

# Predicting wader mortality and body condition from optimal foraging behaviour

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In order to assess the future impact of environmental change, ecologists must be able to provide accurate predictions under new environmental conditions. The difficulty with this is that there is often no way of knowing whether the empirical relationships upon which model predictions are based will hold under the new conditions. As a consequence, such predictions are of uncertain accuracy.

Behaviour-based models have been developed in an attempt to overcome this problem. These predict how individual animals will alter their behaviour in order to respond to future environmental change. Their central assumption is that, no matter how much the environment changes, each individual will behave in a manner that maximises its own fitness. Because of this, model animals are expected to respond to environmental change in the same way as real animals. By following the behaviour and ultimate fate of each individual, a behaviour-based model is able to predict the population consequences of the optimal decisions of individuals. These models should therefore provide a reliable means of predicting how animal populations will be influenced by environmental change.

Behaviour-based models contain more parameters than traditional demographic models, but this does not mean that they will take any longer to parameterise and adapt to a particular situation. In fact they can often be developed much more quickly.

I describe how behaviour-based models have been developed for non-breeding wader populations and how they have been used to predict the consequence of environmental change in terms of the mortality rate and body condition of waders.

## INTRODUCTION

Many human activities affect or destroy the habitats used by wader populations (e.g. agricultural intensification, industrial development, land-claim, resource harvesting, recreation, salt production). Their coastal habitats may also be particularly vulnerable to sea level rise caused by climate change. Decisions are often required on how best to maintain these populations and to reconcile their protection with economic and other activities. To do this, policy makers need to know how bird populations will respond to environmental change, ideally before it happens. The difficulty with predicting the consequences of new circumstances is that there is often no way of knowing whether the empirical relationships upon which models are based, typically measured over a relatively narrow range of population sizes or environmental conditions, will hold under the new conditions for which predictions are required.

Environmental change at a non-breeding site can affect wader population size by changing (i) the size of the fat reserve needed for successful migration and breeding and (ii) the risk of starvation during the non-breeding season. If an environmental change is not predicted to affect present-day rates of fat storage or survival, there would be no reason to be concerned for the birds (Goss-Custard *et al.* 2002). If, on the other hand, fat storage and survival were predicted to decline, population size would be expected to decrease, by

an amount that depends on the strength of any compensatory density-dependent reproduction on the breeding grounds (Goss-Custard & Durell 1990) and the presence of alternative wintering or passage sites (Pettifor *et al.* 2000a).

Behaviour-based models are useful tools for predicting the influence of environmental change and different policy options on the survival and body condition of waders (Goss-Custard *et al.* 1995a,b, Stillman *et al.* 2000a, 2001). They predict population level changes, such as mortality rate, from the combined behavioural responses of the individual animals within the population. They predict the changed intake rates of birds forced by environmental change to alter their diet and/or to redistribute themselves over resource patches of varying quality (Goss-Custard *et al.* 2000). They do this by using foraging theory and game theory, which are thought to provide a reliable basis for prediction (Goss-Custard 1996, Sutherland 1996, Goss-Custard & Sutherland 1997).

Behaviour-based models have one particular advantage over traditional demographic models; they should produce more accurate predictions outside the range of conditions for which they are parameterised. The empirical relationships from which demographic models derive their predictions may or may not change as the environment does, but there is no way of knowing this in advance. In contrast, the basis of predictions of behaviour-based models – fitness maximization – does not change, no matter how much the environment changes (Goss-Custard 1996, Sutherland 1996, Goss-



Custard & Sutherland 1997). Animals in behaviour-based models are likely, therefore, to respond to environmental change in the same way that real ones would.

The simplest behaviour-based models are the spatial depletion models, originally developed by Sutherland & Anderson (1993), and recently applied to waders (e.g. Gill *et al.* 2001). These models assume that all individuals within a population are identical (i.e. when feeding in the same place, they all consume prey at the same rate), that individuals do not store fat reserves and that interference (the short-term, reversible decline in intake rate due to the presence of competitors (Goss-Custard 1980)) is absent. They predict the manner in which an animal population spreads out between patches as successive ones are depleted. Spatial depletion models are not used to predict mortality rate or body condition. This is because, as they assume that all individuals are identical, they either predict that all will die or all survive. They cannot predict body condition because they do not incorporate fat reserves. Instead of mortality or body condition, they predict the maximum number of bird-days that can be supported by a habitat. However, many, inefficient or subdominant birds may die before the maximum bird-days carrying capacity is reached (Goss-Custard *et al.* 2001, 2002, Goss-Custard, this volume). This will happen if individual variation in survival occurs either through variation in foraging ability or susceptibility to interference (Goss-Custard *et al.* 2001).

