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# Critical thresholds of disturbance by people and raptors in foraging wading birds

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## ABSTRACT

Intertidal areas support during the non-breeding season many wading birds Charadrii that may often take flight in response to the presence of people or of birds of prey on their intertidal feeding and roosting grounds. Disturbance can cause birds to spend energy flying away and to lose feeding time while relocating to different feeding areas, where the increased bird densities may intensify competition from interference and, if of sufficient duration, from prey depletion. Until now, there has been no method for establishing how frequently birds can be put to flight before their fitness is reduced. We show how individual-based behavioural models can establish critical thresholds for the frequency with which wading birds can be disturbed before they die of starvation. It uses oystercatchers *Haematopus ostralegus* in the baie de Somme, France where birds were put to flight by disturbance up to 1.73 times/daylight hour. Modelling shows that the birds can be disturbed up to 1.0–1.5 times/h before their fitness is reduced in winters with good feeding conditions (abundant cockles *Cerastoderma edule* and mild weather) but only up to 0.2–0.5 times/h when feeding conditions are poor (scarce cockles and severe winter weather). Individual-based behavioural models enable critical disturbance thresholds to be established for the first time.

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## 1. Introduction

To maintain fitness, the many wading birds Charadrii that congregate outside the breeding season on European coasts must survive until spring by avoiding death from starvation or from enemies (disease, but probably mainly predators) and also accumulate sufficient body reserves to reach their frequently distant breeding grounds in good condition. These threats to bird fitness can be exacerbated by disturbance arising from both natural and human sources. Birds of prey (raptors) not only eat wading birds but also disturb them on the frequent occasions when attacks fail. Wading birds put to flight by rap-

tors or disturbed by people may spend significant amounts of energy flying away and those that had been foraging when disturbed also lose feeding time while moving to alternative feeding areas (Quinn, 1997), where interference competition may be immediately intensified because of the increased density at which birds then forage. Indeed, if the disturbance is long-lasting or very frequent, competition could also be increased through increased rates of prey depletion in the alternative feeding areas. The lower intake rates resulting from increased competition between birds not only reduces the chances that birds will avoid starvation but may also cause them to feed more frequently in places where they are at

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the greatest risk from land-based raptors (Cresswell, 1994, 1995, 1996; Whitfield, 1985, 2003a,b).

Most studies of disturbance and wading birds have focussed on measuring the effect of disturbance on the observable behaviour, and sometimes the underlying physiology, of the birds and have not been able to measure its impact on a component of their fitness, the real measure of how disturbance (or any other change in the environment) affects birds (Goss-Custard et al., 2002; Goss-Custard, 2003). A few examples will suffice to illustrate the many studies of this kind that have been carried out. Measurements have been made on (i) species differences in the responses of birds to an approaching person (Blumstein et al., 2003) and, in particular, the distances at which they take flight (de Boer and Longamane, 1996); (ii) the effect that the detection of an approaching person has on the intensity with which the birds feed (de Boer and Longamane, 1996); (iii) potentially harmful physiological responses, such as elevated corticosterone levels (Fowler, 1999); (iv) the amount of parental care given to oystercatcher chicks when parents are disturbed by humans (Verhulst et al., 2001); (v) the short distance displacement and subsequent return of birds (Pfister et al., 1992); (vi) the numbers of birds in a locality (Burton et al., 1996); (vii) the distribution of birds between different feeding sites (Burton et al., 2002), sometimes with food abundance also being taken into account and over a range of spatial scales (Gill et al., 2001a); (viii) the under-exploitation of resources in areas that are frequently disturbed (Gill et al., 2001a), and (ix) whether wading birds can compensate for the losses of time and energy resulting from disturbance by altering their behaviour or by habituation (Smit and Visser, 1993; Triplet et al., 1999a; Urfi et al., 1996). But as Gill et al. (2001b) point out, it is very difficult unambiguously to interpret the implications of many of these findings for the effect that disturbance might have on the abundance of the birds. For example, that a bird changes its behaviour and foraging location, or does not exploit all of its potential food supply, does not necessarily mean that its chances of surviving the winter have been reduced. Rather, we need to be able to assess whether the frequency with which birds are being disturbed is high enough significantly to reduce a component of fitness. For wintering wading birds, this has only been done for oystercatchers *Haematopus ostralegus* on the Exe estuary, using an individual-based and behaviour-based model (West et al., 2002).

This paper shows how behaviour-based models, in which individual birds vary in respects that are believed to affect their fitness, can produce very simple policy guidelines for deciding when the frequency with which birds are put to flight by disturbance reaches the level at which bird fitness begins to be reduced – the ‘critical threshold for disturbance’. This individuals-based approach to ecology is applied increasingly to solve applied problems of ecological management (Grimm and Railsback, 2005).

Typically, as a human disturber approaches, wading birds raise their heads and may start to walk away, sometimes while feeding. Eventually, they stop feeding and then may take flight, either returning later to the area from which they were disturbed or moving to somewhere else. They often do not resume feeding immediately after they land but rest and preen for a period. The data available (i) on the distance

from people at which birds begin to become disturbed and then fly away and (ii) on the amount of potential foraging time lost and the extra energy expended by shorebirds in each of these phases of disturbance suggest that the birds’ responses vary between species, between places and between different phases of the non-breeding season (e.g., Blumstein et al., 2003; de Boer and Longamane, 1996; Smit and Visser, 1993). In predicting the impact of disturbance on wading birds, it is therefore necessary to have available a number of site-specific and species-specific estimates of the parameters that describe the local response of the birds to disturbance.

