zeros gives a positive number. Only when the
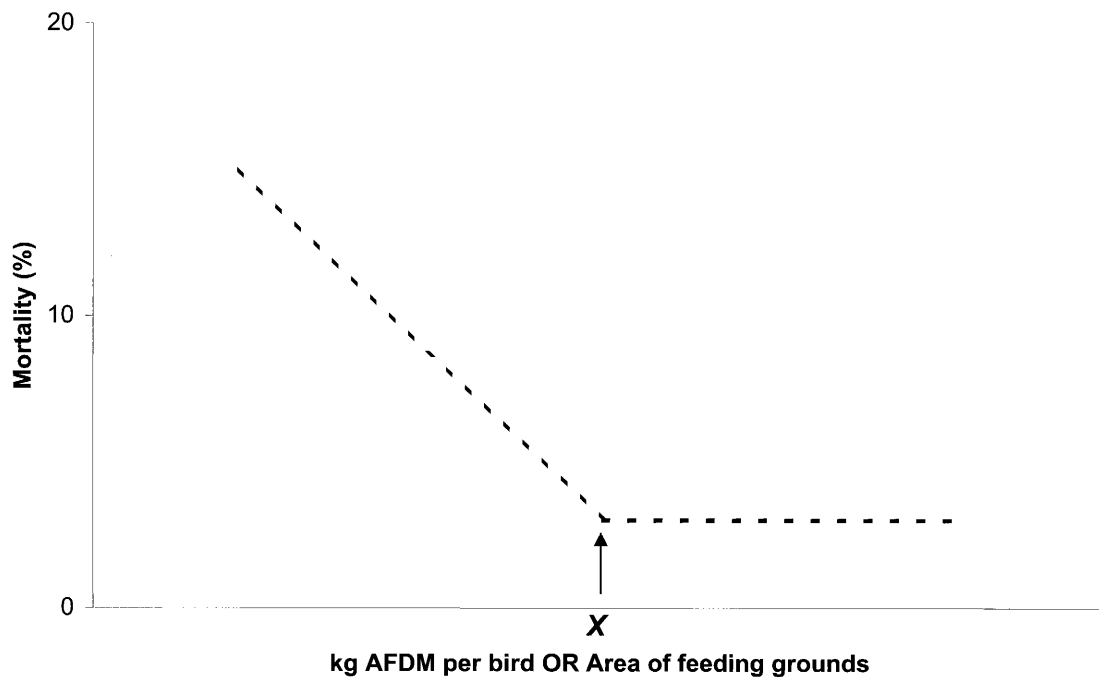
Fig. 4. A diagram showing how shorebird fitness might decrease as the feeding conditions deteriorate. Fitness is measured as the mortality rate during the non-breeding season but it could also be portrayed as the proportion of birds failing to achieve their target body mass in spring, just prior to migration. The feeding conditions deteriorate either because total tonnage of food decreases (expressed here as the kgAFDM/bird available at the start of the non-breeding season) or because the area of the feeding grounds decreases. The arrow shows the inflection point below which further deterioration in the feeding conditions so intensifies competition between birds that an increasing proportion lose fitness. The inflexion point in this example occurs when the kgAFDM/bird has the value X. The carrying capacity of the site is reached when the amount of food per bird reaches X because, from then on, shorebird fitness decreases. (Adapted from Goss-Custard & Durell 1990)

birds' density occurs near to or to the left of the inflexion point will a further deterioration in the feeding conditions reduce fitness and thus population size.

How do we know where present-day wader populations lie along this function? One way is to plot winter mortality rate (or spring body condition) against the quantity of food per bird (or population size if food varies little between winters). But this is very difficult to do for a single species in one estuary, let alone in many species in many estuaries. Furthermore, this can only be done for present-day coastal management policies so the functions would often not be applicable to new scenarios for which policy-makers require advice (Goss-Custard & Durell 1990, Goss-Custard et al. 1995). For the majority of coastal management scenarios, it is necessary to predict how a change in management would change the density-dependent fitness function itself.

As far as I am aware, the only approach yet devised to derive or predict the density-dependent functions is to use behaviour-based models in which individual model birds differ realistically in competitive abilities (e.g. Goss-Custard et al. 1995). [Note that spatial depletion models are also behaviour-based but do not have individuals that differ; the birds are aggregated into a single class]. Individuals behaviour-based models (IBBMs) can be used to generate density-dependent functions for new coastal management scenarios by running a series of simulations across a range of initial (autumn) population sizes. They can also give direct predictions of the number of birds – if any – whose fitness would be reduced by a wide variety of changes in coastal management (Stillman et al. 2001, West et al. 2002, 2003). Recent advances enable such models to be constructed well within

the amount of time usually devoted to environmental impact studies (Stillman & Caldow 2001), and for any wader species, and not just the oystercatchers on which the approach was developed (Morrisey et al. in press, Durell et al. in press). Further details of this approach can be found in Goss-Custard & Stillman 2002, Stillman, this volume).

