Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model

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Abstract

To assess the long-term effects of human disturbance on birds, ways of predicting its impacts on individual fitness and population size must be found. In this paper we use a behaviour-based model to predict the impact of human disturbance on oystercatchers (*Haematopus ostralegus*) on their intertidal feeding grounds in the Exe estuary in winter. The model predicted that, for the same overall area disturbed, numerous small disturbances would be more damaging than fewer, larger disturbances. When the time and energy costs arising from disturbance were included, disturbance could be more damaging than permanent habitat loss. Preventing disturbance during late winter, when feeding conditions were harder, practically eliminated its predicted population consequences. Although disturbance can cause increased mortality, it was not predicted to do so at the levels currently occurring in the Exe estuary. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Environmental-impact assessment has become influential in determining whether certain human activities should be regulated, or even allowed to occur, in an area of conservation value. Often, an important consideration is the effect of human disturbance on birds (Gill et al., 1996; Hill et al., 1997). To date, most studies have looked at the effects of disturbance on one or more aspects of bird behaviour (e.g. Owens, 1977; Yalden, 1992; Fitzpatrick and Bouchez, 1998), or on local bird numbers and distribution (e.g. Tuite et al., 1984; Draulans and van Vessem, 1985; Pfister et al., 1992). Such studies measure the immediate effects of disturbance but not their impact on fitness (the survival chances and/or reproductive success of individuals) and population size, which conservation managers aim to influence.

Madsen's (1998a,b) 12-year study of hunting in two Danish wetlands partly addressed the long-term consequences of disturbance. By combining studies of bird numbers and distribution with experimental manipulation, he showed that refuges from hunting increased

species diversity and bird density. However, it was not clear whether this local increase in numbers meant that the total population had also increased, and in many situations a study of such scope and longevity is not practical.

Gill et al. (1996) proposed a more rapidly conducted way of assessing the impacts of disturbance. They used the trade-off between resource-use and risk of disturbance to measure the extent to which disturbance caused an under-use of resources. However, this approach does not enable the effect of disturbance on bird fitness and population size to be predicted. In addition, Gill et al. noted that a change in local circumstances, such as an increase in population size at the site, could change the birds' tolerance to disturbance, making prediction to new circumstances unreliable. An example is Owens' (1977) study of brent geese (*Branta bernicla bernicla*) in which birds avoided disturbed areas early in the winter but exploited them later after resources elsewhere had become depleted.

Owens' finding suggests that the impact of disturbance on birds may be inversely related to their density. As bird numbers increase and intraspecific competition for food intensifies, tolerance to disturbance may increase as undisturbed resources are depleted more rapidly or

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made less profitable by interference competition. Without including such density-dependent effects, one cannot confidently predict the effects of disturbance on the birds. Birds displaced by disturbance will move to other feeding areas, thus intensifying density-dependent processes, such as competition for food and risk of infection by parasites, which will also affect undisturbed birds. It has been suggested that the role of density dependence may be particularly important in understanding the impacts of local disturbance at larger spatial scales (Hill et al., 1997).

Even at a local level, interpretation of disturbance-related changes in behaviour can be difficult. For example, the distance at which birds fly off when approached has been used as a measure of sensitivity to disturbance. It is usually assumed that birds that do not fly away until an approaching person is close to them are the least sensitive to disturbance (e.g. Burger, 1981), but the opposite might be true (Ward, 1990; Hill et al., 1997; Gill et al., 2001). Birds that allow people to approach closely might be reluctant to leave a food source because they are having difficulty meeting their energy requirements and are less able to compensate for the costs of flying away. In contrast, birds that flush easily might be those that are most able to compensate for disturbance and, in terms of survival, are least affected by it. This ambiguity involved in interpreting behavioural responses means that another approach is needed to evaluate the fitness consequences of disturbance (Goss-Custard et al., 1995).

One such approach is to regard disturbance as comparable in its effects to those arising from habitat loss, a common conservation issue addressed by empirical and theoretical studies (e.g. Dolman and Sutherland, 1995; Goss-Custard et al., 1995). Both disturbance and habitat loss can displace birds to other feeding areas, thus leading to an increase in bird density in those areas. In some circumstances, this approach may work. Lower levels of disturbance tend to be due to static factors (e.g. industrial development), to which birds tend to habituate (Hockin et al., 1992). Those birds that do not habituate leave the area permanently, in which case the effects of disturbance are indeed equivalent to habitat loss. However, when disturbance is neither static nor continuous, the habitat-loss analogy no longer applies and different factors must be considered: (1) temporarily displaced birds incur the costs of lost foraging time and additional energy expenditure; (2) the severity and duration of the disturbance may be variable and unpredictable; and (3) disturbed birds may be able to compensate by feeding for longer when disturbance is absent, or on other prey types outside normal feeding times.

