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When enough is not enough: shorebirds and shellfishing

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In a number of extensive coastal areas in northwest Europe, large numbers of long-lived migrant birds eat shellfish that are also commercially harvested. Competition between birds and people for this resource often leads to conflicts between commercial and conservation interests. One policy to prevent shellfishing from harming birds is to ensure that enough food remains after harvesting to meet most or all of their energy demands. Using simulations with behaviour-based models of five areas, we show here that even leaving enough shellfish to meet 100% of the birds' demands may fail to ensure that birds survive in good condition. Up to almost eight times this amount is needed to protect them from being harmed by the shellfishery, even when the birds can consume other kinds of non-harvested prey.

Keywords: shellfish harvesting; oystercatchers; density-dependent survival; interference competition; prey depletion; behaviour-based modelling

1. INTRODUCTION

Large numbers of mollusc-eating birds (e.g. the oystercatcher *Haematopus ostralegus* and eider duck *Somateria mollissima*) congregate outside the breeding season in a limited number of extensive coastal areas (e.g. Wash, Wadden Sea) where they mainly eat shellfish, particularly the cockle *Cerastoderma edule* and mussel *Mytilus edulis*. As these rather large birds mainly eat the larger-sized cockles and mussels, which are also harvested by people, a conflict often arises between commercial and conservation interests (Goss-Custard *et al.* 2000; Ens 2000, 2003). When low stocks of shellfish occur, shellfishers may blame the birds while conservationists may blame the shellfish industry, and evaluating the two viewpoints may require a substantial research programme (Horwood & Goss-Custard 1977).

The increased importance attached to the conservation value of coastal areas has caused the emphasis of this debate to shift from the possible impact of birds on shellfisheries to the possible impact of shellfisheries on shorebirds. This is the issue discussed here. The largest numbers of birds that depend on commercially exploited shellfish occur in Europe during autumn and winter, over which period the birds must survive in good condition to migrate to the breeding grounds the following spring. Although the birds can eat alternative prey species when shellfish are scarce, these prey often do not enable birds to survive as well, and in such good body condition, as when shellfish are abundant, as has been demonstrated for both the Wadden Sea (Camphuysen *et al.* 1996, 2002; Smit *et al.* 1998) and Wash (Atkinson *et al.* 2003). The wintering populations of oystercatchers in both these important areas have declined in recent years following a number of winters with low shellfish stocks.

If bird populations are to be maintained, sufficient shellfish to meet their demands must remain for them after harvesting. But what constitutes a sufficient quantity of shellfish? A common approach has been to base this decision on the biomass of shellfish required by the whole bird population to satisfy its energy demands. The policy in the Dutch Wadden Sea, for example, has been to reserve for the birds in years of low shellfish stocks a biomass of shellfish equivalent to 70% of the birds' requirements, on the assumption that the remainder will be obtained from non-harvested prey species (CWSS 2002).

Using oystercatchers as our example, we show that, unless their intake rate on the alternative prey is high enough, even providing 100% of the population's needs in autumn as shellfish biomass is insufficient to enable all of the birds to survive autumn and winter. In the systems considered, as much as almost eight times this amount must be reserved for each bird.

2. MATERIAL AND METHODS

This conclusion was reached from simulations with behaviour-based models of oystercatchers in five areas: Wash (Stillman *et al.* 2003); Exe estuary (Stillman *et al.* 2001; West *et al.* 2002); Burry Inlet (West *et al.* 2003); Bangor flats (Caldow *et al.* 2004); and Baie de Somme (J. D. Goss-Custard and P. Triplet, unpublished data, using data given in Triplet *et al.* (1998)). These are site-specific versions of a general process-based model developed and tested for Exe estuary oystercatchers (Stillman *et al.* 2000). Details of parameter values in each model are given in the above sources. The models consider individual birds that use optimization decision rules to decide how to obtain most rapidly their daily energy requirements, which, in the model as in reality, depend on the ambient temperature. Individuals vary in competitive ability, and each bird takes into account the decisions made by competitors in deciding when (e.g. night or day), where (e.g. which shellfish bed) and on what