In this paper, I describe a behaviour-based model that incorporates fat reserves, individual variation and interference. It is therefore able to predict mortality rate and body condition, and be applied to systems in which interference is important, as well as those in which it is not. I describe how this model has been parameterised for different systems and used to predict the consequences of environmental change for the mortality rate and body condition of non-breeding wader populations on a range of sites.

## THE MODEL

The model is individuals-based and tracks the foraging location, body condition and ultimate fate of each individual within the population. During each day, each bird in the population must consume enough food to meet its energy demands. It attempts to do this by feeding in those locations and at those times of the day where and when its intake rate is maximised. Although all individuals decide on the same principle, intake rate maximization, the actual decisions made by each differ. Their individual choices depend on their particular competitive ability, which depends on two characteristics. Interference-free intake rate is the rate at which an individual feeds in the absence of competition and measures its basic foraging efficiency. Susceptibility to interference measures how much interference from competitors reduces its intake rate as bird density rises. Survival is determined by the balance between an individual's daily rates of energy expenditure and consumption. Energy expenditure depends on metabolic costs plus any cost of thermoregulation at low temperatures. Energy consumption depends both on the time available for feeding and intake rate while feeding. When daily energy consumption exceeds daily expenditure, individuals accumulate energy reserves or maintain them if a maximum level has already been reached. When daily requirements exceed daily consumption, individuals draw on their reserves. If reserves fall to zero, an individual

starves, the only source of mortality in the model. Stillman *et al.* (2000a, 2001) describe the model in detail and Stillman *et al.* (2000a) perform a sensitivity analysis of the model.

## TESTING THE MODEL

The model was originally developed for Eurasian oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis* in the Exe estuary, UK, and has been most thoroughly tested for this system (Stillman *et al.* 2000a, 2001). The model was developed by comparing its predicted mortality rate with the observed rate on the Exe estuary during 1976–81. As a test of the model, its predicted mortality rate was compared with the observed rates during 1981–91, a period when the oystercatcher population increased and there was a density-dependent increase in the mortality rate. The model successfully predicted this increase, even though it was only developed to predict the mortality rate when the population size was considerably lower (Stillman *et al.* 2000a). Furthermore, the underlying behaviour of the birds, such as the amount of time spent feeding on mussels and their impact on them, the distribution of birds throughout the estuary and the changes in body mass through the season (Stillman *et al.* 2000a). This demonstrated the potential of this model in particular, and behaviour-based models in general, to predict with accuracy to new circumstances outside the range of conditions for which they were parameterised.

## PARAMETERISING THE MODEL

Although the model was developed as part of a long-term field study, only a small fraction of the data collected during that study was used to parameterise the model. The model is being applied to a range of wader conflicts, and has been parameterised for a range of sites and species (Table 1). Usually it can be applied to a new site in less than a year because general relationships can be used to predict the behaviour of birds at the site. What needs to be measured at a new site is the abundance of food and its distribution throughout the site and exposure through the tidal cycle. Food abundance and distribution can be measured from a survey of the site at the start of the non-breeding season. Changes in the abundance of food through that season can be measured by repeated surveys on a reduced scale. The exposure of food through the tidal cycle can be derived from local knowledge or new measurements, or predicted through the use of tidal models.

The foraging behaviour of waders does not need to be measured directly, but instead can be predicted from general relationships derived from a wide range of species and sites. The size ranges of prey consumed have been derived from a literature review (J.D. Goss-Custard, unpublished data). The interference-free food intake rate (*IFIR*) of each species can be calculated from the following functional response.

$$IFIR = \frac{IFIR_{max} B}{B_{50} + B} \quad (\text{eqn 1})$$

where  $B$  = biomass density of prey within the size range consumed,  $IFIR_{max}$  = maximum intake rate when prey are superabundant and  $B_{50}$  = prey biomass density at which intake rate is 50% of its maximum. The value of  $IFIR_{max}$  can be calculated from body and prey mass using the following equation.