The necessary data are available for that majority of oystercatchers using the Reserve Naturelle in the baie de Somme, France that start the winter eating cockles *Cerastoderma edule* but turn to ragworms *Hediste diversicolor* if the shellfish become depleted. Disturbances arise from overflying raptors, from cockle-fishers over a one-two month fishing season in early winter and from people undertaking a wide range of recreational activities at all times of the winter. Using data from Triplet et al. (1998, 1999a, 2002), we model three winters which varied greatly in the abundance and quality of the initial cockle stocks, in the weather conditions and in the number of oystercatchers that arrived late in the winter from The Netherlands, from where they had been driven by severely cold weather.

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## 2. Methods

### 2.1. Model

We used a version of a general process-based model developed and tested for mussel-feeding oystercatchers in the Exe estuary (Stillman et al., 2000, 2001). The model is individuals-based as it tracks the diet, foraging location and body condition of each individual within the population and whether or not it starves before the end of winter.

The food supply is distributed between a number of discrete patches, each of which may differ in the type (prey species), quantity (numerical density) and quality (size and energy content) of the food items it contains as well as in the duration of the time for which it is exposed through spring and neap tidal cycles. During each 24-h day, each bird must consume enough food to meet its energy demands that vary daily according to the ambient temperature. An individual attempts to do this by feeding in the locations, times of the day (day or night) and stages of the tidal cycle where its intake rate is currently the highest. Although all individuals make these choices using the same optimisation principle – intake rate maximisation – the actual decisions made by each animal differ. This is because their individual choices depend on their individual competitive abilities, which in turn depend on two characteristics. The *interference-free intake rate* is the rate at which an individual feeds in the absence of interference competition and measures an animal’s basic foraging efficiency. The *susceptibility to interference* measures by how much interference from competitors reduces an individual’s intake rate as bird density rises and this, in turn, depends on the animal’s social dominance in contests over food items and feeding sites. The model is therefore game

theoretic in that each animal responds to the decisions made by competitors in deciding when, where and on what to feed.

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 (e.g., the duration of the exposure period of the food patches) and on the intake rate while feeding which, in turn, depends on the profitability of the prey and on the individual's susceptibility to interference. 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 an individual's reserves fall to zero, it starves, the only source of mortality in the model, and the main source of oystercatcher winter mortality in the wild (Goss-Custard et al., 1996).

The model also incorporates those aspects of the seasonal change in the food supply that affect oystercatchers. The overwinter reduction in the mass of individual prey animals is included and their numerical density is reduced daily through depletion by the birds themselves and by other mortality agents, such as storms. If shellfishing occurs, the daily shellfish harvest is also deducted daily from the shellfish stocks present. Birds disturbed by shellfishers that harvest by hand-picking and by other disturbers, such as walkers, spend time and energy relocating to an undisturbed shellfish bed (West et al., 2002).

Stillman et al. (2000, 2001) describe in more detail the model processes and its many parameters, many of which are detailed below. When modelling a particular site, such as the baie de Somme, most of the parameters are obtained from the literature: e.g., the energy costs of thermoregulation and of flight when disturbed; the relationship between dominance and susceptibility to interference (Stillman, 2003). The remaining parameters are necessarily site-specific and are estimated from local field studies: e.g., the area and exposure times of patches; the densities and energy content of the prey and their overwinter mortality due to storms; the daily ambient temperature. Stillman et al. (2000) provide a sensitivity analysis and tests of model predictions and Stillman (2003) lists the many countries, sites, shorebird and wildfowl species and applications where the model is being, or has been, applied. More recent information, and a visual representation of the model, are available at: <http://www.dorset.ceh.ac.uk/shorebirds/>.

## 2.2. Parameters for the environment, food supply, bird population and feeding behaviour

Only those parameters differing from those used for the Burry Inlet (West et al., 2003), and the methods used to determine them, are detailed here. The tidal cycle comprised 10 stages: high water, 2.394 h; tide receding, 0.975 h; first low water stage, 2.1 h; six 1-h low water stages; tide advancing, 0.975 h. The two main cockle beds were the 'rive gauche' and the 'rive droite', situated either side of a creek called La Maye and had a combined surface area of 160 ha. They were situated at a high shore-level and were exposed over high tide on neaps and only covered for a short period on springs. A

third low-lying cockle bed (43 ha) was covered over high water on all tides and was exposed on springs only over low water but also on neaps as the tide ebbed and flowed.