There will be a point, however, at which the costs of disturbance are too great to be offset by supplementary feeding (Hill et al., 1997), whereupon local and national populations may decrease as survival rates decline.

There is a need to devise ways to evaluate and predict the overall impacts of disturbance on individual fitness and population size, taking into account its time and energy costs and the compensatory responses of the birds. Here, we show how a behaviour-based individuals model is able to quantify the potential impacts of various sporadic disturbances on individual survival and long-term population-size in an overwintering wading bird, the oystercatcher (*Haematopus ostralegus*). We also demonstrate how the model can be used both to explore whether current levels of disturbance affect bird fitness and population size, and to evaluate alternative policy options for managing the disturbance on an estuary.

2. Methods

2.1. The model

Simulations were run using a slightly modified version of a model of oystercatchers eating bivalve molluscs and earthworms (Lumbricidae) on the Exe estuary (Stillman et al., 2000). The Exe is a relatively small estuary in SW England on which oystercatchers from several breeding populations further north in Britain and Europe spend the winter. The main food supply for most of the oystercatchers that overwinter in the Exe comprises 10 intertidal beds of edible mussel (*Mytilus edulis*). Some birds supplement their intake by feeding on *Scrobicularia plana* (da Costa) and *Cerastoderma edule* (L.) at higher levels of the shore when the mussel beds are submerged, and on earthworms in nearby pastures at high tide. The area around the Exe is heavily populated and most of the estuary is easily accessible, so it is well-used by walkers, bait collectors, shellfishers and people in boats.

The model predicts where birds will feed and what their intake rates will be using game theory and foraging theory, which are thought to provide a reliable basis for prediction (Goss-Custard and Sutherland, 1997). The decision principles on which the behavioural responses of model birds are based, such as maximization of intake rate are unlikely to be affected by disturbance, even if the particular choices made by individuals do change. Model birds are therefore believed likely to respond to disturbance in the same way as real birds. Individuals in the model differ in their foraging efficiency and social dominance, which, in turn, determines by how much interference competition reduces their intake rate. The model includes four tidal stages of different duration, each of which represents a discrete 'time-step' within the model; high tide, receding tide, low tide, and advancing tide. The four tidal stages last a total of 12.44 model 'hours'. The model follows the location, foraging behaviour and body condition of

each individual at each stage of each tidal cycle from 1 September, by which time most adults have returned to the estuary from the breeding grounds, to 15 March, by when most adults have left for the breeding grounds. Individuals decide what prey to take, where, and at what stages of the tide to forage in order to maximise their intake rate, taking into account the quality of each feeding area ('patch') available at a given tidal stage, their own feeding efficiency and the location and dominance of all other individuals. Once an individual has acquired its immediate needs, it stores any extra food consumed as body reserves, which can be drawn on if it ever fails to obtain its daily requirements from foraging. The maximum amount of body reserves an individual can carry is limited by a target weight, derived from weights of oystercatchers ringed on the Exe, which varies through the course of the winter. If an individual uses up all its body reserves, it dies from starvation.

The model includes some real biological details, such as temperature-related energy requirements, prey-assimilation efficiency, prey energy density and night feeding efficiency, which are important for accurate prediction (Stillman et al., 2000). There are 12 separate feeding patches in the model. The main feeding habitat in the model is the 10 mussel beds, which are only accessible to birds during the 'low tide' tidal stage. In reality, mussel beds vary in quality as feeding areas owing to differences in mussel flesh-content, size and density; the model simulates this variation. The model also takes account of the supplementary bivalve resources and earthworms in the adjoining pastures where availability is temperature-related. Parameter values used in the model are detailed in the Appendix of Stillman et al. (2000).

At the start of each tidal stage, the model determines the ideal feeding location for each bird in random order, taking into account the quality of each exposed patch and the social dominance of other birds already placed on those patches. The birds then 'feed' for the duration of that tidal stage on their chosen patch.