In the absence of a standard classification scheme for models, IBBMs cannot be placed in an easily recognised category. Because it is process-based, and therefore unlike habitat association models, an IBBM is not a "top-down" or "phenomenological" model based on the description and classification of phenomena but not with processes. Nor is it a conventional "bottom-up" or "mechanistic and deterministic" ecological "box" model in which the outputs from each of a sequence of empirically determined equations form the inputs to the next and, finally, the prediction of the model as a whole.

Probably the most appropriate category for IBBMs is the "complex stochastic" process-based models sometimes used in atmospheric physics and sedimentology. There are some box model elements, but the fundamental feature of such models is that they use a stochastic procedure and a complex operation based on first principles, such as a Newtonian law, to derive the most probable prediction. They are "complex" because (i) an analytical solution is not yet mathematically tractable, and (ii) a simulation process generates, evaluates and selects from the alternative solutions available. Current IBBMs are complex because they use simulation to determine how each individual can optimise its choice of diet and feeding location, using a rate-maximising, optimisation principle which is believed to be related to fitness; in due course,

model decisions may be based directly on fitness consequences by using life history theory. They are "stochastic" because the combinations of competitive characteristics ascribed to each individual bird is drawn at random from empirically determined distributions and because the sequence in which individuals are considered in successive daily iterations is chosen at random. To some biological modellers (who might suffer from "physics envy"), IBBMs appear too complex and cumbersome because they are simulation rather than analytical models and require more than a few parameters. However, we have not found an analytical mathematics that can capture the necessary biological processes and natural history details (which represent the survival strategies of the birds involved) in such a way as to realistically and reliably predict how fitness is affected by changes in coastal management. This is surely a more appropriate criterion than "analytical elegance" with which to evaluate the usefulness of these models.

SOME FINAL POINTS

Habitat quality

Habitat association and bird-days carrying capacity models provide a measure of habitat quality. Habitat association models predict the effects of environmental change on habitat quality, using bird density (i.e. bird usage) as the measure of habitat quality. They produce essentially the same predictions as aggregated behaviour-based models, such as spatial depletion models, which measure habitat quality as bird-days instead of bird-density.

Indeed calculating the maximum number of bird-days that can be supported by a site may prove to be just a complicated way of calculating how much food there is now, or will be in the future. If one bird needs 1 kg per day and there is 1000 kg of food available, then the food supply in principle will support 1000 bird-days. If the food supply is predicted to decrease to 800 kg, then both the food supply and the bird-days it can support are predicted to decrease by 20%. Nothing seems to be gained by expressing this change in habitat quality in terms of bird-days rather than simply in terms of the size of the food supply. One could equally well just say that the food supply is predicted to decrease by 20%, and that habitat quality is therefore predicted to deteriorate by that amount.

Both approaches do not predict the effects of an environmental change on fitness, demographic rates or population size. The difference between them, however, is that habitat association models are likely to over-estimate the impact of a deterioration in the feeding conditions on the birds. In contrast, the bird-days carrying capacity approach is likely to under-estimate the effect because fitness may be much reduced before carrying capacity is reached. In my opinion, using such an approach to advise policy-makers may not advance the cause of wader conservation and certainly is at odds with the precautionary principle.

Carrying capacity

There are two widely used definitions of carrying capacity: (i) the maximum bird-days that the food supply can support and (ii) the maximum number of birds surviving to the end of the non-breeding season (Goss-Custard et al. 2002). Both of these are perfectly sound definitions of carrying capacity but are very poor guides for policy because fitness can be so

seriously reduced before carrying capacity, however defined, is reached (Goss-Custard et al. 2002).

Figs 3 and 4 suggest an alternative way of defining carrying capacity in waders and, indeed, in other taxa. The inflexion point (shown by the arrow) defines the conditions in which further deterioration in the feeding conditions would start to reduce fitness. It enables one to make statements such as: "To maintain the wader population at its present level in this site (or in these sites) – i.e. to maintain its carrying capacity – we should not let the quantity of food per bird present in autumn fall below X kgAFDM (ash-free dry mass)". The quantity X can be viewed as the carrying capacity, the quantity of food below which further reductions should be resisted if we wish to maintain the birds at their present level of fitness. [If in practice the inflexion point is not so clear-cut as illustrated in Fig. 4, one could define carrying capacity as the kgAFDM/bird at which fitness starts to decrease below its current average levels.] This very simple approach is now being applied to a number of wader species, including oystercatchers on the Wash (Stillman et al. in press).