The food supply was sampled monthly from October to February in 12 (1995–96) or 19 (1996–97 and 1997–98) quadrats, measuring  $25 \times 25 \text{ m}^2$ , that were situated across the cockle beds to provide a representative sample from which the food supply in each of the three cockle patches used in the model could be estimated (Triplet et al., 1998). Ten randomly placed cores of sediment,  $200 \text{ cm}^2$  in area and 5 cm deep, were taken in each quadrat on each sampling occasion and the contents were sieved through a mesh of 1 mm gauge. The maximum length of each retained cockle was measured by calliper to the nearest 1 mm. A separate sample of cockles, ranging from 58 to 173 in number, was taken from the cockle beds each month to determine the allometric relationship between cockle length and ash-free dry mass (AFDM) by drying the flesh extracted from individual cockles at  $90^\circ \text{C}$  and burning in a muffle furnace at  $550^\circ \text{C}$ , both to a constant mass. From this allometric relationship, the mean AFDM of all the cockles in the size range of 15–40 mm normally taken by oystercatchers (Goss-Custard et al., submitted) was calculated from the length-frequency distribution obtained from the core sampling to estimate the mean size and energy content of the cockles available to oystercatchers in each patch/month/year. In addition, the overwinter decline in the AFDM of individual cockles was calculated as the mean percentage decrease between October and February of cockles of lengths 15, 20, 25, 30 and 35 mm. The mean numerical density of 15–40 mm cockles was also calculated for each patch/month/year to determine the number of cockles available to the birds in each patch. A large proportion of the cockles 15–40 mm long that were present in October disappeared over the winter for reasons other than shellfishing and predation by oystercatchers; probably, storms washed the cockles away. The proportion of the initial numbers of cockles that disappeared this way was calculated for each winter by comparing cockle density in October with that in February, having first removed the losses attributable to oystercatchers (10–15%) and shellfishing (4–6%), as calculated by the model and confirmed, in the case of shellfishing, from fishery statistics.

The initial (Oct. 1st) densities and sizes (mean ash-free dry mass (AFDM) of cockles in the oystercatcher size-range (15–40 mm)) in each patch was specified in the model along with their overwinter (until Feb. 28th) (i) mortality due to causes other than oystercatchers and shellfishing, and (ii) reduction in mean cockle mass due to flesh-loss by individual cockles and the disappearance of large cockles.

The fourth feeding patch was the ragworm bed (160 ha) where depletion was assumed not to occur as birds turned to this prey so late in the winter. Therefore, only the birds' intake rate on ragworms had to be specified. This was obtained from an empirically derived equation that reliably predicts the intake rate of a shorebird from the masses of the bird and of its prey (Goss-Custard et al., submitted). Using the mean mass of the ragworms in the size range consumed by oystercatchers that were present during the winter 2000/01 – the only estimate available – intake rate on ragworms was estimated as 0.957 mgAFDM/second. For want of data, the intake rate on ragworms was assumed to be the same in each of

the three winters modelled. Sensitivity tests were conducted to explore the likely consequences of this assumption.

The size of the oystercatcher population was determined during routine counts made at the high tide roost (Triplet et al., 1998). The age-composition and feeding methods used by the birds when opening cockles was determined at close-quarters from hides situated close to a sub-sample of the quadrats used to sample the cockle food supply (Triplet et al., 1998). The size and age-composition of the population varied between years but, in all winters, the majority (>93%) opened cockles by stabbing the bill between the valves of the cockle, the remainder hammering a hole in the shell. It is important to specify the feeding technique in oystercatchers as it affects both the intake rate and susceptibility to interference of the bird (Triplet et al., 1999b). This paper is only concerned with birds in the Reserve that started by eating cockles and does not include the several hundred immatures that ate ragworms from the start.

The daily mean temperature used in the model was calculated as the mean of the minimum and maximum temperature recorded by Météo France at Hourdel on the southern shore of the baie de Somme. Data on the numbers of shellfishers and their daily allowable catch were obtained from the local fishery statistics, as detailed in Triplet et al. (1998). The procedures used to record the frequency with which oystercatchers were disturbed and the time costs associated with each disturbance are described in Triplet et al. (1999a).

### 2.3. Representing disturbance

As in reality, shellfishing disturbance occurred during the first (2 h) low-water stage and only in daylight on weekdays during the six week fishing season in early winter. Other disturbers (human and raptor) occurred in each tidal stage throughout the winter, but only in daylight.

In the model, a disturber (or a group of disturbers of the same kind, such as shellfishers) arrived on the specified patch at the beginning of the specified tidal stage and stayed for a specified time. All the birds on the patch flew up before alighting on the same or another patch, each bird choosing the patch that was now, for it, the most profitable. Each disturbed bird incurred a specified energy cost as they flew up but no time cost as flight-time was so short (ca. 30 s). Birds roosted before resuming feeding, using a winter-average 'recovery' time from Stillman and Goss-Custard (2002). Birds remaining on the disturbed patch could not feed in a circular 'exclusion zone' around the disturber while the disturber remained: 2 h for shellfishers, 20 min for other human disturbers and 2 min for raptors. Afterwards, birds re-occupied the exclusion zone at a rate that increased through the winter (Stillman and Goss-Custard, 2002).