**Table 1.** Systems and environmental issues to which the behaviour-based model has been, or is being (\*) applied.

Site	Wader species	Prey species	Issue	References
Bahia de Cadiz, Spain	dunlin, curlew sandpiper, redshank, black-winged stilt, avocet, curlew	polychaetes, bivalves, <i>Hydrobia</i> spp.	disturbance, shellfishing habitat loss	*
Baie de Seine, France	dunlin, oystercatcher, curlew	polychaetes, cockles <i>Cerastoderma edule</i>	habitat loss and creation	Durell <i>et al.</i> in press
Baie de Somme, France	dunlin, oystercatcher, curlew	polychaetes, cockles, <i>Hydrobia</i> spp., <i>Corophium</i> spp.	hunting, disturbance, shellfishing	*
Burry Inlet, UK	oystercatcher	Cockles, mussels <i>Mytilus edulis</i>	shellfishing	West <i>et al.</i> 2003
Exe estuary, UK	oystercatcher, dunlin, redshank, black-tailed godwit, curlew	polychaetes, cockles, mussels, scrobicularia	disturbance, shellfishing	Stillman <i>et al.</i> 2000a, 2001; West <i>et al.</i> 2002a Stillman <i>et al.</i> (submitted)
Humber estuary, UK	dunlin, ringed plover, knot, redshank, grey plover, black-tailed godwit, bar-tailed godwit, oystercatcher, curlew	oligochaetes, polychaetes, cockles, <i>Macoma balthica</i> , <i>Hydrobia</i> spp., <i>Corophium</i> spp.	habitat loss, sea level rise	*
Menai Straights, UK	oystercatcher	mussels	shellfishing	*
Strangford Lough, UK	oystercatcher	cockles	shellfishing	West <i>et al.</i> 2002b
The Wash, UK	oystercatcher	cockles, mussels	shellfishing	*

$$\log_{10}(IFIR_{\max}) = a + b \log_{10}(M_{\text{spec}}) + c \log_{10}(M_{\text{prey}})$$

(eqn 2)

where  $M_{\text{spec}}$  = average body mass of the bird species and  $M_{\text{prey}}$  = mean ash-free dry mass of prey within the size range. The values of  $B_{50}$ ,  $a$ ,  $b$  and  $c$  have been calculated from a review of a wide range of wader-prey systems (J.D. Goss-Custard, unpublished data).

The strength of interference competition within each species can be predicted from previous studies of a range species, the predictions of an interference model (Stillman *et al.* 1997, 2002), the foraging behaviour of individual species and the mobility and predator escape responses of different prey. Interference is assumed to be absent in species consuming very small, non-mobile prey (e.g. *Hydrobia* spp.). This is because these can be consumed quickly (<5–10s), minimising interference through prey stealing (Stillman *et al.* 1997), and cannot escape, eliminating interference through prey depression, which happens when prey can rapidly move into a protective burrow or shell when they detect a predator. (Yates *et al.* 2000, Stillman *et al.* 2000b). Interference in a species consuming small, mobile prey (e.g. Polychaetes and *Corophium* spp.) is assumed to occur through prey depression, as these prey can escape when they detect a predator. The strength of interference through prey depression has been measured in *Corophium*-feeding redshank (Yates *et al.* 2000) or can be predicted from an interference model (Stillman *et al.* 2000b). For species consuming large prey that take a relatively long time (>5–10s) to consume, interference is assumed to occur both through actual prey stealing and the need to avoid prey stealing. Hence it depends on dominance,

being absent for the most dominant birds and strongest for the least dominant. The strength of interference over large prey has been measured in some systems or can be predicted for others using a behaviour-based interference model (Stillman *et al.* 2002).

## PREDICTING THE CONSEQUENCES OF ENVIRONMENTAL CHANGE

The model is able to predict the consequences of environmental change caused by factors such as habitat loss, disturbance, shellfishing, recreation, climate change and sea level rise. The model represents the feeding habitats of birds as a number of discrete patches, each of which, at any point in time, has a certain area exposed by the tide and a certain abundance and quality of invertebrate food. To determine the effect of a change in the environment, the model is initially parameterised and run for the current-day environmental conditions. These simulations are used to predict the current mortality rates and body conditions of birds. At this stage, the model's predictions are compared with as much empirical data as possible in order to assess the accuracy of its predictions. If data are available on the mortality rate and body condition of birds, these are compared with the model's outputs. For example, these tests were possible when the model was applied to the Exe estuary oystercatchers (Stillman *et al.* 2000a). If these data are not available, as is often the case, empirical data on the distribution of birds throughout a site, prey selection or the proportion of time birds spend feeding are compared with predictions. This assesses how well the model describes the underlying behaviour from which mortality and body condition are predicted. These tests were made when the model was applied to oystercatchers in the



Burry Inlet, UK, and showed that the model accurately predicted changes in the distribution of birds, the proportion of cockles and mussels in the diet and the proportion of the tidal cycle spent feeding (Table 1, West *et al.* 2003).