Intraspecific competition and interference

The arguments made here hinge on the occurrence in waders of individual variations in competitive ability; i.e. in basic foraging efficiency and/or in success in interference competition in one of its several forms (Goss-Custard 1980, Goss-Custard et al. 2002). This is not an easy assumption to test but, so far, properly designed studies have found strong evidence in favour; post-Darwin, perhaps we should not really be surprised by that.

We have understood for 20–25 years now that the study of competitive processes is central to the problem of predicting the effect on birds of changes in coastal management (Goss-Custard 1977, Zwarts & Drent 1981, Goss-Custard & Durell 1990). Despite this, rather few studies on individual variation in competitive abilities and interference competition have actually been carried out. One reason for this is that marked individuals are often difficult to follow on the many large intertidal areas of NW Europe: the solution to this is to choose small and more-or-less isolated study areas. Marked birds also increase the chances that interference competition will be detected because its effect may only be detectable in subdominant birds (Ens & Goss-Custard 1984). A second reason is that interference may only occur during periods of poor feeding conditions when birds are hungry enough to risk injury by attacking other birds, as was found in oystercatchers eating cockles in the baie de Somme (Triplet et al. 1999). This is probably why, in oystercatchers feeding on mussels on the Exe estuary, interference was absent in autumn when the feeding conditions were good but intense in January and February when the feeding conditions were at their worst (Goss-Custard & Durell 1987), and birds were at risk of dying of starvation (Goss-Custard et al. 2001). [Sadly this means that interference may need to be studied in the field at the least comfortable period of the winter for wader ecologists!] A final reason is that birds will actively attempt to reduce the chances that they will experience interference competition by, for example, avoiding coming too close to conspecifics, unless they are forced to do so by a reduction in feeding space (Yates et al. 2000). It is therefore perhaps not surprising that interference is not easy to detect and that studies have to be carefully targeted to be able to do so.

There also sometimes seems to be a belief that interference only occurs in oystercatchers because they eat large prey that can be profitably stolen, yet this now seems highly unlikely. The prey of many waders have anti-predator responses which take them out of reach of the birds, a form of interference for which there has been evidence for over 20 years (Goss-Custard 1976) and that has now been modelled in redshank using a behaviour-based model (Yates *et al.* 2000). Fighting for food items and feeding sites is also common in waders other than oystercatchers eating mussels (Goss-Custard 1980), especially when feeding conditions are poor (e.g. in knots *Calidris canutus* on the Wash in winter (Goss-Custard 1977)). The prey items do not have to be large either, as seems sometimes to be assumed. Common cranes in Spain *Grus grus* experience competition when eating small cereal grains (Stillman *et al.* 2002). Given its central importance for predicting the effect of changes in coastal management on waders, it is to be hoped that more workers will make the heavy investment required to investigate its strength and occurrence across species and systems. In the meantime, and for the sake of conserving waders, we should perhaps adopt the precautionary principle and assume that, on present evidence, it is likely to be widespread.

Competition is also likely to be involved when birds choose one area rather than another to spend the non-breeding season and when to change their choice if feeding conditions deteriorate. Atkinson *et al.*'s (2003) study of Wash oystercatchers lend strong support to the long-suspected idea that bird numbers on one coastal area depend greatly on decisions made by prospecting juveniles (Goss-Custard *et al.* 1977), and this decision is very likely to be influenced by the intensity of the competition in different sites. Richard Caldow's pioneering multi-site model of the World population of the dark-bellied brent goose (in Pettifor *et al.* 2000) illustrates how, by changing sites, birds can reduce the effect of a deterioration in the feeding conditions in one site on their fitness, and thus population size, by in effect spreading the resulting increase in competitive pressure across a number of sites. But we are still unsure of the decision rules used by birds in these circumstances, and for realistic and confident prediction, we should find out what they are. Amongst the many exciting research challenges that lie ahead for those wader ecologists who are tackling head-on the problem of predicting how wader fitness will be affected by changes in coastal management, is investigating, by both theoretical and empirical means, the basis upon which waders decide to stay in one area or to move to seek another.

As other articles in this volume have pointed out, monitoring and predicting demographic rates is the key to both understanding the factors that have affected wader populations and to predicting the effect of changed coastal management upon them (Boyd, this volume; Minton, this volume; Sandercock, this volume; Boyd & Piersma 2001). It is astonishing that, despite decades of intensive ringing, there are very few estimates of demographic rates, especially within one period of the annual cycle, even of survival in the non-breeding season, a period of the annual cycle to which so much effort has been applied. This is important not only because population size in waders is likely to be very sensitive to the survival rate but also because we need more estimates of demographic rates in the non-breeding season – and not for the year-round as a whole – with which we can calibrate and test the predictions of models that predict fitness and demographic rates. Unless we are able quantitatively and

reliably to predict the effect of changed coastal management on the fitness of waders, and thus their demography, can we really claim that we have a full understanding of their biology during the non-breeding season and that we are able to forecast how changed coastal management will affect their numbers?

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