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Table 1. The biomass (kgAFDM) of shellfish per oystercatcher in autumn at which the probability of starving reaches 0.5%. (The value in square brackets in column (iii) is the actual kgAFDM bird⁻¹ that was initially present in the winter(s) modelled; the value for the Exe is the mean over 7 years. The year(s) modelled are shown in brackets in column (i). The value in square brackets in column (iv) is the gross consumption by one bird taking into account the amount that is wasted. The ratios between the shellfish biomass required per bird in autumn to ensure a probability of mortality of less than 0.5% and the biomass actually consumed by a single bird from autumn to spring are shown in columns (v) and (vi). In column (v), the AFDM of the shellfish in autumn was used to calculate the gross biomass required per bird, whereas in column (vi), the biomasses required and consumed take into account, respectively, the overwinter loss of flesh in individual shellfish and the wastage of flesh while the birds are feeding; they are therefore 'net' of these losses of flesh. The birds' intake rates on alternative prey are shown in column (vii). The period modelled was 1 September to 15 March (196 days) in all systems except the Baie de Somme, where it was 1 October to 28 February (151 days).)

(i) system	(ii) predominant shellfish	(iii) biomass density at which mortality reaches 0.5% (kgAFDM bird ⁻¹)	(iv) biomass consumed by one bird over autumn and winter (kgAFDM)	(v) biomass required/biomass consumed gross	(vi) net	(vii) intake rate of alternative intertidal prey (mgAFDM s ⁻¹)
Exe estuary (1976–82)	mussel	61 [75.7]	7.88 [9.13]	7.74	5.35	0.673
Bangor flats (1999)	mussel	50 [71.6]	7.79 [9.62]	6.42	4.08	0.867
Burry Inlet (2000)	cockle	44 [90.6]	7.88 [9.27]	5.58	3.56	0.693
Wash (1994)	cockle	20 [54.2]	7.93 [7.93]	2.52	1.89	0.673
Baie de Somme (1996)	cockle	33 [21.4]	6.56 [7.72]	5.03	3.60	0.957

(e.g. cockles or mussels or alternative prey species) it should feed. Because, in winter, shellfish are more profitable than other prey species for oystercatchers (Zwarts *et al.* 1996), the birds attempt first to obtain their requirements from shellfish alone but, should they fail, they eat other intertidal invertebrates over low water (all five systems) or terrestrial prey, such as earthworms, over high water on the Exe, Burry and Bangor. Once an individual has obtained its current daily energy requirement, it stores subsequent consumption as body reserves up to a daily limit. A bird uses its reserves if it fails to obtain its daily requirement from current foraging. It starves to death if its body reserves are ever used up.

The models incorporate those aspects of shellfishing that affect oystercatchers (Goss-Custard *et al.* 2000). The shellfish harvest is deducted from the shellfish stocks present, which are also depleted by the birds, mortality agents such as storms and an overwinter decrease in the flesh content of individual shellfish. Birds disturbed by shellfishers that harvest by hand picking spend time and energy relocating to an undisturbed shellfish bed (West *et al.* 2002). Field tests of model predictions are given in the references where the particular models are published.

The sizes of shellfish stocks in autumn vary annually either because the areas they occupy vary or because their densities vary, or both. We varied only the size of the shellfish beds since this was sufficient to make our main point. Importantly, this also most closely replicates the potentially serious long-term impact of large-scale harvesting techniques, notably suction dredging and trawling, which render intertidal flats unsuitable for cockles (Piersma *et al.* 2001) and mussels (Stillman *et al.* 2001), respectively. The data for shellfish abundance, bird numbers and ambient temperature for each system were taken either from a typical autumn and winter or from the average of several seasons (table 1).

3. RESULTS

The best measure of the impact of environmental change on birds is its effect on individual fitness and thus on population demographic rates (*per capita* rates of survival and reproduction) and population size (Goss-Custard & Durell 1990; Goss-Custard *et al.* 2002; Sutherland & Norris 2002). For shorebirds in the non-breeding season, this means predicting the probability of birds surviving until spring with sufficient body reserves to migrate to the breeding grounds. Although our models predict body reserves (Stillman *et al.* 2001; West *et al.* 2003), model predictions of survival rates only are required to make our main point.