The model has been used to predict the density-dependent mortality and survival arising from habitat loss and shellfishing (Goss-Custard et al., 2000; Stillman et al., 2001). Disturbance from a mobile source, such as a walker or bait-digger ('disturber'), has some of the same effects as collecting shellfish by hand. Important differences are that shellfish are not removed during disturbance, and that shellfish collection is more likely than other types of disturbance to be concentrated on areas of high mussel quality, which are also preferred by oystercatchers.

2.2. Including costs of disturbance

In the model, disturbance first affects birds by preventing them from feeding within a circular area of specified radius around the disturber (the 'disturbance area'), thus temporarily reducing the area of the disturbed patch accessible to birds. This potentially increases bird density and consequently interference competition on the remaining part of that patch and elsewhere. This effect was included here using values of the disturbance radius measured on the Exe by Stillman et al. (2001). Having been disturbed, oystercatchers fly some distance before settling and then rest for a time before resuming feeding. The times spent in flight and in resting before resuming feeding (the 'time costs') were values recorded for oystercatchers by Triplet et al. (1999) on the baie de Somme, France; these are very similar to unpublished values from the Exe (R. A. Stillman, unpublished information). Typically, birds spent 1 min in flight after being disturbed and did not resume feeding until 30 min after the disturbance had occurred. While flying, a bird incurred an additional energy cost of 1 kJ, equivalent to the energy expended in flying for 1 min (Zwarts et al., 1996). Disturbance costs were applied to individual birds for the tidal-stage in which the disturbance occurred. The model was designed to simulate birds being disturbed at their preferred feeding patch, thus incurring costs and possibly having to move to an undisturbed patch. At each tidal stage, the model distributed birds without accounting for potential costs and reduction in available patch area caused by any disturbance. Next, the model redistributed the birds, this time taking into account which patches were disturbed and thus had less than their full area available for feeding. After this, birds fed on the patch they finally occupied for the whole tidal stage. Disturbed birds lost 30 min feeding time and incurred an energetic cost of 1 kJ. Thus, only individuals that would otherwise have visited the disturbed patches suffered direct costs, although some or all undisturbed individuals may have been penalised indirectly through an increase in bird density on undisturbed patches.

2.3. The scenarios

Simulations were run to explore the effects of different types and intensities of disturbance and the mitigating effects of some regulations that might be placed on people to reduce disturbance. Disturbance was confined to mussel beds, the main feeding areas. The upshore feeding area and the meadow were left undisturbed. Disturbers were distributed over the mussel beds at random, avoiding each other where possible to ensure disturbance areas did not overlap. Simulations were run with either 10 or 50% of the total area of mussels disturbed. The model was run for each of these two conditions and with two types of disturbance, 'major' and 'minor' disturbers, as described in Table 1. A person walking across a mussel bed would be a major disturber and affect birds at 100 m distance. Minor disturbers

Table 1
Types of mobile, unpredictable human disturbance occurring commonly on estuaries

Type	Characteristics	Examples
Major	Disturbs a relatively large area Moves frequently and/or rapidly	Walker on feeding grounds Dog on or near feeding grounds Boating near feeding grounds
Minor	Disturbs a smaller area Moves frequently and/or rapidly	Amateur bait digger Walker near feeding grounds Crab collector

represented people moving around or near to mussel beds. To reflect this in the model, the area affected by a minor disturber was 10% of that affected by a major disturber. This meant that, for example, 10% of the estuary could be disturbed and denied to the birds either by two major disturbers or by 20 minor disturbers. The comparator habitat-loss simulations were run with 10 and 50% of average-quality habitat permanently removed.

Initially, disturbance was applied over every low tide, day and night, throughout the whole simulation period. This is an extreme condition as, in reality, disturbance is uncommon on the Exe at night and at neap tides (Goss-Custard and Verboven, 1993). Different restrictions were then imposed on disturbers. Disturbance was prevented at night, during neap tides and then during the second part of the winter, from 1 December, when declining temperature and declining food quality combine to make survival more difficult for oystercatchers (Goss-Custard et al., 1996). These restrictions were first imposed separately, then all together.

