Population consequences of winter habitat loss in a migratory shorebird. II. Model predictions

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Summary

1. This paper models empirically how habitat loss in winter might affect the size of the European population of oystercatchers Haematopus ostralegus ostralegus. It explores how a density-dependent mortality rate in winter interacts with a density-dependent production rate in summer to determine the total, year-round population size following a loss of winter habitat which itself leads to intensified competition for food and hence increased winter mortality rates.

2. Simulations over a range of probable parameter values show that the density at which winter mortality becomes density-dependent, $c_W$, simply determines the point at which population size is affected as habitat is gradually removed. The population is affected sooner in the more widely fluctuating Continental subpopulations than in the less variable Atlantic subpopulations.

3. Once winter density reaches $c_W$, the consequences depend on the slope, $b_W$, of the density-dependent winter mortality function. In all subpopulations, the reduction in population size increases sharply as $b_W$ increases, but only at low values; above a certain level, further increases in $b_W$ make less difference. Because of their higher reproductive rate, inland subpopulations are initially less affected by winter habitat loss than coastal subpopulations. These conclusions are robust over a range of assumptions about competition for territories in summer and age difference in mortality in winter.

4. Adding density-dependent fledging success to the basic model reduces the effect of winter habitat loss on population size, but only when low proportions of the habitat are removed. A higher mortality rate in females, whether only in post-fledging young birds or in birds of all ages, makes little additional difference to the population consequences of habitat loss.

5. Field studies on winter habitat loss in migratory bird populations should first test whether density has already reached the critical level, $c_W$; i.e. whether some birds already die of food competition. The parameter $b_W$ should then be estimated to determine whether its probable value lies in the range within which predictions are sensitive or insensitive to its precise value. Whether the summer density-dependent functions are linear or curvilinear needs also to be explored, as does the effect of interactions between subpopulations which have different fledgling production rates but share the same winter habitat.

Key-words: density-dependent mortality, Haematopus ostralegus, intertidal zone, oystercatcher, population dynamics.

Introduction

Many hundreds of thousands of shorebirds Charadrii arrive in late summer and autumn from their breeding grounds to the north and east to winter on the estuaries and coastal flats of north-west Europe (Smit & Piersma 1989). Because of the open and unsheltered nature of the terrain, shorebirds have high energy demands (Kersten & Piersma 1987) and, in cold and windy weather, many may die of
starvation. Conservationists are concerned that activities on estuaries, ranging from dog-walking to large-scale reclamation, might make it even more difficult for shorebirds to obtain their food requirements. These activities prevent shorebirds from using intertidal areas and so remove winter habitat. The question, therefore, is whether displaced shorebirds are able successfully to re-establish themselves on the flats that remain. The predictions required range in scale from the local, as when the effect on bird numbers on a particular shore is being explored (Goss-Custard & Yates 1992), to the global, when the size of an entire subspecies population throughout the year across the whole of its range is being considered (Goss-Custard 1993). This paper investigates how the equilibrium population size of a world subspecies population might be affected by various amounts of winter habitat loss, given different assumptions about the strengths of the all-important density-dependent functions operating in summer as well as in winter.

Habitat loss causes a re-distribution of birds and an increase in density in the areas that remain (Goss-Custard 1977, 1980, 1993; Sutherland & Goss-Custard 1991). The effect this has on their survival and breeding success will depend on how much interference and depletion competition are intensified and so decrease the rate at which individuals can feed (Goss-Custard 1980). Fig. 1a shows how the proportion starving might change as densities increase with decreasing intertidal area. Initially, there is no competition so that increases in bird density due to habitat loss do not affect the density-independent proportion ($m_W$) starving. But eventually, a point, $c_W$, is reached at which mortality begins to increase and so becomes density-dependent. From then on, mortality increases by $b_W$ for every unit increase in bird density resulting from habitat loss.

Unfortunately, the values of $b_W$ and $c_W$ have not been measured in any species in one estuary, let alone over an entire wintering range. Using an empirical model whose parameter values are derived in Goss-Custard et al. (1995d), this paper investigates how the values of $c_W$ and $b_W$ affect the impact of winter habitat loss on the equilibrium size of the global population of one species of shorebird, the European subspecies of the oystercatcher Haematopus o. ostralegus. Since competition for territories in summer causes the reproductive rate also to be density-dependent (Goss-Custard et al. 1995d), it asks how changes in a density-dependent mortality rate in winter, due to habitat loss, interact with a density-dependent production rate in summer to determine the total population size throughout the year. As very few estimates are available for the parameters $b_T$ and $c_T$ of the territory competition function (Fig. 1b), a range of values was again assumed in the simulations. The model was therefore used to explore the sensitivity of the population equilibrium size to habitat loss under different assumptions of the intercept and slope of the density-dependent functions in both the summer and winter.

**The model**

**Structure and Parameters**

A review of oystercatcher field studies (Goss-Custard et al. 1995d) identified parameter values that were quite well established, and others that were not. Birds breeding in the Atlantic and Continental regions were kept separate and, within each, birds bred either in coastal or inland sites. The model assumed that coastal and inland birds from one region wintered in the same coastal feeding areas. For each of the four subpopulations, Table 1 gives the model values for the density-independent clutch size and subsequent mortalities, which varied annually within ±2 SD of the mean values shown. In the basic model, summer density dependence was assumed only to arise from competition for breeding territories, as shown in Fig. 1b. A later version also included density-dependent fledging success.

**Simulation Procedure**

In exploratory model runs without winter density
Table 1. Parameter values for each of the four subpopulations used in the basic population model. Mean annual values for clutch size and all subsequent mortalities are shown. Standard deviation (SD) are the same across all four subpopulations and refer to annual variations. From Goss-Custard et al. (1995d).