Figure 1 shows oystercatcher mortality from autumn to spring as a function of the abundance of shellfish in the autumn, expressed as kg ash-free dry mass (AFDM) bird⁻¹. Where shellfishing occurred later during autumn and in winter, the harvest was deducted from the initial shellfish stock. The quantity kgAFDM bird⁻¹ therefore represents the shellfish biomass that the birds could actually use over the whole non-breeding period.

At high shellfish abundance (70–120 kgAFDM bird⁻¹), the probability of starving over the winter is extremely low and independent of shellfish stock (figure 1). The probability increases sharply below this range but the increase begins at different shellfish abundances in the different systems modelled. The dotted horizontal line in figure 1 shows the 0.5% starvation probability. Depending on the system, the mortality curve crosses this line at 20–61 kgAFDM bird⁻¹ (table 1, column (iii)), or at 2.5–7.7 times the gross food requirement (i.e. allowing for assimilation efficiency) of a single oystercatcher over the whole

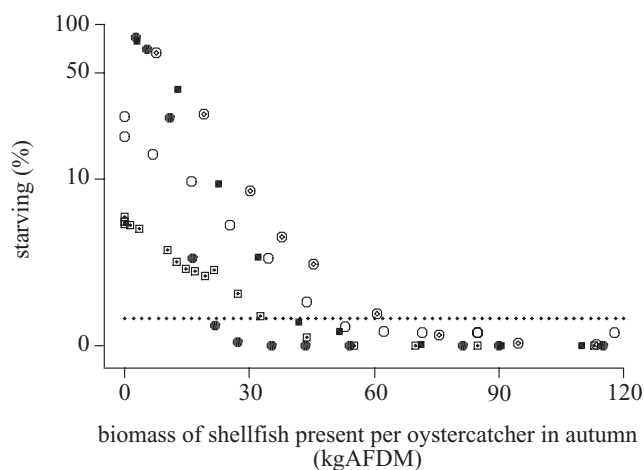


Figure 1. The probability of oystercatchers starving between autumn and the following spring in relation to the shellfish stocks present in autumn. Each symbol is the mean of five simulations in one of the five oystercatcher–shellfish systems modelled (details in table 1): Wash (solid circle); Burry Inlet (solid square); Baie de Somme (dotted square); Exe estuary (double circle); and Bangor flats (single circle). The horizontal dotted line represents a mortality rate of 0.5%. Cockle biomass is for animals more than 15 mm long, whereas mussel biomass is for animals 30–60 mm long, these being the sizes from which oystercatchers obtain most of their intake.

period modelled (column (v)). The 0.5% starvation probability seems to be reached at higher shellfish abundances where mussels (open and double circles in figure 1), rather than cockles, are the predominant shellfish. Below these threshold values, starvation probability rises rapidly to reach levels that, with no shellfish present, depend on:

- (i) oystercatcher intake rates on alternative prey;
- (ii) the duration of the exposure period, the average time for which the uppermost flats are exposed over the tidal cycle; and
- (iii) whether birds can feed over high tide.

Oystercatchers leave scraps of flesh in the shells and, during daylight, also have shellfish stolen from them by kleptoparasites, e.g. gulls (*Laridae*). These sources of ‘wastage’ require each bird to find up to an additional 20% flesh, depending on the system. Furthermore, individual shellfish lose 33–50% of their flesh mass from autumn to spring. The decline in flesh mass is approximately linear, so the average loss over the winter as a whole is half of the total reduction in flesh content that occurs from autumn to spring. Column (vi) in table 1 shows the ratios between the net amount a bird requires to survive (i.e. taking wastage and flesh loss into account) and the amount it actually consumes. The values of 1.9–5.4 are still well above unity. Thus, flesh wastage and loss only partly explain why the food supply in autumn must exceed by so much the amount that the birds will actually consume if most of the birds are to survive until spring.