2.4. Output measures

The impact of disturbance was measured both as the number of birds surviving and as the percentage starving over a single winter at different population sizes. In addition, the effect of a predicted increase in winter mortality on the equilibrium population size (EPS) in the long-term was also explored. The number of survivors and mortality rate were obtained over a range of initial autumn population sizes because the effect of disturbance was expected to increase as population density, and thus competition for food, intensified. The resulting density-dependent functions for the number of survivors enable us to explore the effect of disturbance on the carrying capacity in this system (Goss-Custard et al., in press). The density-dependent mortality functions show the effects of disturbance on the probability that an average individual will die, one component of fitness. The effects on EPS were calculated because, in long-lived birds, population size is very sensitive to changes in the average mortality rate (Goss-Custard, 1981), even though density-dependent summer reproduction com-

pensates somewhat for decreased per capita survival rates in winter (Goss-Custard and Durell, 1990). The effect of disturbance on EPS was calculated using a demographic model described by Goss-Custard et al. (1995), which includes density-dependence in the reproductive rate. The density-dependent mortality function for disturbance of a given intensity was inserted into this model and the effects over 200 years were calculated. The initial autumn population size in these simulations was 1500 birds, similar to the average numbers occurring on the mussel beds of the Exe during much of the study period.

2.5. Sensitivity analysis

To test the sensitivity of the model to the values of the time and energy costs of disturbance, simulations were re-run with costs halved and with costs doubled. The range of time costs covered by this, from 15 min to 60 min, was similar to that observed by Triplet et al. (1999). Time and energy costs were varied together. In these simulations, 10 and 50% of the estuary was affected by minor disturbers at two initial bird population sizes of 1500 and 7500 birds.

3. Results

3.1. Continuous disturbance and survival

Continuous disturbance throughout every low water period of the simulation period had very little effect on the number of birds surviving the winter at autumn population sizes below the range recorded on the estuary over recent years (Fig. 1), regardless of the type and extent of the disturbance. At greater population sizes, disturbing 10% of the total feeding area had less effect than disturbing 50%. However, the way in which disturbance occurred had a big influence. Minor disturbers reduced the number of survivors more than major disturbers, although both disturbed the same total area.

If only 10% of the estuary was disturbed, there was a marked effect on the number of survivors with minor disturbers (Fig. 1(a)), but little effect in the case of
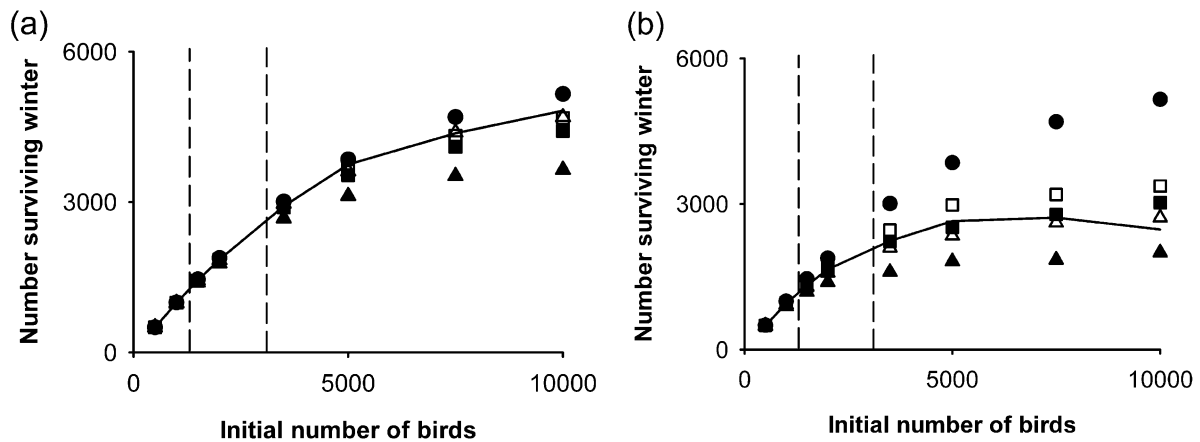
Fig. 1. Density-dependent survivorship function with (a) 10% or (b) 50% of the total mussel area continuously disturbed or removed; (filled circles) no disturbance or habitat removal; (filled squares) major disturbers with costs; (open squares) major disturbers without costs; (filled triangles) minor disturbers with costs; (open triangles) minor disturbers without costs; (solid line) average-quality habitat removed. Dotted lines show the range of bird numbers seen on the Exe in recent years.

major disturbers. Even with minor disturbers, the numbers of birds surviving were similar to the numbers surviving in simulations with no disturbance if time and energy costs were omitted. In simulations that included costs, however, fewer birds survived. This effect was most apparent with minor disturbers, which inflicted the costs over a greater number of mussel beds, but did not disturb a greater overall area.