Shellfishers did not overlap in space with other human disturbers or with each other; in practice, the whole patch fell inside their combined exclusion zone for the whole 2 h. Model limitations limited to one the number of disturbers – additional to shellfishers – per tidal stage on each day of the week yet, to achieve the observed frequency of disturbance, there had to be up to three. To approximate this, the energy and time costs per disturber were increased according to the number of disturbances per tidal stage being represented. If one

disturber costs 1 kJ and 30 min, two disturbers during a 1 h tidal stage cost 2 kJ, because all birds fly up twice, even if the second disturbance occurs immediately after the first. However, the two recovery times (i.e., 30 + 30 min) could not be summed because this would assume the second disturber always arrives just as birds resume feeding following the first disturbance. In fact, the second disturber could arrive at any time during the recovery period, or afterwards up until the end of the tidal stage; the model required that the whole of the disturbance event had to take place within the specified tidal stage. It was therefore assumed that the combined recovery time from two disturbances would be 30 + 15 min because there would only be a 50:50 chance that the second disturbance occurred after the birds had resumed feeding. By the same logic, three disturbances in a tidal stage cost 3 kJ and 30 + 15 + 7.5 min.

In reality, cockle-eaters and ragworm-eaters intermingled but may not have interfered with each other. Accordingly, in the model, they were spatially separated by providing additional ragworm patches the same size as cockle patches and subjected to the same disturbance: thus, the same number of cockle-fishers occurred in the ragworm patches as in the cockle patches because, in reality, shellfishers disturb both ragworm-eaters and cockle-eaters. Based on the general model of disturbance of Stillman et al. (2002), the interference threshold ( $D$ ) and slope ( $m$ ), respectively, were 100 birds/ha and 0.25 in cockle-eaters and 300 birds/ha and 0.50 in ragworm-eaters.

## 3. Results

In most simulations, only 'other human' disturbers were used in addition to shellfishers, comparison between human and raptor disturbers being made subsequently. All results are the means of 10 simulations.

### 3.1. 1996–97

As Table 1 shows, cockles were at typical autumn densities and of typical mean length and flesh-content. AFDM decreased by 31%, partly because shellfishing removed the larger ones but mainly because individual cockles lost mass. Most cockles disappeared over the winter (99.1%), primarily from causes other than shellfishing and oystercatcher predation which, between them, accounted for only about 15% of the loss. The parameter in the model that represents these cockle losses,  $k$ , is the  $-\log_{10}$  proportion of the density that would survive until the end of the winter in the absence of shellfishing and depletion by oystercatchers. As only 1% of cockles remained by the end of the winter, and most disappeared from unknown causes,  $k$  was given the value of 2. In the absence of their preferred shellfish prey, all cockle-eaters switched to ragworms during January, in the model as in reality. Mudflats froze for 2–3 days in late winter during a long cold spell during which 7000 Dutch adult cockle-eaters joined the 500 immature and 2700 adult cockle-eaters in the Reserve; their provenance from The Netherlands is extremely well-known from ringing studies (Hulscher et al., 1996). Based on the body mass of oystercatchers leaving The Netherlands during a severe spell of cold weather

**Table 1 – The observed frequencies of disturbance by people and raptors and the critical disturbance thresholds**

Year	Feeding conditions									Critical disturbance threshold (disturbances/h)	Observed frequency of disturbance	
	C/m <sup>2</sup>	C%	M	M%	Nt	Ns	Dr	T	Du		From people (disturbances/h)	From raptors (disturbances/h)
1995–96	1420	65	128	58	11	4	2–4	–5.35	3050	1.0–1.5	?	?
1996–97	573	99	321	31	19	2	7 and 12	–9.10	7000	0.2–0.3	0.967	?
1997–98	569	99	238	0	7	3	2–3	–1.30	0	0.5–0.6	0.384	0.204–1.584

The feeding conditions are shown; cockle densities etc. refer to the average across the two main cockle beds. C/m<sup>2</sup> = cockles > 14.9 mm long/m<sup>2</sup> on October 1st; C% = % overwinter decline in cockle density; M = mean AFDM of cockles > 14.9 mm long on October 1st; M% = % overwinter decline in mean cockle mass; Nt = total number of days with mean daily temperature <0 °C; Ns = number of cold spells during which contiguous days had mean temperatures <0 °C; Dr = range in the duration of the cold spells in days; T = lowest daily temperature; Du = number of Dutch oystercatchers arriving during cold weather. No data on disturbance frequencies were available for 1995–96, but the value from the previous winter was 0.513/h (Triplet et al., 1999a). The frequency of disturbances due to raptors was only recorded during one winter, when it increased from October to February over the range shown.

(L. Zwarts, unpublished information) and the likely energetic cost of flying to the Somme, Dutch birds were estimated to have had an arrival a body mass of 402 g. The sudden decrease in oystercatcher numbers that was observed in February 1996 is likely to have been due to the departure of the birds that had come from The Netherlands during the severe spell of weather. In the model, it was therefore assumed that the Dutch birds left the Somme in mid-February, just before the local birds.

The difficult feeding conditions in 1996–97 due to the prolonged period of very severe weather in January and the almost complete disappearance of the cockles by the end of the winter made this winter the most appropriate for making extensive sensitivity tests. Although some sensitivity analyses were carried out on some of the assumptions made about key processes (e.g., whether or not birds eating ragworms experienced interference competition), most were done on the values of particular parameter values about which there was some uncertainty as to their real value.