Birds starve below the threshold values of shellfish biomass even though they can take alternative prey at the constant overwinter rates shown in column (vii) of table

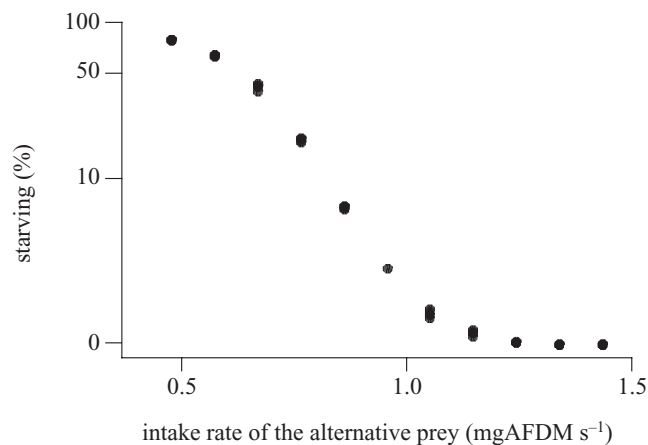


Figure 2. The probability of oystercatchers in the Baie de Somme starving between autumn 1996 and the following spring in relation to their intake rate of the alternative prey to cockles, the ragworm *Nereis diversicolor*. The actual intake rate, and the value used in the model simulations shown in figure 1, was 0.957 mgAFDM s⁻¹ (table 1).

1. The intake rate of alternative prey can be critical for survival, as demonstrated using the Somme model (figure 2). This system was chosen because, in the particular winter modelled, cockle stocks were almost completely exhausted, both in reality and in the model, by late winter, whereupon, in the model as in reality, most birds switched to the only available alternative prey, the ragworm *Nereis diversicolor* (Triplet *et al.* 1998). The percentage of birds starving increased sharply as the intake rate of worms fell below the observed rate of 0.957 mgAFDM s⁻¹ and fell to zero at higher intake rates (figure 2). As would be expected, the impact of inadequate shellfish stocks on oystercatcher survival depends critically on their intake rate of the alternative prey.

4. DISCUSSION

On the five major estuaries modelled so far, between 2.5 and 7.7 times the shellfish biomass that will be consumed by oystercatchers must be available in autumn if most birds are to survive until spring. Only part of this high demand is caused by overwinter flesh loss in individual shellfish and by wastage during foraging. The main reason is that by reducing the area of the shellfish beds, and therefore reducing the biomass of shellfish available per oystercatcher, interference competition for food is intensified. The increased density of birds increases the frequency with which dominant birds attack subdominants to steal food items and feeding locations of both mussels (Stillman *et al.* 1997) and cockles (Triplet *et al.* 1999). Reducing shellfish stocks also increases competition because shellfish stocks are depleted earlier in the winter. The same processes are likely to occur in other large shellfish-eating birds, such as the common eider, in which interference competition also seems to occur (Nehls & Ketzenberg 2002).

Figure 1 is actually a density-dependent function in which bird density is expressed as the ratio of bird numbers to initial shellfish stocks. Our findings support the argument that predicting the effect of changes in feeding conditions (and of other kinds of environmental

change) on birds (and other animals) depends on being able to predict how the dependence of demographic rates on density will be affected (Goss-Custard 1977, 2003; Goss-Custard & Durell 1990; Goss-Custard & Sutherland 1997; Sutherland & Norris 2002).

It might be thought that a few percentage points increase in the oystercatcher mortality rate from its typical base level of 1% (Atkinson *et al.* 2003) might not matter. In fact, population size in such long-lived animals is very sensitive to the annual mortality rate (Goss-Custard *et al.* 1996). The rapid increase in mortality rate as shellfish stocks fall below the threshold confirms that conservation managers should assess the impact of shellfishing (and other environmental change) in terms of how it will affect bird fitness rather than in terms of the total number of bird days that the food supply can, in principle, support (Goss-Custard *et al.* 2002; Goss-Custard 2003; Stillman *et al.* 2003). The same point applies to other bird groups if individuals vary in competitive ability.

