Predicting the effect of disturbance on coastal birds

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Assessments of whether disturbance is having a deleterious effect on populations have often measured behavioural responses to disturbance and assumed that populations with a larger behavioural response are more susceptible to disturbance. However, there is no guarantee that the behavioural response to disturbance is related to the population consequence, measured in terms of decreased reproduction or increased mortality. Individual-based models, consisting of fitness-maximizing individuals, are one means of linking the behavioural responses to disturbance to population consequences. This paper reviews how individual-based models have been used to predict the effect of disturbance on populations of shorebirds and wildfowl at several European sites, and shows how these models could be improved in the future by incorporating a range of alternative responses to disturbance.

There is considerable debate into the effects of human disturbance on animal populations (e.g. Hockin *et al.* 1992, Hill *et al.* 1997). Assessments of whether disturbance is having a deleterious effect on populations have often relied on measuring behavioural responses to disturbance, such as the closest distance to which a disturbance source is approached or the time for animals to return after disturbance has ceased, and assumed that populations with a larger behavioural response are more susceptible to disturbance (Gill *et al.* 1996, 2001a). However, there is no guarantee that the behavioural response to disturbance is related to the population consequence, measured in terms of decreased reproduction or increased mortality (Gill *et al.* 1996, 2001a). For example, birds that show a large behavioural response to disturbance may do so simply because they have alternative feeding or breeding sites to move to. The impact of disturbance needs to be measured in terms of its effect on population size, rather than simply in terms of behaviour (Gill *et al.* 2001a, Gill 2007). In migratory shorebirds and wildfowl, population size is a function of the interaction between (1) mortality and reproductive rates in the breeding ranges and (2) mortality rate in the non-breeding range, including

migratory routes (Sutherland 1996, Goss-Custard & Sutherland 1997). Therefore, the best measure of the impact of disturbance on population size is one which, directly or indirectly, determines these demographic rates (Goss-Custard *et al.* 2002). For migratory shorebirds and wildfowl during the non-breeding season, this means that the impact of disturbance should be measured in terms of its effect on two factors: (1) the storage of fat reserves needed to fuel migration in spring and to breed successfully after the birds have reached the breeding grounds, and (2) the number of birds that die during the non-breeding season (Goss-Custard *et al.* 2002).

Individual-based models, consisting of fitness-maximizing individuals, are one means of predicting fat storage and mortality rates and hence can be used to link the behavioural responses to disturbance to population consequences [see Norris & Stillman (2002) for a discussion of the advantages of this behaviour-based approach over traditional regression or demographic models]. Recently, such individual-based models have been used to predict the effect of habitat loss, sea-level rise and disturbance on coastal bird populations at several European sites (Goss-Custard *et al.* 1995a, 1995b, 2004, 2006, Stillman *et al.* 2000, 2001, 2003, 2005b, West *et al.* 2003, Caldow *et al.* 2004, Durell *et al.* 2005). These models track the behavioural decisions and locations of all animals within a population, and predict population

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parameters, such as mortality rate, from the fates of all individuals. Importantly, the decisions made by model animals are based on optimal foraging theory and game theory, which are thought to provide a reliable basis for prediction (Sutherland 1996, Goss-Custard & Sutherland 1997). Model individuals are designed always to behave in order to maximize their own chances of survival and reproduction, no matter how much the environment changes. Therefore, model animals are expected to respond to environmental change in the same ways as real ones would (Sutherland 1996, Goss-Custard & Sutherland 1997). In this paper, we review the use of individual-based models to predict the effect of human disturbance on coastal shorebird and wildfowl populations.

INDIVIDUAL-BASED MODELS OF COASTAL BIRDS

Why develop individual-based models?

There were two reasons for developing individual-based shorebird and wildfowl models. First, many responses by birds to environmental change are behavioural (Goss-Custard & Durell 1990); for example, they change feeding location when disturbed. Secondly, models must often predict how demography may be affected by as yet untried management scenarios and policy options, which therefore lie outside the present-day empirical range. The difficulty with this is that there is often no way of knowing whether the empirical relationships upon which traditional regression and demographic models are based will hold under new conditions, meaning that predictions are of uncertain accuracy (e.g. Norris & Stillman 2002). To have confidence in predictions outside of past empirical ranges, models need to operate on basic principles, underpinned by theory, that will still apply in the new scenarios rather than on present-day empirical relationships, which may no longer hold in the scenarios for which predictions are required.