To predict the consequences of environmental change, appropriate alterations are made to the model's parameters and simulations run to predict mortality rate and body conditions under the new environmental conditions. Change caused by habitat loss is simulated by altering the area of one or more of the habitat patches. Loss of habitat that is above or below average quality may be simulated by changing the quality of remaining patches as well as their area. This approach was taken to simulate the effect on dunlin, oystercatcher and curlew of potential habitat loss from the Baie de Seine, France, which may be caused by a proposed port extension (Table 1, Durell *et al.* in press). Habitat loss may be compensated for by habitat creation schemes, and the relative benefits of difference schemes can be simulated by adding to the model new habitat, of varying quality and exposure through the tidal cycle. Again this approach was taken to assess the likely benefit of a proposed mitigating measure in the Baie de Seine (Table 1, Durell *et al.* in press).

Human disturbance excludes birds from areas that would otherwise be used for feeding or roosting, increases the energy demands of birds by causing them to take flight and reduces the amount of time they have to feed. The effect of disturbance can be modelled by excluding birds from some patches, by reducing the time they have to feed and by increasing their energy needs. The model has been used to predict the effect of disturbance on oystercatchers on the Exe estuary (Table 1, West *et al.* 2002a). The predictions were that the current level of human disturbance on this estuary had no influence on oystercatcher mortality or body condition, but that greatly increased levels would cause more birds to die.

Shellfishing has a range of effects on coastal birds, some negative and some positive (Goss-Custard *et al.* 2000). Mussel and cockle *Cerastoderma edule* fishing removes the large-sized shellfish that are also eaten by birds, such as the oystercatcher, and hence reduces the amount of food available to them. If shellfishing activity occurs at low tide when waders are feeding, it can also disturb birds and force them to spend energy flying away or to move to poorer quality habitat. In contrast, when artificial shellfish beds are created in the intertidal zone by dredging mussels from deep waters, the amount of food available to birds is increased. Damaged shellfish left in intertidal areas after harvest can also provide additional feeding opportunities for birds. The effects of shellfishing can be simulated by changing the abundance of the food supply for birds (to account for depletion or the creation of new beds) or by excluding birds from all or part of some patches (to account for disturbance). This approach has been used to predict the effect of the current intensities of shellfishing on the Exe estuary and Burry Inlet, UK (Table 1, Stillman *et al.* 2001). In both these estuaries, the model predicted that the current, low intensity of shellfishing was highly unlikely to be increasing the mortality rate in the oystercatcher populations. However, the model also predicted the points at which increases in the intensity of fishing would start to increase oystercatcher mortality rates.

Climate change will affect the energy demands of waders and may alter the distribution and abundance of prey populations and hence the types of prey available. Sea level rise may reduce the area and change the type of habitat, par-

ticularly if the current position of the coastline is maintained. Coastal realignment schemes may offset habitat loss, but newly created habitat may differ from that which is lost. The model can be used to predict how any of these changes will affect the mortality rate and body condition of waders. The required data are predictions of the expected temperature, and the expected abundance and availability of prey under a climate change scenario. As these predictions themselves are likely to be uncertain, the model can be used to determine the sensitivity of wader populations to changes in each of these predictions.

## DISCUSSION

The model described in this paper was originally developed and tested for oystercatchers feeding on mussels in the Exe estuary and was able to predict accurately the density-dependent mortality rates of oystercatchers in that system (Goss-Custard *et al.* 1995a,b, Stillman *et al.* 2000a). However, the Exe oystercatchers have been the subject of a long-term study (e.g. Goss-Custard 1996) and, although only a small part of the overall research on the Exe was used to parameterise the model, some of the data used in the Exe model are not usually available in other areas and for other species. To be of applied value, such behaviour-based models must be able to produce accurate predictions using existing data or data that can be collected within a relatively short time scale. The general relationships described in this paper have made this possible for wader species, and the model has been applied to conservation problems at several sites, typically taking less than a year to develop for each. The most time-consuming aspect has been surveying the food supply. Apart from their numbers, no new data are needed for the birds, as their optimal foraging behaviour and physiology can be predicted from the general relationships.