Our results from five diverse systems suggest that providing just the quantity of food that oystercatchers actually need to consume may generally not safeguard their fitness or numbers: providing enough food therefore is not enough. The Dutch Wadden Sea policy of providing 70% of the birds' requirements as shellfish in winters when shellfish stocks are poor may therefore not protect the birds as much as intended. Among other factors that affect how much food a bird can obtain in a 24-hour period (e.g. duration of exposure period, availability of terrestrial prey), whether or not this is the case will depend on the birds' intake rates of alternative prey and, unfortunately, very few estimates are available for Wadden Sea oystercatchers (Zwarts *et al.* 1996). However, the increased mortality rates of both oystercatchers (Camphuysen *et al.* 1996; Smit *et al.* 1998) and eiders (Camphuysen *et al.* 2002; Ens *et al.* 2002) in the Wadden Sea in years when shellfish stocks are low strongly implies that switching to alternative prey does not maintain bird fitness. The same applies to the Wash, a similar large embayment, where the oystercatcher mortality rate is very high in winters of shellfish scarcity (Atkinson *et al.* 2003), despite the widespread presence of alternative intertidal prey.

The results from the five systems suggest a simple policy guideline for managing shellfisheries to sustain oystercatchers: shellfish stocks measured in autumn should not be allowed to fall below 2.5–8 times the biomass that the birds need to consume. If this rule can indeed be applied to the Dutch Wadden Sea, the present policy for winters of shellfish scarcity may provide only between one-quarter and one-tenth of the shellfish required to maintain bird fitness in years of shellfish scarcity, depending on the relative contribution from cockles and mussels. Policy should also aim to maintain stocks above the critical threshold levels in the long term and not just in the current season. Some shellfishing techniques, e.g. hand picking, have no demonstrable effect on long-term shellfish abundance, so stocks can probably be reduced each winter to the threshold values. But intensive suction dredging of cockles and trawling of mussels are strongly suspected to reduce shellfish stocks (and those of the alternative prey species) in the long term by reducing recruitment (Stillman *et al.* 2001; Piersma *et al.* 2001). If molluscivorous birds are to be protected, policy should prevent the cumulative impact of

harvesting over successive years from reducing autumn shellfish stocks to below the threshold values.

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REFERENCES

- Atkinson, P. W., Clark, N. A., Bell, M. C., Dare, P. J., Clark, J. A. & Ireland, P. L. 2003 Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. *Biol. Conserv.* **114**, 127–141.
- Caldow, R. W. G., McGrorty, S., Stillman, R. A., Goss-Custard, J. D., Durell, S. E. A. le V. dit, West, A. D., Beadman, H. A., Kaiser, M. J., Mould, K. & Wilson, A. 2004 A behaviour-based modelling approach to predicting how best to reduce shorebird–shellfish conflicts. *Ecol. Applications* (Submitted.)
- Camphuysen, C. J., Ens, B. J., Heg, D., Hulscher, J. B., van der Meer, J. & Smit, C. J. 1996 Oystercatcher *Haematopus ostralegus* winter mortality in The Netherlands: the effect of severe weather and food supply. *Ardea* **84A**, 469–492.
- Camphuysen, C. J. (and 11 others) 2002 Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. *Biol. Conserv.* **106**, 303–317.
- CWSS 2002 *Shellfish fisheries. An overview of policies for shellfish fishing in the Wadden Sea*. Wilhelmshaven, Germany: Common Wadden Sea Secretariat.
- Ens, B. J. 2000 Berekeningsmethodiek voedselreservering Waddenzee. Alterra-rapport 136. Wageningen: Alterra.
- Ens, B. J. 2003 What we know and what we should know about mollusc fisheries and aquacultures in the Wadden Sea. In *Challenges to the Wadden Sea* (ed. W. J. Wolff, K. Essink, A. Kellermann & M. A. van Leeuwe), pp. 121–147. Groningen: Ministry of Agriculture, Nature Management and Fisheries/University of Groningen.
- Ens, B. J., Borgsteede, F. H. M., Camphuysen, C. J., Dorrestein, G. M., Kats, R. K. H. & Leopold, M. F. 2002 Eideendensterfte in de winter 2001/2002. Alterra-rapport 521. Wageningen: Alterra.
- Goss-Custard, J. D. 1977 The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). *J. Appl. Ecol.* **14**, 721–739.
- Goss-Custard, J. D. 2003 Fitness, demographic rates and managing the coast for shorebird populations. *Wader Study Group Bull.* **100**, 183–191.
- 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 edn (ed. J. R. Krebs & N. B. Davies), pp. 373–395. Oxford: Blackwell Science.
- Goss-Custard, J. D., Durell, S. E. A. le V. dit, Clarke, R. T., Beintema, A. J., Caldow, R. W. G., Meininger, P. L. & Smit, C. 1996 Population dynamics of the Oystercatcher. In *The Oystercatcher: from individuals to populations* (ed. J. D. Goss-Custard), pp. 352–383. Oxford University Press.
- 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* (ed. M. Gosling & W. G. Sutherland), pp. 65–82. Cambridge University Press.