History of model development

Over the last decade, a sequence of individual-based models has been developed to predict the consequences of environmental change for shorebird and wildfowl populations (Fig. 1). The first two shorebird models (Goss-Custard *et al*. 1995a, 1995b, Clarke & Goss-Custard 1996) described in increasing detail the Oystercatcher–shellfish system in the Exe estuary, UK. The third shorebird model was also primarily developed for Eurasian Oystercatchers *Haematopus ostralegus* on the Exe estuary (Stillman *et al*. 2000, 2001), but was subsequently parameterized for Oystercatchers and other shorebirds in Strangford Lough, Menai Strait, Dee estuary, Humber estuary, The Wash and Burry Inlet in the UK, and Baie de Somme and Baie de Seine in France. In parallel, Pettifor *et al*. (2000a) developed individual-based models for migratory Barnacle *Branta leucopsis* and Brent Goose *B. bernicla* populations. Although these models were developed for shorebirds and wildfowl, the principles on which the models are based – that animals attempt to maximize their chances of survival and reproduction – apply to any system, and the types of environmental issues that the models are designed to address are not restricted to the coast. This was the incentive to develop a much more flexible model (Stillman *et al*. 2005a), capable of being applied to a much wider range of species and environmental issues. To date, this model has been applied to shorebirds in the Exe estuary, Poole harbour and Southampton Water in the UK, Baie de Somme, France, and Bahia de Cadiz, Spain (Stillman *et al*. 2005a, 2005c), Brent Geese in western Europe (Stillman *et al*. 2005a) and Black Scoter *Melanitta nigra* in the Irish Sea (Kaiser *et al*. 2005).