With 50% of the estuary disturbed, the pattern was different (Fig. 1(b)). The number of birds surviving was substantially lower with disturbance than without it. Even when birds incurred no costs, just preventing access to half the total feeding area at any one time was enough to cause many fewer birds to survive the winter. Including the cost of disturbance decreased the numbers surviving even further. However, it is clear that with a large area disturbed it was the reduction in available feeding area, and not the time and energy costs, that was the more damaging element of disturbance.

3.2. Continuous disturbance, mortality rate and equilibrium population size

The most obvious effects of disturbance on the numbers of birds surviving the winter were at large population sizes, which are unlikely to be seen normally on the Exe (Goss-Custard et al., 1997). Over the present-day range of population sizes, the effect appeared to be rather small (Fig. 1). However, with the results expressed as the mortality rate, disturbance had a much more noticeable effect, even at present-day population sizes (Fig. 2); a decrease in survival rate from 98 to 96% may appear small, but actually represents a doubling in mortality rate, from 2 to 4%. Calculating the long-term cumulative effect of the predicted increases in mortality rate on the equilibrium population size (EPS) showed that major disturbers on 10% of the estuary would

cause only a 2% reduction in the present-day EPS of 1500 birds, whereas minor disturbers would reduce EPS by 8% (Table 2). With 50% of the estuary disturbed, both types of disturber would have a substantially larger effect on EPS (Table 2).

3.3. Comparison of continuous disturbance and habitat removal

The possibility that continuous disturbance of a fixed proportion of the birds' feeding area might be equivalent to the permanent removal of habitat is also explored in Figs. 1 and 2. With 10% of the estuary disturbed or permanently removed, and with no disturbance costs incurred by the birds, the numbers (Fig. 1) and percentage of birds dying (Fig. 2) from disturbance and habitat removal were indeed approximately the same. However, when costs were included and when the population was large, disturbance caused a greater percentage of birds to starve than did habitat loss. This indicates that, when a small area is affected by disturbance, costs are an important factor, causing substantially higher mortality than is caused by losing the equivalent amount of feeding area through habitat removal.

With 50% of the estuary affected and disturbance costs included, minor disturbers again had a greater effect than habitat removal. At this level of disturbance, major disturbers caused approximately the same amount of mortality as habitat removal when costs were included, but were less damaging without costs.

3.4. Regulating disturbance

Fig. 3 shows the predicted mortality rate at an initial autumn population size of 1500 birds when various hypothetical regulations were applied to restrict dis-
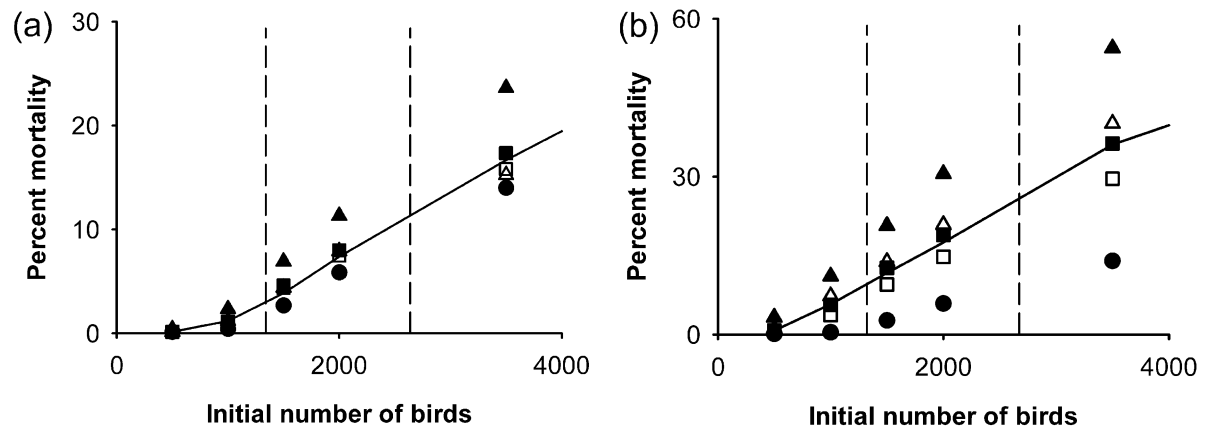
Fig. 2. The density-dependent mortality function over the range of birds found on the Exe, with (a) 10% or (b) 50% of total mussel area continuously disturbed or removed; (filled circles) no disturbance or habitat removal; (filled squares) major disturbers with costs; (open squares) major disturbers without costs; (filled triangles) minor disturbers with costs; (open triangles) minor disturbers without costs; (solid line) average-quality habitat removed. Dotted lines show the range of bird numbers seen on the Exe in recent years.