- Goss-Custard, J. D., Stillman, R. A., West, A. D., Caldow, R. W. G. & McGrorty, S. 2002 Carrying capacity in overwintering migratory birds. *Biol. Conserv.* **105**, 27–41.
- Horwood, J. W. & Goss-Custard, J. D. 1977 Predation by the oystercatcher, *Haematopus ostralegus* (L.), in relation to the cockle, *Cerastoderma edule* (L.), fishery in the Burry Inlet, South Wales. *J. Appl. Ecol.* **14**, 139–158.
- Nehls, G. & Ketzenberg, C. 2002 Do common eiders *Somateria mollissima* exhaust their food resources? A study on natural mussel *Mytilus edulis* beds in the Wadden Sea. *Danish Rev. Game Biol.* **16**, 47–61.
- Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J. J., Dekker, R. & Essink, K. 2001 Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *J. Appl. Ecol.* **38**, 976–990.
- Smit, C. J., Dankers, N., Ens, B. J. & Meijboom, A. 1998 Birds, mussels, cockles and shellfish fishery in the Dutch Wadden Sea: how to deal with low food stocks for eiders and oystercatchers? *Senckenbergiana maritima* **29**, 141–153.
- 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., West, A. D., Durell, S. E. A. le V. dit, Caldow, R. W. G., McGrorty, S. & Clarke, R. T. 2000 Predicting to novel environments: tests and sensitivity of a behaviour-based population model. *J. Appl. Ecol.* **37**, 564–588.
- Stillman, R. A. (and 10 others) 2001 Predicting oystercatcher mortality and population size under different regimes of shellfishery management. *J. Appl. Ecol.* **38**, 857–868.
- Stillman, R. A., West, A. D., Goss-Custard, J. D., Durell, S. E. A. le V. dit, Yates, M. G., Atkinson, P. W., Clark, N. A., Bell, M. C., Dare, P. J. & Mander, M. 2003 A behaviour-based model can predict shorebird mortality rate using routinely collected shellfishery data. *J. Appl. Ecol.* **39**. (In the press.)
- Sutherland, W. J. & Norris, K. 2002 Behavioural models of population growth rates: implications for conservation and prediction. *Phil. Trans. R. Soc. Lond. B* **357**, 1273–1284. (DOI 10.1098/rstb.2002.1127.)
- Triplet, P., Fagot, C., Bacquet, S., Desprez, M., Lengignon, A., Locquet, N., Sueur, F. & Oget, E. 1998 Les relations Coque, Huitrier-pie, Homme en Baie de Somme. Report. Abbeville, SC: Syndicat Mixte pour l'Aménagement de la Côte Picarde.
- Triplet, P., Stillman, R. A. & Goss-Custard, J. D. 1999 Prey abundance and the strength of interference in a foraging shorebird. *J. Anim. Ecol.* **68**, 254–265.
- West, A. D., Goss-Custard, J. D., Stillman, R. A., Caldow, R. W. G., Durell, S. E. A. le V. dit & McGrorty, S. 2002 Predicting the impacts of disturbance on wintering waders using a behaviour based individuals model. *Biol. Conserv.* **106**, 319–328.
- 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. J. 2003 The Burry shellfishery and oystercatchers: using a behaviour-based model to advise shellfishery management policy. *Mar. Ecol. Prog. Ser.* **248**, 279–292.
- Zwarts, L., Ens, B. J., Goss-Custard, J. D., Hulscher, J. B. & Durell, S. E. A. le V. dit 1996 Causes of variation in prey profitability and its consequences for the intake rate of the Oystercatchers *Haematopus ostralegus*. *Ardea* **84**, 229–268.