Model tests

If individual-based models are to be of applied value they need to produce accurate predictions. Each of the models listed in Figure 1 was tested as thoroughly as possible using all data available for each study system. Although the tests varied between sites, data were typically available to test the predicted distribution of birds throughout a site and the major prey species consumed by birds. Typically, patch selection and prey choice were accurately predicted for the majority of species (e.g. Durell *et al*. 2005, Stillman *et al*. 2005b). For some sites, data were available on overwinter mortality rates and the proportion of the time spent feeding each day (an important indicator of the difficulty birds are having in surviving winter). Both overwinter mortality and the proportion of the time spent feeding were accurately predicted in all cases (Fig. 2). These accurate predictions increase confidence that the models provide realistic descriptions of the real world, and therefore that predictions for novel scenarios, which cannot be tested, are also likely to be accurate.
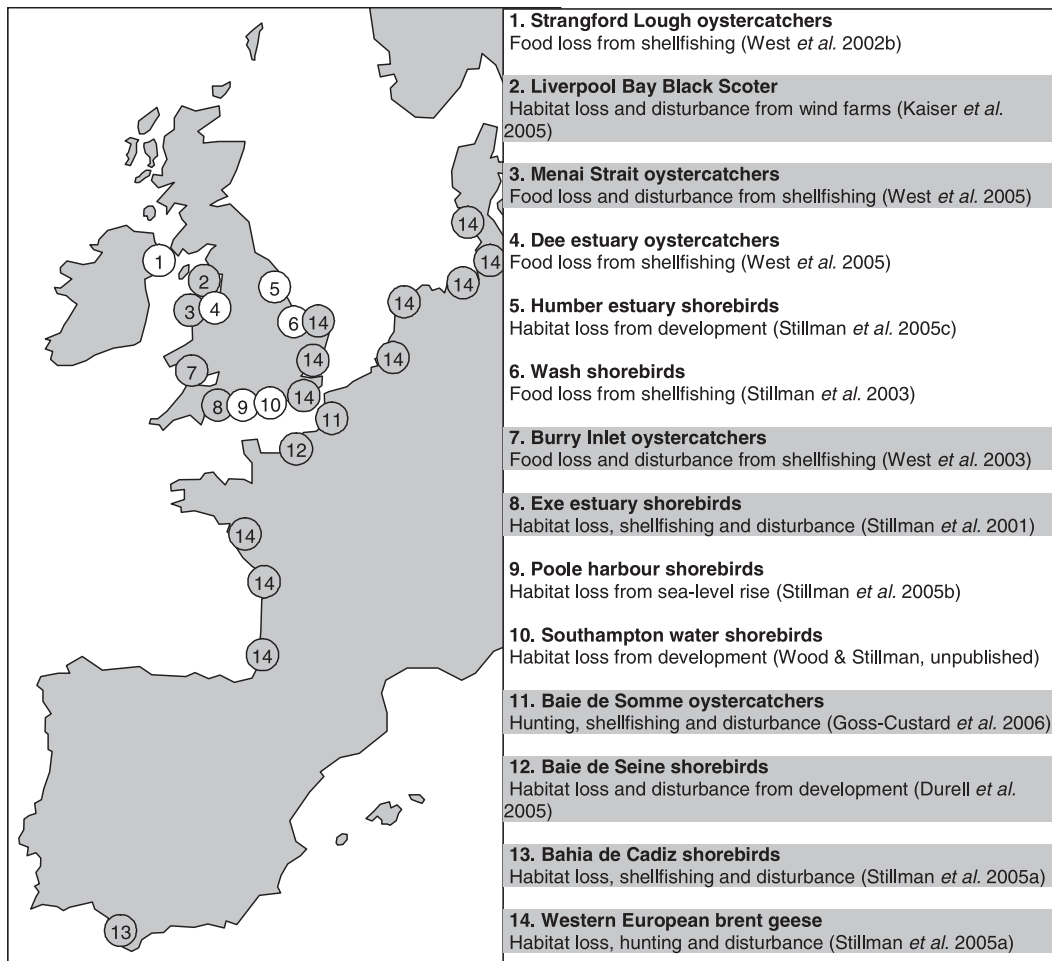
Figure 1. Shorebird and wildfowl systems for which individual-based models have been developed. The figure describes the environmental issue addressed in each system and highlights in grey shading those systems in which the effect of human disturbance has been incorporated.

The figure contains a map with the following legend:

1. Strangford Lough oystercatchers
Food loss from shellfishing (West *et al.* 2002b)

2. Liverpool Bay Black Scoter
Habitat loss and disturbance from wind farms (Kaiser *et al.* 2005)

3. Menai Strait oystercatchers
Food loss and disturbance from shellfishing (West *et al.* 2005)

4. Dee estuary oystercatchers
Food loss from shellfishing (West *et al.* 2005)

5. Humber estuary shorebirds
Habitat loss from development (Stillman *et al.* 2005c)

6. Wash shorebirds
Food loss from shellfishing (Stillman *et al.* 2003)

7. Burry Inlet oystercatchers
Food loss and disturbance from shellfishing (West *et al.* 2003)

8. Exe estuary shorebirds
Habitat loss, shellfishing and disturbance (Stillman *et al.* 2001)

9. Poole harbour shorebirds
Habitat loss from sea-level rise (Stillman *et al.* 2005b)

10. Southampton water shorebirds
Habitat loss from development (Wood & Stillman, unpublished)

11. Baie de Somme oystercatchers
Hunting, shellfishing and disturbance (Goss-Custard *et al.* 2006)

12. Baie de Seine shorebirds
Habitat loss and disturbance from development (Durell *et al.* 2005)

13. Bahia de Cadiz shorebirds
Habitat loss, shellfishing and disturbance (Stillman *et al.* 2005a)

14. Western European brent geese
Habitat loss, hunting and disturbance (Stillman *et al.* 2005a)

MODELS INCORPORATING HUMAN DISTURBANCE

How disturbance is incorporated

Several direct or indirect effects of disturbance can be incorporated into individual-based models. Disturbance can exclude birds from part of the habitat and so decrease the area of available habitat. It can also cause birds to cease feeding and so decrease the total amount of time available for feeding. If disturbance causes birds to take flight, it can increase energy demands. By decreasing habitat area, disturbance causes more food to be consumed in undisturbed patches, and so indirectly affects food abundance.