Table 2
Percentage change from an undisturbed Exe estuary equilibrium population size (EPS) of 1500 oystercatchers arising from different amounts and kinds of disturbance

Type of disturber	% Estuary disturbed	% Change in EPS due to disturbance
None	0	0
Major	10	−2.1
Minor	10	−7.7
Major	50	−24.7
Minor	50	−39.0

turbance. Restrictions were first applied separately, then all three were applied together. Although the magnitude of the effect depended on the type of disturber and the area disturbed, the pattern was always the same.

All three restrictions caused a noticeable drop in the level of mortality caused by disturbance. Preventing disturbance during neap tides was the least effective restriction, but still reduced mortality substantially. The most effective restriction was to ban disturbance during the second half of winter. This was almost as effective as introducing all three restrictions together, and reduced mortality to levels only slightly above that predicted when there was no disturbance at all.

3.5. Sensitivity analysis

Predicted mortality increased linearly with increasing costs over the range examined in all the scenarios tested (Fig. 4). With 10% of the estuary disturbed, introducing disturbance with no costs increased mortality by only a small amount. But when costs were included and increased to double the observed values, mortality increased by more than threefold at initial autumn population sizes of both 1500 and 7500 birds (Fig. 4(a)). With 50% of the estuary disturbed, introducing disturbance with no costs caused a large increase in mortality, especially at a population size of 7500 birds (Fig. 4(b)). Adding increasingly large costs caused a further increase in mortality of up to 10% at both bird population sizes.

4. Discussion

4.1. Effects of different kinds of disturbance and of habitat removal

The model's predictions for the effect of disturbance on mortality rate cannot yet be tested directly because no field estimates of an increase in mortality due to disturbance have been made in any wintering oystercatcher population. However, the model's predictions for the winter mortality rate without disturbance have been tested successfully for mussel-feeding oystercatchers on the Exe estuary (Stillman et al., 2000). The model was calibrated using data from the early years of the study and then used to predict mortality rates for subsequent years when the amount of prey and the number of birds using the estuary were different. During those years there was an increase in bird numbers and a corresponding density-dependent increase in mortality. Although no data from observations at the higher population sizes were used in its development, the model correctly predicted the observed increases in mortality rate. This suggests that the model reasonably captures the main processes and parameter values that determine mortality rates in this system. Its ability to predict to circumstances outside the range with which it was developed suggests that it may provide a sound base for exploring the effects of disturbance in this system.

We have considered mobile, unpredictable disturbances whose consequences for bird survival have previously been impossible to predict, and to which birds are least likely to habituate (Hockin et al., 1992). Comparing the effects on survival rates of disturbance without costs with those of the permanent removal of an equivalent area of habitat show that, when the area affected was small, the consequences for survival were similar. However, when a larger area was disturbed, habitat removal had a larger effect than cost-free disturbance because habitat removal reduced the overall amount of food, whereas disturbance only made some
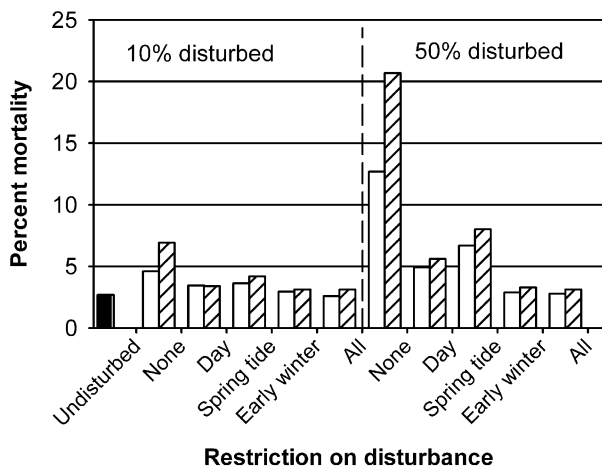

Fig. 3. The percentage of an initial autumn population of 1500 oystercatchers that die from starvation over the winter in relation to the restrictions imposed on disturbance from people. 'Day' = disturbance only allowed during the day and not at night; 'Spring tide' = disturbance only allowed on spring tides; 'Early winter' = disturbance only allowed before 1 December. 'All' = disturbance only allowed during daylight on spring tides before 1 December. Solid bar = no disturbance, white bar = major disturbers, hatched bar = minor disturbers.

fraction of it unavailable at any one time. The amount of food remaining at the end of winter would therefore have been greater when habitat was disturbed than when it was removed.