This paper has focused on one model, but other behaviour-based models have been developed (see reviews in Sutherland (1996), Goss-Custard & Sutherland (1997), Pettifor *et al.* (2000b) and Norris & Stillman (2002)). In particular, several spatial depletion models have been used to address a number of wader and wildfowl conservation issues (e.g. Gill *et al.* 2001). Although based on the same general principles, the model described in this paper differs from spatial depletion models in three main ways. First, it includes food competition through interference as well as depletion, whereas spatial depletion models only include depletion. Second, individuals in the model may differ in foraging efficiency and susceptibility to interference, whereas all individuals are assumed to be identical in spatial depletion models. Third, the model includes the storage of reserves as fat whereas fat reserves are not incorporated in spatial depletion models. The consequences of these differences are that the model is able to predict how environmental change influences the mortality rate and body condition of birds, and hence can be used to predict how these changes affect population size. In contrast, spatial depletion models are not used to predict mortality or body condition, but the maximum number of bird-days a site can support. As a means of evaluating alternative policy options, this measure has a potential disadvantage, since many birds may starve or lose condition before the full bird-days capacity of a site is reached (Goss-Custard *et al.* 2001, 2002, Goss-Custard, this volume).

Behaviour-based models contain more parameters than demographic models. The single parameters of demographic



models, such as mortality rate during the non-breeding season, are replaced by several parameters describing the underlying behaviour and physiology from which mortality rate is predicted. However, this does not mean that behaviour-based models will take longer to develop. Demographic models must take at least one season to develop, longer if the influence of between-season variation in the environment or population size is to be incorporated. The most time-consuming aspect of applying the behaviour-based model to a new system has been measuring the food supply, which has usually taken part of one season. The model has been applied quickly because general relationships have been used to predict the behaviour and physiology of the birds. Although new data can be measured from the birds to refine or test predictions, this is not essential. Further work to identify general rules in the behaviour of waders and other species should increase the range of environmental problems to which behaviour-based models can be applied.