If prey quality differs between disturbed and undisturbed patches, disturbance can also have the indirect effect of changing the quality of food available to birds. One or more of these effects were incorporated into each of the models that have incorporated disturbance (Fig. 1).

Measuring disturbance parameters

Individual-based models have been parameterized by measuring behavioural responses to disturbance, such as the distance from which birds are excluded from a disturbance source, the time taken to return after disturbance has ceased, and the amount of time flying and energy cost during a disturbance. Figure 3
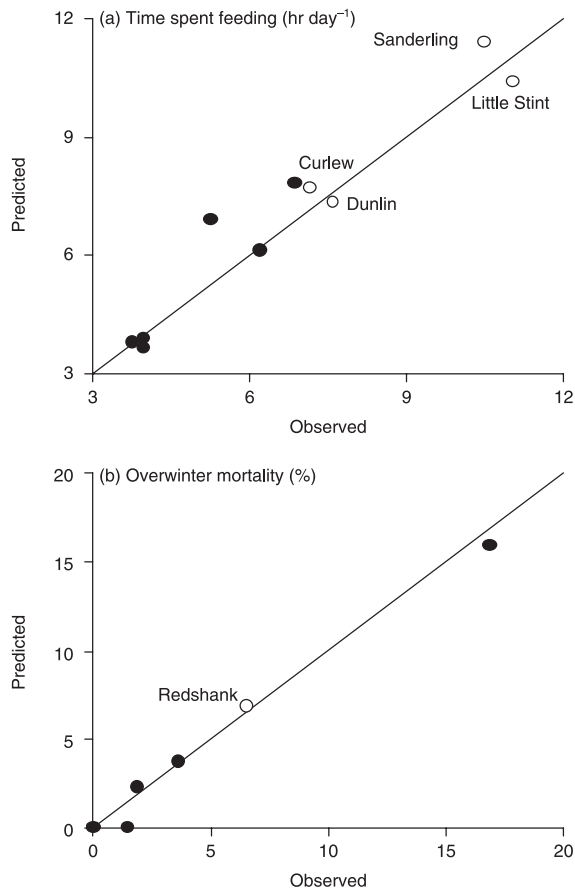
Figure 2. Tests of individual-based shorebird models. Comparisons between model predictions and (a) the observed amount of time spent feeding by an average bird over a single daylight tidal cycle (closed symbols: Oystercatchers; open symbols: Little Stint *Calidris minuta*, Sanderling *C. alba*, Dunlin *Calidris alpina* and Curlew *Numenius arquata*; data from the Exe estuary, Burry Inlet and Bangor flats in the UK, Seine estuary, France, and Bahia de Cadiz, Spain) and (b) the observed winter mortality rates of Oystercatchers (closed symbols; data from the Burry Inlet, Exe estuary and the Wash in the UK) and Redshank *Tringa totanus* (open symbol; data from the Rhymney flats of the Severn estuary, UK).

Figure 3. Example of data that can be used to parameterize individual-based models of disturbance. Experiments were performed on Oystercatchers feeding on a mussel bed. Relationships are shown between stage of the season and (a) the distance around a stationary observer from which birds were excluded and (b) the time taken for birds to return to the observer's location after the observer left the mussel bed. The lines show relationships fitted using linear regression and both show significant seasonal reductions in the response to disturbance. Adapted from Stillman & Goss-Custard (2002).