Including the time and energy costs of disturbance into the model had a major effect on the comparison between the effects of habitat removal and disturbance, even though the costs used in these simulations were not large (30 min of lost feeding time and an extra energy expenditure equivalent to 1 min of flying). Even at relatively low levels, disturbance with costs increased the mortality rate by more than permanent habitat removal. The time and energy costs arising from disturbance reduced survival rates even when a large proportion of the estuary remained undisturbed. At a higher level of disturbance, the importance of costs varied according to how the disturbances were distributed in space. With numerous minor disturbers, including costs caused disturbance to have a greater effect than habitat removal: when there were fewer, major disturbers, the costs of disturbance were offset by the benefit of having a greater overall prey resource. Accordingly, the effect of disturbance was less than that of permanent habitat removal.

The simulations showed clearly that there was a difference between the impact of minor and major disturbers. Although potentially preventing access to the same area of resources, numerous minor disturbers had a greater detrimental effect than a few major ones on annual mortality and therefore equilibrium population size. This arose because minor disturbers spread out over a greater number of patches. When costs were incurred by disturbed birds, more birds therefore suffered these direct costs of disturbance. Even when there were no disturbance costs, minor disturbers had a greater effect on population size than major ones. With
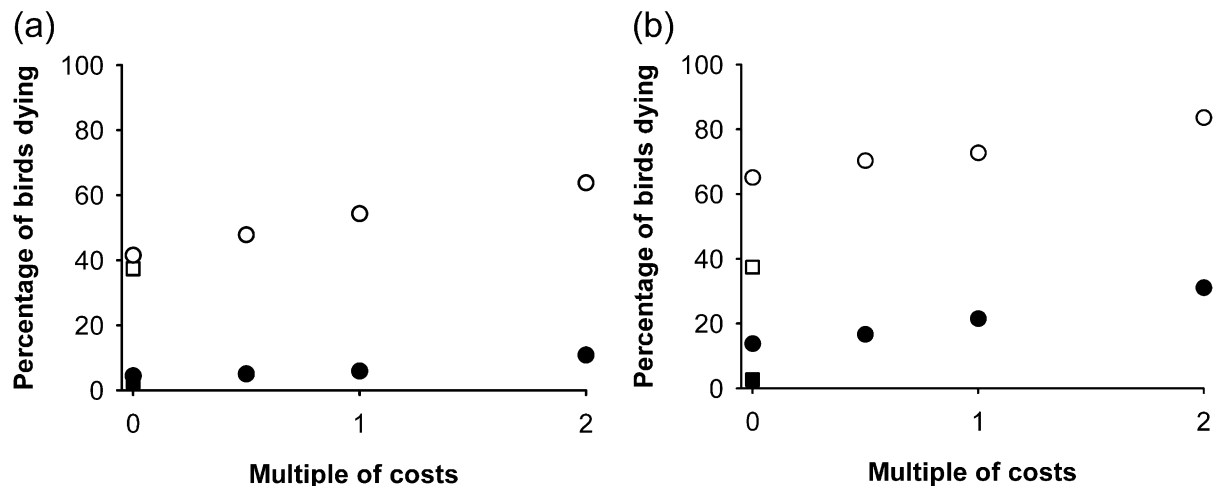

Fig. 4. The effect on the overwinter mortality rate of changing disturbance costs with (a) 10% or (b) 50% of the estuary disturbed by minor disturbers for 1500 (filled circles) and 7500 (open circles) birds. The mortality rates with no disturbance (squares) are included for comparison. 1 = values used in the normal simulations; i.e. a time cost of 30 min/tide and an energy cost of 1 kJ/tide. 2 = twice the normal values; i.e. a time cost of 60 min/tide and an energy cost of 2 kJ.

numerous minor disturbers and no costs, most birds still suffered the indirect consequences of disturbance through increased competitor density in undisturbed feeding areas. Major disturbers occupied fewer patches, so more birds escaped the indirect consequences, especially when the major disturbers happened to be on less preferred patches. This has potentially important implications for the management of disturbance; a large, noisy disturbance (e.g. water-skiing) in one part of an estuary might appear very damaging as it disturbs birds over a large area, yet people walking quietly across the feeding areas in several places may have a much greater effect. Similarly, a group of bait-diggers could cause less disturbance than the same number of individuals spread throughout an estuary.