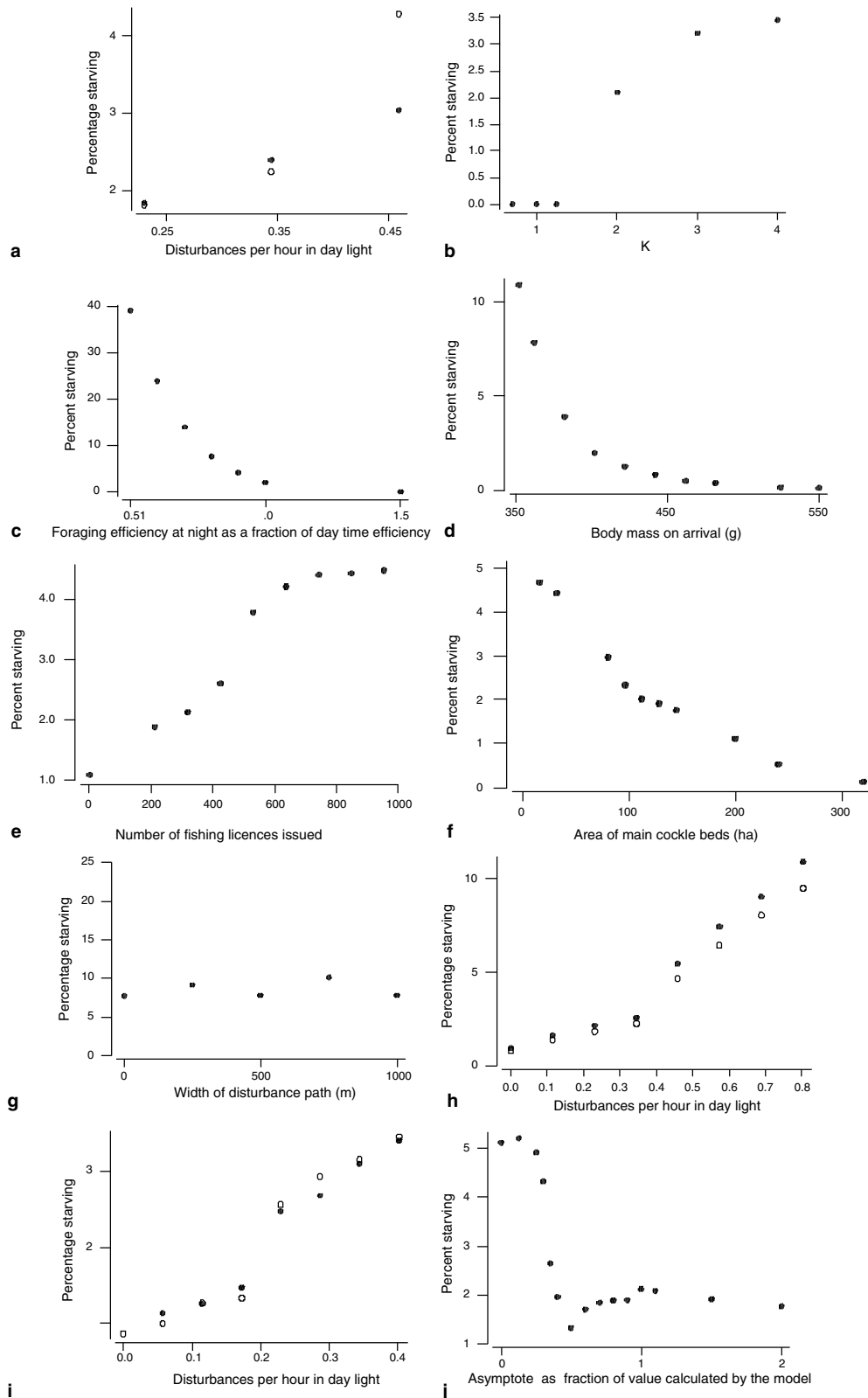
In the sensitivity tests, the range in the parameter value that was used was chosen to at least encompass the probable range in which the true value would lie. Most of the findings are shown as graphs in Fig. 1 (sensitivity tests) and Fig. 2 (main results) because the frequently non-linear effect of varying a parameter could not be portrayed in any other way. In the following discussion of the sensitivity of the model to parameter values, the values in brackets show, first, the value that was chosen for the simulations that gave the main results and, second, the range over which mortality was either sensitive or insensitive to the values used.