shows the data (Stillman & Goss-Custard 2002) used to parameterize a model of the effect of shellfishing disturbance on Oystercatcher mortality rate on the Exe estuary (Stillman *et al.* 2001). Experiments were designed to mimic the disturbance caused by stationary fishermen. An observer walked to a fixed location on the mussel bed and measured the size of the area from which Oystercatchers were excluded. After a fixed amount of time, the observer then walked off the mussel bed and recorded the time
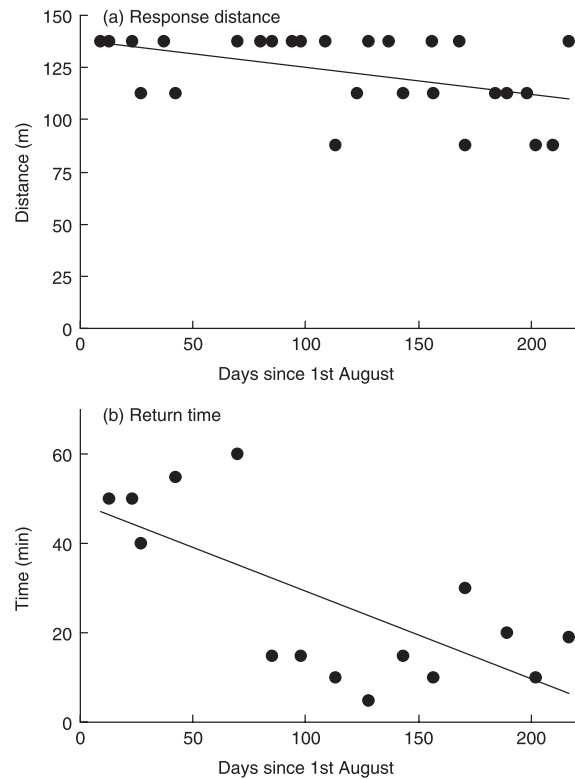
for birds to return. Experiments were conducted throughout winter to account for the seasonal trend in response to disturbance, in which birds responded less in late winter when their energy demands were higher and food quality lower. Within the model the amount of disturbance caused by shellfishing was calculated from the number of fishermen on a mussel bed multiplied by the area from which birds were observed to be excluded, and the time for which fishermen were present plus the observed amount of time taken for birds to return after disturbance. Similarly, data on disturbance distance, time to return after disturbance and the energy cost of flight during disturbance were used to parameterize a model of shorebirds in the Baie de Seine, France (Durell *et al.*

2005). These examples show how simple data on the behavioural response to disturbance, frequently measured in many studies (e.g. Smit & Visser 1993), can be used to parameterize individual-based models.

Example applications

Disturbance from human activities

Shellfishing and recreation can cause disturbance to shorebirds when they occur during low tide and in places in which shorebirds feed or roost. West *et al.* (2002a) used a modified version of the original Exe estuary model to study the effect of human disturbance on wintering Oystercatchers. In the original model (Stillman *et al.* 2000), the only effect of disturbance was to reduce the area of patches available to birds, thus increasing bird density. The version used by West *et al.* (2002a) was modified to include the time and energy costs of disturbance – energy expended flying away from the disturber and feeding time lost as a result of the disturbance. The model predicted that, for a given overall area disturbed, disturbance was more detrimental if it arose from many small-scale sources rather than fewer, larger-scale sources (Fig. 4). When the time
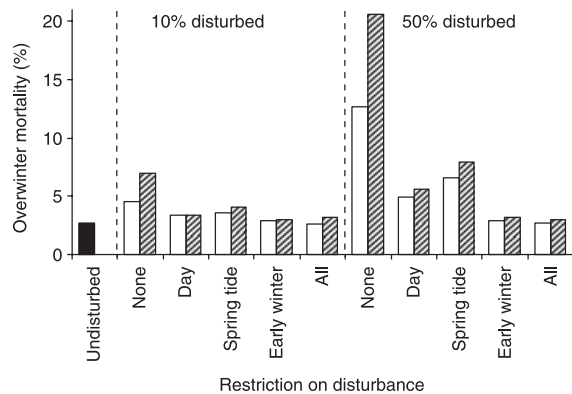
and energy costs arising from disturbance were included, disturbance could be more detrimental than permanent habitat loss. The model also predicted how to minimize the impact of disturbance. Preventing disturbance during late winter, when feeding conditions were worse, practically eliminated its predicted population consequences (Fig. 4). Although disturbance can increase mortality, it was not predicted to do so at the levels currently occurring in the Exe estuary. This example shows how individual-based models can both assess the current impact of disturbance on shorebird mortality and predict how this may change in the future.