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## REFERENCES

- Durell, S.E.A. le V. dit, Goss-Custard, J.D., Stillman, R.A., Triplet, P., Fagot, C. & Aulert, C. (in press) Les conséquences de la création de Port 2000 au Havre sur les Limicoles: première version d'un modèle prédictif. *Alauda*.
- Gill, J.A., Sutherland, W.J. & Norris, K. 2001. Depletion models can predict shorebird distribution at different spatial scales. *Proceedings of the Royal Society of London. Series B*, 268, 369–376.
- Goss-Custard, J.D. 1980. Competition for food and interference amongst waders. *Ardea* 68: 31–52.
- Goss-Custard, J.D. ed. 1996. *The Oystercatcher: from individuals to populations*. Oxford University Press, Oxford.
- Goss-Custard, J.D. & Durell, S.E.A. le V. dit. 1990. Bird behaviour and environmental planning: approaches in the study of wader populations. *Ibis* 132: 273–289.
- Goss-Custard, J.D. & Sutherland, W.J. 1997. Individual behaviour, populations and conservation. In: *Behavioural ecology: an evolutionary approach* (4th edition) (eds J.R. Krebs & N.B. Davies), pp. 373–395. Blackwell Science, Oxford.
- Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A. le V. dit & Sutherland, W. J. 1995a. Deriving population parameters from individual variations in foraging behaviour: I. Empirical game theory distribution model of oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. *J. Anim. Ecol.* 64: 265–276.
- Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T. & West, A.D. 1995b. Deriving population parameters from individual variations in foraging behaviour: II. Model tests and population parameters. *J. Anim. Ecol.* 64: 277–289.
- Goss-Custard, J.D., Stillman, R.A., West, A.D., Caldow, R.W.G. & McGrorty, S. 2002. Carrying capacity in overwintering migratory birds. *Biol. Cons.* 105: 27–41.
- Goss-Custard, J.D., Stillman, R.A., West, A.D., McGrorty, S., Durell, S.E.A. le V. dit & Caldow, R.W.C. 2000. Role of behavioural models in predicting the impact of harvesting on populations. In: *Behaviour and Conservation* (eds M. Gosling & W.J. Sutherland). Cambridge University Press, Cambridge. pp. 65–82.
- Goss-Custard, J.D., West, A.D., Stillman, R.A., Durell, S.E.A. le V. dit, Caldow, R.W.G., McGrorty, S. & Nagarajan, R. 2001. Density-dependent starvation without significant food depletion. *J. App. Ecol.* 70: 955–965.
- Norris, K.J. & Stillman, R.A. 2002. Predicting the impact of environmental change. In: *Conserving bird biodiversity* (eds K.J. Norris & D. Pain). Cambridge University Press, Cambridge. pp. 180–201.
- Pettifor, R.A., Caldow, R.W.G., Rowcliffe, J.M., Goss-Custard, J.D., Black, J.M., Hodder, K.H., Houston, A.I., Lang, A. & Webb, J. 2000a. Spatially explicit, individual-based behaviour models of the annual cycle of two migratory goose populations – model development, theoretical insights and applications. *J. App. Ecol.* 37: Supplement 1, 103–135.
- Pettifor, R.A., Norris, K.J. & Rowcliffe, J.M. 2000b. Incorporating behaviour in predictive models for conservation. In: *Behaviour and Conservation* (eds M. Gosling & W.J. Sutherland). Cambridge University Press, Cambridge. pp. 198–220.
- Stillman, R.A., Goss-Custard, J.D. & Caldow, R.W.G. 1997. Modelling interference from basic foraging behaviour. *J. Anim. Ecol.* 66: 692–703.
- Stillman, R.A., Goss-Custard, J.D. & Alexander, M.J. 2000b. Predator search pattern and the strength of interference through prey depression. *Behav. Ecol.* 11: 597–605.
- Stillman, R.A., Goss-Custard, J.D., West, A.D., Durell, S.E.A. le V. dit, Caldow, R.W.G., McGrorty, S. & Clarke, R.T. 2000a. Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *J. App. Ecol.* 37: 564–588.
- Stillman, R.A., Goss-Custard, J.D., West, A.D., McGrorty, S., Caldow, R.W.G., Durell, S.E.A. le V. dit, Norris, K.J., Johnstone, I.G., Ens, B.J., van der Meer, J. & Triplet, P. 2001. Predicting oystercatcher mortality and population size under different regimes of shellfishery management. *J. App. Ecol.* 38: 857–868.
- Stillman, R.A., Poole, A.E., Goss-Custard, J.D., Caldow, R.W.G., Yates, M.G. & Triplet, P. 2002. Predicting the strength of interference more quickly using behaviour-based models. *J. Anim. Ecol.* 71: 532–541.
- Stillman, R.A., West, A.D., Goss-Custard, J.D., Caldow, R.W.G., McGrorty, S., Durell, S.E.A. le V. dit, Yates, M.G., Atkinson, P.W., Clark, N.A., Bell, M.C., Dare, P.J. & Mander, M. (submitted). An individual behaviour-based model can predict shorebird mortality using routinely collected shellfishery data. *J. App. Ecol.*
- Sutherland, W.J. 1996. *From individual behaviour to population ecology*. Oxford University Press, Oxford.
- Sutherland, W.J. & Anderson, C.W. 1993. Predicting the distribution of individuals and the consequences of habitat loss – the role of prey depletion. *J. Theor. Biol.* 160: 223–230.
- West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldow, R.W.G., Durell, S.E.A. le V. dit & McGrorty, S. 2002a. Predicting the impacts of disturbance on wintering wading birds using a behaviour-based individuals model. *Biol. Cons.* 106: 319–328.
- West, A.D., Stillman, R.A. & Portig, A. 2002b. *Modelling of the interaction between oystercatchers and shellfish in Strangford Lough, Northern Ireland*. Centre for Ecology and Hydrology Report, pp. 23.
- West, A.D., Goss-Custard, J.D., McGrorty, S., Stillman, R.A., Durell, S.E.A. le V. dit, Stewart, B., Walker, P., Palmer, D.W. & Coates, P. 2003. The Burry shellfishery and oystercatchers: using a behaviour-based model to advise on shellfishery management policy. *Mar. Ecol. Prog. Ser.* 248: 279–292.
- Yates, M.G., Stillman, R.A. & Goss-Custard, J.D. 2000. Contrasting interference functions and foraging dispersion in two species of shorebird (Charadrii). *J. Anim. Ecol.* 69: 314–322.