The overwinter mortality rate in initially cockle-eating oystercatchers was sensitive to: (i) intake rate on ragworms (0.957 mgAFDM/second; 0.96–0.67 (Fig. 1 in Goss-Custard et al., 2004)); (ii) energy cost of disturbance (see below); (iii) duration of the post-disturbance recovery (see below); (iv) whether birds were disturbed on consecutive or alternate days (Fig. 1(a)); (v) value of  $k(2; 0-4)$  (Fig. 1(b)); (vi) efficiency of night-feeding on both cockles and ragworms as a fraction of daytime efficiency (1; 0.5–1.5) (Fig. 1(c)); (vii) body mass of arriving Dutch birds (402 g; 350–450 g) (Fig. 1(d)); (ix) number of shellfishers (106; 0–500) (Fig. 1(e)); (x) area of the main cockle beds (160 ha; 16–320 ha) (Fig. 1(f)); (xi) time a disturber remained (see below); (xii) severity of the winter weather (see below); (xiii) whether the mean AFDM of cockles declined or

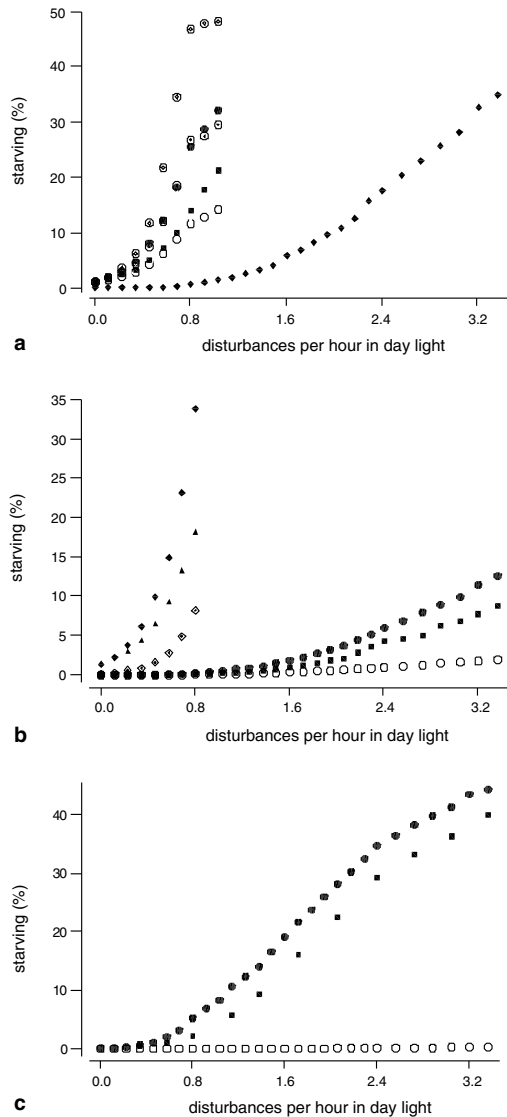
remained at the October level (see below), and (xiv) the duration of the exposure period (see below).

The mortality rate was not very sensitive to (i) the width of the path disturbed by a raptor flying overhead (166.5 m; 50–1000 m) (Fig. 1(g)); (ii) the radius of the circle disturbed by people (166.5 m; 100–200 m) – the mean% starving over 15 simulations across a wide range of scenarios, for a radius of 100 and 200 m, respectively, were  $6.91\% \pm 1.17$  and  $6.84\% \pm 1.17$ , paired t-test,  $p = 0.568$ ;  $t = 0.59$ ;  $df = 14$ : (iii) whether or not interference occurred amongst ragworm-eating birds (Fig. 1(h)); (iv) whether all birds, or only the birds feeding at the time, suffered the time and energy costs of disturbance (Fig. 1(i)); and (v) asymptote of the functional response of cockle-eating birds, except at extreme values below of those calculated by the model (0.5–2 times the value calculated by the model) (Fig. 1(j)).

The effects of the energy and time costs of disturbance, and of the duration of the disturber's stay, are shown in Fig. 2(a). A 30 second flight would cost 1 kJ for an oystercatcher in level flight (West et al., 2003) but 4 kJ for one flying upwards (Nudds and Bryant, 2000). As the amount of level and vertical flight made by disturbed oystercatchers was unknown, the values of 4 and 1 kJ represent the extremes. There was also uncertainty about the duration of the length of time it took the birds to resume feeding after they had landed following a disturbance: the observed 'recovery time' varied between 15 and 30 min, depending on season (Triplet et al., 1999a). Accordingly, it was set at 30 min with the 4 kJ energy cost and at 20 min with the 1 kJ energy cost. The effects of doubling or trebling the observed length of stay of disturbers, or of reducing it to 0.033 h (2 min) to simulate the rapid disturbance caused by raptors, are also shown in Fig. 2(a), with an energy cost of 1 kJ and recovery time of 20 min. Between them, these scenarios probably encompass the reality of the Somme cockle beds that winter and show that, in all cases, mortality rate began to rise rapidly as the frequency of disturbance flights rose above a critical threshold of approximately 0.3/h. This low value was mainly due to the severity of that winter and the associated influx of competing Dutch birds. With no influx and the daily temperature over the 21 days of the actual cold spell set at the average for a normal winter of 3.9 °C (range 0.20–9.30), rather than the actual average of –3.7 °C (range –9.1 to 0.4), the mortality rate only increased above frequencies of about 0.8. disturbances/h.



**Fig. 1** – Sensitivity of model predictions on mortality to some parameter values. (a) Whether disturbances occurred on consecutive (open circle) or alternate days (closed circle); (b)  $k$ -mortality rate of cockles due to factors other than oystercatchers and shellfishers; (c) foraging efficiency at night as a fraction of daytime efficiency; (d) body mass of arriving Dutch birds in mid-winter; (e) the number of shellfishers licenced to fish; (f) area of the main cockle beds; (g) width of the path disturbed by one raptor; (h) whether ragworm-eaters were subjected to interference (closed circle) or not (open circle); (i) whether all birds were disturbed (closed circle) or only those that were actually feeding at the time (open circle); (j) the value of the asymptote of the functional response in cockle-eating birds, expressed as a fraction of the value calculated by the model equation.