In the Baie de Somme, France, a similar model was used to predict how the effect of disturbance on Oystercatcher mortality interacts with food abundance (Goss-Custard *et al.* 2006). In this model, the birds were unaffected by up to three disturbances per hour, provided that cockle stocks were high. However, if, as sometimes happens in the Baie de Somme, large amounts of the cockle stock die in midwinter, the model predicted disturbances should be kept below one per 2 h to prevent increased Oystercatcher mortality (Fig. 5). Thus, the consequences of a given level of disturbance depended on the environmental circumstances prevailing at the time.

Disturbance from industrial developments

Industrial developments such as windfarms or ports cause habitat loss, but may also act as disturbance sources in which either the development itself or the
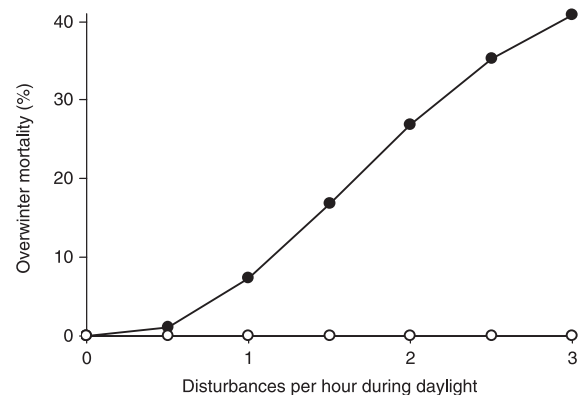

Figure 4. The percentage of an initial autumn population of 1500 Oystercatchers on the Exe estuary, UK, that were predicted to die from starvation over the winter, in relation to the restrictions imposed by disturbance from people. 'None' = disturbance allowed day and night throughout winter; 'Day' = disturbance only during the day; 'Spring tide' = disturbance only on spring tides; 'Early winter' = disturbance only before 1 December; 'All' = disturbance only during daylight on spring tides before 1 December. Solid bar = no disturbance, white bar = few large sources of disturbance, hatched bar = numerous small sources of disturbance. Either 10% (left bars) or 50% (right bars) of the habitat was disturbed in the absence of disturbance restrictions. Adapted from West *et al.* (2002a).

Figure 5. The interaction between food abundance and the effect of disturbance on the predicted percentage overwinter mortality rate of Oystercatchers in the Baie de Somme, France. Open circles – no overwinter cockle mortality, solid circles – high overwinter cockle mortality. Adapted from Goss-Custard *et al.* (2006).

traffic to and from the development displace birds, reduce their feeding time or increase their energy demands (e.g. Burton 2007).

Kaiser *et al.* (2005) used an individual-based model to predict the effect of offshore windfarms on the mortality rate of Black Scoters in Liverpool Bay, UK. It is proposed to construct up to five windfarms in the Bay, from Shell Flat in the north to Rhyl Flats in the south. Liverpool Bay is one of the most important wintering sites for Scoters in England and Wales (Oliver *et al.* 2001) and there is concern that the development of windfarms in these areas will displace the birds into less favourable feeding areas or alter the seabed habitat such that the preferred food of the ducks is no longer available. The model takes account of the changing depth of water over the ducks' food supply and the energetics of diving to reach that food. It incorporates disturbance due to shipping lanes and assumes that Scoters are excluded from a 2-km buffer around windfarms. Proposed windfarms do not overlap shipping lanes and so are an additional source of disturbance. Scoter mortality rate was predicted to increase if all proposed windfarms were developed. However, it was the presence of the proposed windfarm on Shell Flat which, in combination with the others, led to increased Scoter mortality. This happened because the 2-km buffer around the Shell Flat windfarm excluded birds from an area of relatively food-rich, shallow water. The other windfarms were positioned in less suitable Scoter feeding habitat. The negative effect of the Shell Flat windfarm was negated if: (1) the radius of the buffer zone was smaller than 2 km, (2) Scoter redistributed to currently unused but apparently profitable feeding areas within Liverpool Bay or (3) Scoter fed during the hours of darkness as well as during daylight. These simulations showed how individual-based models can be used to assess the relative impacts of a range of possible windfarm developments.