The results show that, when the population size and intensity of disturbance are sufficiently high, disturbance can increase mortality rate, and thus reduce equilibrium population size. It has this effect because it increases interference competition and energy requirements while reducing the time available for foraging. However, the results also show that disturbance on the Exe at present is most unlikely to increase mortality rate above the normal level. Most disturbance is actually caused by single individuals walking over low tide on between two and four mussel beds during daytime on spring tides (Goss-Custard and Verboven, 1993; Goss-Custard et al., 1997). This approximates the simulations with 10% of the feeding area disturbed by major disturbers on spring tides in daylight, which showed no increase in the mortality rate. We conclude that, although disturbance can increase mortality rate, it does not do so at the levels of disturbance that have occurred in recent years on the mussel beds of the Exe estuary.

4.2. Effects of regulating and restricting the frequency of disturbance

The simulations in which disturbance was restricted to daytime, spring tides or early winter, showed how this type of model can be used to evaluate the efficacy of different estuary-management policies. Preventing access by people during darkness reduced the impact of disturbance because oystercatchers can compensate for daytime disturbance by feeding at night. In species which cannot feed at night this restriction would have no effect but, conversely, it would be much more important in primarily night-feeding species. Where disturbance does occur at night, perhaps from shooting or illegal shellfishing, restricting access could therefore be an effective management tool. In the model simulations, restricting disturbance to spring tides was a less effective mitigation, possibly because birds could incur disturbance costs over 2-week periods before they were able to feed free from disturbance. Preventing disturbance in late winter proved very effective, almost

entirely eliminating the predicted population consequences. Birds could compensate for disturbance early in winter when feeding conditions were good and energy requirements low, but not at the end when conditions were harder.

4.3. Model sensitivity

The model's predictions were sensitive to the values of time and energy costs of disturbance, except when the population size was large and a large amount of the estuary was disturbed. The extra energy cost caused by disturbance in these simulations was very small compared to the birds' overall daily energy requirement; 1 min of flying uses energy equivalent to 0.3% of total daily requirement. It is therefore very likely that the time costs, which represented up to 8% of the total feeding time available on the mussel beds, were the main cause of the increased mortality.

Triplet et al. (1999) observed that the time oystercatchers took to resume feeding after a disturbance declined during the course of winter, from 60 min at the start of winter to 20 min at the end. They considered that this was more likely to be a response to worsening climatic conditions than to be a habituation to disturbance. The sensitivity analysis showed that additional mortality was predicted to occur with a time cost as low as 15 min per tide, applied throughout winter. This suggests that, even if birds on the Exe habituated to unpredictable disturbance or modified their response to it during cold weather, they would be unable entirely to compensate for the costs of disturbance.

4.4. Model applications

Although developed and tested for one wader species on one estuary, the model was designed to be easy to apply to other estuaries, species and scenarios. Indeed, the model used in this paper is currently being applied to oystercatchers feeding on a range of prey on estuaries in England, Wales, Northern Ireland and France. Research in progress should soon enable the model to be applied to a wide range of other wader species and wildfowl. Much of the basic information required to parameterise the model, such as the functional responses, the likelihood of interference occurring and bird energy expenditure, can be obtained from the literature. The site-specific data required would in many cases already be monitored, e.g. prey abundance in areas of conservation importance, or would be easily available, e.g. weather. Other parameters, such as patch exposure times and the availability of alternative sources of food, can be obtained with minimal fieldwork or local knowledge. The parameters required to include disturbance are (1) the frequency of disturbance, (2) the distance at which birds respond to a disturbance, (3) the time taken

to resume feeding after a disturbance, which is readily observable, and (4) the time required to fly to, and therefore energetic cost of moving to, an undisturbed area, which can be calculated from literature values of flight costs (Tucker, 1971; Flint and Nagy, 1984; Nudds and Bryant, 2000). Because they utilise the results of research carried out over many years, models of this kind can be applied to new species and systems within the time scale of most environmental impact assessments, as their application to the European populations of two species of geese has recently demonstrated (Pettifor et al., 2000).

The model can be used to predict a much wider range of disturbance scenarios than have been examined here. For example, disturbance can be restricted to certain areas within an estuary; it can be greater on some days of the week than others; it can also incorporate several different types of disturbance occurring at the same time. Properly parameterised, this model's predictions can provide answers to what is often an important question for estuary managers—how will a change in policy affect bird survival and population size? We support the conclusion of Hill et al. (1997) that this type of model can be used to explore how disturbance might best be managed, spatially and temporally, and thereby reduce its consequences for birds where birds and human activities must co-exist.

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