**Fig. 2** – Percentage of oystercatchers starving and the frequency of disturbance flights over three winters. (a) 1996–97: In closed symbols, the energy cost of disturbance ( $ec$ ) = 4 kJ and recovery time ( $rt$ ) = 0.5 h: (closed circle), duration of stay by disturber ( $d$ ) = 0.33 h; (closed square),  $d$  = 0.033 h; (closed diamond),  $d$  = 0.33 h but with no cold spell or influx of Dutch birds. In open symbols,  $ec$  = 1 kJ and  $rt$  = 0.33 h: (open circle),  $d$  = 0.33 h; (dot circle),  $d$  = 0.67 h; (circle circle);  $d$  = 1 h. (b) 1995–96: In closed symbol, 57.7% overwinter decline in mean prey size: (closed circle), energy cost of disturbance ( $ec$ ) = 4 kJ, recovery time ( $rt$ ) = 0.5 h, duration of stay by disturber ( $d$ ) = 0.33 h; (closed square),  $ec$  = 4 kJ,  $rt$  = 0.5 h, but  $d$  = 0.033 h; (closed diamond),  $ec$  = 4 kJ,  $rt$  = 0.5 h,  $d$  = 0.033 h;  $d$  = 0.33 h but exposure time ( $ET$ ) reduced from 12.444 to 8.1 h; (closed triangle), same but  $ec$  = 1 kJ,  $rt$  = 0.33 h. In open symbols, there is no decline in prey size: (open circle),  $ec$  = 4 kJ,  $rt$  = 0.33 h,  $d$  = 0.33 h; (open diamond), same but  $ET$  reduced to 8.1 h. (c) 1997–98: In closed symbols, there is a 95% overwinter cockle mortality whereas in open symbols there is no loss of cockles. In (closed circle) and (open circle),  $ec$  = 4 kJ and  $rt$  = 0.5 h.  $d$  = 0.33 h, whereas in (closed square),  $d$  = 0.033 h.

### 3.2. 1995–96

In this year, cockles were initially extremely abundant but small (Table 1). Even so, mean flesh content decreased over the winter by 57.7%, not because individuals lost mass but because the larger ones disappeared. By February 28th, 65% of cockles >15 mm had disappeared, primarily from causes other than shellfishing and oystercatcher predation, so  $k$  = 0.95. In the model as in reality, some oystercatchers switched to ragworms at the very end of the winter. There was no prolonged severe spell and only 3050 Dutch adult oystercatchers joined the 635 immature and 3335 adult cockle-eaters wintering in the Reserve, but not until mid-February.

Mortality did not begin to increase until 1–1.5 disturbances/h, whether disturbers remained for 0.33 h (people) or 0.033 h (raptors) (Fig. 2(b)). This high critical disturbance threshold was partly due to the very long exposure period of the cockle beds of the baie de Somme: with this reduced to the more typical value for European estuaries of 8.1 h, mortality rate increased sharply at very low frequencies of disturbance whether the energy and time costs were 4 kJ and 0.5 h or 1 kJ and 0.33 h. Fig. 2(b) also shows that the 57.7% reduction in prey mass that winter had a large effect on mortality, the rate being greatly reduced if there was no overwinter decrease in cockle mass.

### 3.3. 1997–98

Initial cockle stocks were at typical autumn levels and of below-average mean length and flesh-content (Table 1). Individual cockles did not lose mass over that winter but most disappeared from causes other than shellfishing and oystercatchers, so  $k$  = 2. Accordingly, most cockle-eaters switched to ragworms during January, in the model as in reality. There was no prolonged severe spell and no Dutch oystercatchers joined the 883 immature and 3880 adult cockle-eaters in the Reserve.

With maximum time and energy costs, mortality rate did not begin to increase sharply until 0.6 disturbances/h whether the disturber was a person or a raptor (Fig. 2(c)). Without the high rate of cockle loss, however, mortality was unaffected by even very high disturbance frequencies. It was therefore the late-winter switch to ragworms that caused the sensitivity to disturbance.

### 3.4. Conclusions

The simulations for 1995–96 and 1996–97 suggested that, compared with annual variations in the values of the critical threshold of disturbance, the assumptions made about the time and energy costs of disturbance had rather little effect on the values of the critical disturbance thresholds, even though they sometimes greatly affected the rates of mortality once the threshold had been reached. The results shown in Figs. 1(h) and (i) illustrate our many unpublished data showing that the critical threshold was rather little affected by the values used for parameters which had only a rather small influence on the mortality rate.