A model of Dunlin *Calidris alpina*, Oystercatcher and Eurasian Curlew *Numenius arquata* in the Seine estuary, France, was used to predict the effect of habitat loss and disturbance from port development, and possible ways of minimizing the detrimental effect of disturbance (Durell *et al.* 2005). Disturbance excluded birds from the upshore mudflats closest to the development and also disturbed birds from a roost close to the development. Two sets of disturbance simulations were run: (1) with disturbance occurring both day and night and (2) with disturbance occurring in daytime only. Disturbance was assumed

to be continuous throughout these periods. Roost disturbance was incorporated by increasing the daily energy costs of birds due to extra flying time. Additionally, simulations were run to test the effect of a proposed mitigation measure to prevent disturbance from occurring within 150 m of the mudflats. When disturbance excluded birds from the upshore area during both day and night, mortality increased significantly, and the proportion of birds failing to reach their target weights increased significantly in all three shorebirds (Fig. 6). When disturbance excluded birds from the upshore during the daytime only, the effect of disturbance was considerably reduced, with only Dunlin body condition being reduced significantly (Fig. 6). When roost disturbance increased energy costs by the equivalent of 10 min or more extra flying time a day, there was a significant effect on the mortality and body condition of all three shorebird species. Simulating the effect of a buffer zone, which would prevent disturbance from occurring within 150 m of the sea wall, effectively
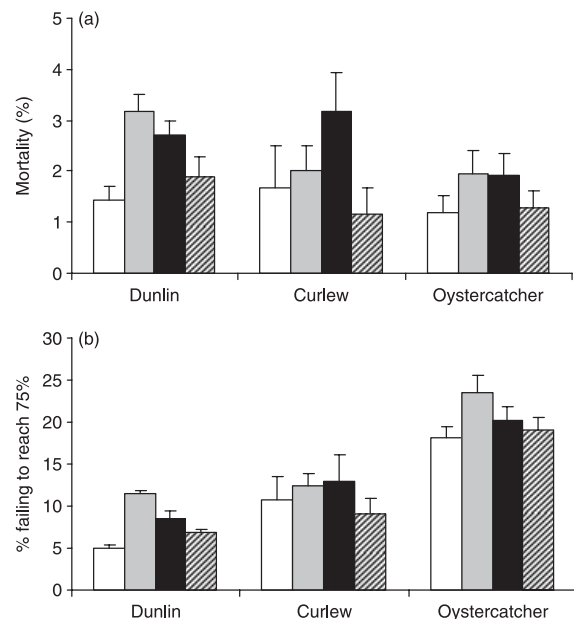

Figure 6. The effect of habitat loss (grey bars), disturbance of feeding birds day and night (black bars) and disturbance of birds during daytime only (striped bars) on (a) mortality and (b) body condition of shorebirds in the Baie de Seine, France. Open bars show mortality and body condition in the absence of disturbance or habitat loss. Disturbance was simulated without habitat loss. Body condition is expressed as the proportion of birds failing to accumulate at least 75% of their target reserves. Bars show means and 95% confidence limits. Adapted from Durell *et al.* (2005).

removed the effect of disturbance on feeding shore-birds. These simulations showed how individual-based models can compare alternative ways of managing disturbance.

DISCUSSION

The behavioural responses of birds to human presence in coastal areas are often very obvious; large bird flocks may be seen flying away from people and areas where people occur often have few birds. However, these large behavioural responses do not necessarily mean that more birds will die, as they may have spare time in which to compensate for disturbance or may simply move to another feeding area after being disturbed (Gill *et al*. 2001a). The individual-based models discussed in this paper can incorporate all of the effects of disturbance and predict whether more birds die or the body condition of birds is decreased by disturbance.

If individual-based models are to be of value in advising coastal management, they must produce accurate predictions and be developed within a relatively short time-scale. Testing predicted mortality rates is difficult because intensive, long-term ringing studies are required to estimate overwinter mortality rates in wild bird populations. Such studies have been conducted at just a few sites and so this limits the number of systems in which model predictions can be tested. The difficulty of measuring overwinter mortality was in fact one of the major reasons for developing individual-based models to predict mortality. However, mortality rate has been accurately predicted for those sites for which suitable data are available, increasing confidence that predictions will also be accurate for sites for which observed data are not available. Models can also be developed relatively quickly (1–2 years including data collection), especially when compared with the time and effort required to develop demographic models (one estimate of mortality rate per year). Disturbance parameters can also be measured within a short time-span, and are available already for species in which the behavioural response to disturbance has previously been measured (e.g. Smit & Visser 1993, Triplet *et al*. 1999, Stillman & Goss-Custard 2002).

We have shown how individual-based models have been used to predict the effect of a wide range of disturbance sources, from localized disturbance caused by people walking on mudflats (e.g. recreation and shellfishing) to larger disturbances from industrial developments (e.g. ports and windfarms). Although

differing in scale, these disturbances have similar effects on the birds. They exclude birds from areas which would otherwise be used for feeding or roosting, increase the energy demands of birds by causing them to take flight and reduce the amount of time they have to feed. Disturbance may also decrease the efficiency with which birds feed or increase the metabolic rate of birds before they take flight, factors which could potentially be incorporated into individual-based models in the future. Individual-based models can be used to assess the effect of present-day disturbance on mortality rate, compare the relative effects of alternative future disturbance scenarios and predict the best ways of managing disturbance.

We have focused on one group of models, but other mechanistic models have been developed (see reviews in Sutherland 1996, Goss-Custard & Sutherland 1997, Pettifor *et al*. 2000b and Norris & Stillman 2002). In particular, spatial depletion models have been used to address a number of shorebird and wildfowl conservation issues (e.g. Sutherland & Allport 1994, Percival *et al*. 1996, Gill *et al*. 2001b). Although based on the same general principles, the individual-based models in this paper differ from spatial depletion models in three main ways. First, they include food competition through interference as well as depletion, whereas spatial depletion models only include depletion. Secondly, individuals may differ in foraging efficiency and susceptibility to interference, whereas all individuals are assumed to be identical in spatial depletion models. Thirdly, the storage of reserves as fat is included whereas fat reserves are not incorporated in spatial depletion models. The main consequences of these differences are that the models in this paper are able to predict how environmental change influences the mortality rate and body condition of birds, and hence can be used to predict how change affects population size.

An assumption of all the models discussed in this paper is that the response to disturbance (e.g. the distance over which birds avoid disturbance or the time to return after disturbance) is unrelated to the difficulty birds are having in surviving winter. For example, Black Scoter were always assumed to avoid windfarms by *c*. 2 km, Oystercatchers assumed to approach a disturbance source no closer than 100 m and shorebirds assumed to spend *c*. 10 min per day flying from disturbances at roosts, irrespective of the frequency of disturbance or the condition of the birds. These disturbance parameters were based on observations of real birds, but it is likely that birds

would approach a disturbance source more closely or return to feed more quickly if they were close to starvation (e.g. Gill *et al.* 1996, Stillman & Goss-Custard 2002). The observed response to disturbance is determined by the birds' experience of disturbance, body condition and the availability of alternative feeding or roosting sites, and is not always measured from birds which are about to starve and have no alternative sites. One way to account for this in future disturbance models would be to run simulations assuming two alternative responses to disturbance: (1) *precautionary simulations* based on the response currently observed in the study species on the study site and (2) *better case simulations* based on the minimum response observed in the study species on any site. The precautionary simulations assume that the response to disturbance on a site is fixed and will not change as animals experience more disturbance or lose condition (i.e. the assumption in current models). The better case simulations assume that birds will respond less as they experience more disturbance and lose condition, but that some minimum response will be reached, as measured by the minimum response observed in the field. To improve estimates of the minimum response to disturbance, more empirical studies are required on birds that are in poor condition.

This paper has reviewed how individual-based models have been used to link behavioural responses to disturbance to overwinter mortality rate in coastal birds. However, disturbance is just one form of environmental change and coastal birds share characteristics with many other species, and individual-based models can be applied to a much wider range of species and environmental issues.

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