The value of the critical threshold was particularly low (0.2–0.3/h) in 1996–97 when a prolonged period of severe weather raised the birds' energy demands at a time when their intake rates were reduced because ice prevented them from feeding for a few days, because the birds competed for cockles with Dutch immigrants and because the cockles disappeared so that the birds switched to the less profitable ragworms. Without severe winter weather and the associated influx of Dutch birds, the critical threshold was higher (0.8–1.0/h in 1996–97; 0.5–0.6/h in 1997–98) and would have been even higher had the birds not been forced to switch to less profitable ragworms at the end of the winter because most cockles disappeared. Accordingly, in 1995–96 when cockles remained until the end of the winter, the threshold was comparatively high (1.0–1.5/h): the threshold would have been higher still if the cockles had not been small at the start of the winter and had not lost mass. The finding that the value of the critical threshold would have been much lower if the exposure period on the baie de Somme had not been so long compared with most other estuaries confirms that it is the balance between the energy demands of the birds and the opportunity to fulfil them – the feeding conditions – that determines whether the value of the critical threshold for disturbance is high or low.

#### 4. Discussion

Oystercatchers wintering in the Reserve Naturelle were disturbed into flight up to 0.513–1.73 times/daylight hour by people and raptors, depending on the winter. The highest disturbance frequency would only have increased mortality a little in a mild winter in which cockles remained abundant throughout (1995–96). Most birds could continue eating cockles throughout the winter and did not have to switch to the less profitable ragworms, even though individual cockles had lost mass. But in a mild winter during which most cockles disappeared, mortality started to increase at 0.5–0.6 disturbances/daylight hour (1997–98), frequencies of disturbance that were common on the baie de Somme. The critical disturbance threshold was only 0.2–0.3 disturbances/daylight hour when, in addition to cockles becoming depleted, a prolonged period of cold weather occurred and many Dutch birds arrived (1996–97). Interestingly, the threshold was much higher without the cold spell and the influx of Dutch birds even though cockles became depleted: the large size of the cockles that winter probably enabled birds to survive for longer before they switched to ragworms.

The critical disturbance thresholds were similar whether the disturbances were caused by people staying for 20 min or by rapidly over-flying raptors and whether they inflicted the maximum or minimum energy and time costs on oystercatchers. Therefore, a quite simple policy rule can be devised for the management of disturbance in the Reserve. A frequency of flying up caused by people and/or raptors in autumn and early winter of <1.5/daylight hour can be allowed. However, if the cockles become considerably depleted by the end of December, especially if they are small, the frequency of disturbance – from both people and raptors – should be kept below 0.5/h. This could mean that in winters with many raptors, people should not be allowed to disturb the birds at

all. Similarly, no disturbance from people should be allowed during a prolonged cold spell with an influx of Dutch birds – in the same way that hunting is already often banned in many places during severe weather.

This policy guideline is practicable for the baie de Somme. It is very easy to detect from a very simple sampling programme when cockles become scarce. It is also straightforward to estimate the frequency with which birds are put to flight by people or by raptors. While it is of course impossible to control the number of disturbances due to raptors, it is possible to see when the disturbance from people causes the total number of disturbances from raptors and people to exceed the critical threshold, whereupon access to the feeding areas by people can then be stopped. Similarly, it is easy to prevent access by people during cold spells, just as hunting and catching birds is also prevented during periods of severe winter weather.

In these simulations, all the birds in the Reserve flew up when disturbed whereas, in reality, only some of them may do so. Because of this, these critical thresholds show how frequently a given group of birds can be repeatedly disturbed before their survival rate is reduced. Model simulations in which only a proportion of birds were disturbed produced, of course, lower mortality rates. The critical thresholds described here are therefore precautionary because they assume that the same birds were repeatedly disturbed.

This example of the baie de Somme has shown that individual-based behavioural models can therefore be used to establish for the first time practicable critical disturbance thresholds. The level of the critical threshold will, of course, depend on estuary-specific features and cannot be regarded as being applicable everywhere – as the simulations in which the exposure time was reduced to 8.1 h illustrated. Thresholds will depend on bird species and the many factors known to affect the ability of wading birds to survive the winter in good condition. By using the oystercatchers of the baie de Somme as the test system, this paper has only demonstrated a capability to determine critical disturbance thresholds rather than provided values for thresholds that will be applicable everywhere. On the other hand, it is now possible to apply this kind of model very rapidly to new systems within the normal length of time available to environmental impact assessments (Stillman, 2003; see also <http://www.dorset.ceh.ac.uk/shorebirds/>).

It is to be hoped that, as such models become increasingly widely deployed to a wider range of taxa and sites, that general policy guidelines that can be applied without modelling the system in question may emerge; for example, the relative levels of disturbance that will affect the fitness of small and large bodied birds in mild and severe winters. The potential value of individuals-based models is not widely realised and many research workers are unfamiliar with their principles and application (Grimm and Railsback, 2005). Nonetheless, the demand from nature managers for the advice that such models can provide is likely to lead to their widespread application, and thus to the development of policy guidelines that are very simple to apply in practice (West et al., 2005). Because estimating the net impact of disturbance on fitness has seldom been possible, most nature managers at the moment make the precautionary assumption that, if the birds'

behaviour and/or physiology is affected, there is a risk that their fitness might also be affected. However, this may often not be the case with the result that the activities of people on the coast may be unnecessarily restricted. In the long run, this could lead to a weakening in public support for attempts to manage the coast to the benefit of wading birds.

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