<table>
<thead>
<tr>
<th></th>
<th>Atlantic Coastal</th>
<th>Atlantic Inland</th>
<th>Continental Coastal</th>
<th>Continental Inland</th>
<th>SDLeaves</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clutch size</td>
<td>2.604</td>
<td>2.750</td>
<td>2.840</td>
<td>2.986</td>
<td>0.0062</td>
</tr>
<tr>
<td>Eggs mortality</td>
<td>0.682</td>
<td>0.598</td>
<td>0.518</td>
<td>0.435</td>
<td>0.0040</td>
</tr>
<tr>
<td>Chick mortality</td>
<td>0.445</td>
<td>0.445</td>
<td>0.796</td>
<td>0.796</td>
<td>0.0046</td>
</tr>
<tr>
<td>Mortality in 1st &amp; 2nd winter</td>
<td>0.200 above adult rate</td>
<td>0.200 above adult rate</td>
<td>0.200 above adult rate</td>
<td>0.200 above adult rate</td>
<td>0.200 above adult rate</td>
</tr>
<tr>
<td>Mortality in 3rd &amp; 4th winter</td>
<td>Same as adult rate</td>
<td>Same as adult rate</td>
<td>Same as adult rate</td>
<td>Same as adult rate</td>
<td>Same as adult rate</td>
</tr>
<tr>
<td>Adult mortality in winter</td>
<td>0.09126</td>
<td>0.09126</td>
<td>0.03855</td>
<td>0.03855</td>
<td>0.00247</td>
</tr>
<tr>
<td>Additional severe winter mortality at all ages</td>
<td>0.07−0.15</td>
<td>0.07−0.15</td>
<td>0.07−0.15</td>
<td>0.07−0.15</td>
<td>0.07−0.15</td>
</tr>
<tr>
<td>Adult mortality in summer</td>
<td>0.010</td>
<td>0.010</td>
<td>0.010</td>
<td>0.010</td>
<td>0.010</td>
</tr>
<tr>
<td>Mortality in 2nd to 4th summer</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

dependent mortality, the coastal subpopulations declined to extinction. Either the fledgling production rate had been under-estimated in coastal sites or the non-breeding season mortality had been overestimated. Both explanations are likely; fledging success may sometimes increase at low breeding densities, and so prevent extinction, and the way adult mortality was measured is very likely to over-estimate the mortality rate (Goss-Custard et al. 1995d). As fledging success may not be widely density-dependent, extinction was avoided in the model by gradually reducing winter mortality rates until the breeding coastal populations in each region stabilized; this only required a reduction of 2%. As removing the summer adult mortality rate made little difference, it was retained at 1%.

To allow for density dependence, population sizes were expressed as densities, yet the area of the breeding range was unknown. The value of $cT$, at which pairs began to be excluded, was therefore estimated indirectly by finding, for a given $bT$ (the slope of the territory competition function), the value which, at stability, produced the observed number of breeding pairs in each subpopulation (Fig. 2), the starting point with all habitat loss simulations. These are provisional estimates of $cT$, especially in the inland habitats where numbers may still be increasing. The winter density-dependent mortality function had the form shown in Fig. 1a. Once density reached $cW$, this additional density-dependent mortality was added to the basic density-independent rate ($mW$ in Fig. 1a), detailed in Table 1. The values for $cW$ were varied from 1 to 2 birds per ha, thus starting with the current value of about 1 per ha in British estuaries (J.D. Goss-Custard, unpublished data). $bW$ measures the increase in percentage mortality per 1 bird per ha increase in bird density. The values used in the simulations varied from 0-001 to 0-10, corresponding to a 0-1% to 10% increase in mortality per 1 bird per ha increase in bird density.

In some simulations, fledging success was made to decrease as the density of breeding territories increased. The slope of this (assumed linear) function was estimated as 174% for every territory per ha increase in breeding density (Goss-Custard et al. 1995d). The intercept was adjusted separately for each of the subpopulations to give the average observed fledging success (Table 1) at a breeding density of 1 territory per ha. This value of territory density was selected for both inland and coastal populations whereas, in reality, densities may be much lower inland (Fig. 3). However, density measurements are difficult to make; on the coast, for example, few studies have included the intertidal feeding territory. On balance, a value of 1 pair per ha seemed appropriate. Tests showed that whether the density-dependent chick mortality function was centered on territory densities of 0-2, 1 or 2-0 per ha made little difference to the predicted population consequences of winter habitat loss.

Although tests showed that it did not affect the outcome, the initial population age structure before winter habitat was removed approximated that on the Exe estuary over five winters (Goss-Custard et al. 1982). Typical population trajectories for the Atlantic and Continental populations are shown in Fig. 4. With density-independent fledging success, large fluctuations occurred in the Continental region because of chance runs of severe winter mortality and the absence of any subsequent compensatory increase in fledgling production. Introducing density-dependent fledging success stabilized the Continental population considerably. The Atlantic population,
Population consequences of habitat loss. II

Fig. 2. The effect of varying $cT$, the density of potential breeding pairs at which competition for territories begins, on the numbers of pairs breeding when the population reaches stability. The different lines refer to various values of $bT$: *, $bT = 0.03$; ●, $bT = 0.05$; •, $bT = 0.7$; ■, $bT = 0.9$. The large open circle denotes the best estimate of $cT$ when $bT$ is set at its best estimate of 0.5. The horizontal dashed line shows the actual numbers of breeding pairs in each of the subpopulations and are: Atlantic inland, 22000; Atlantic coastal, 85500; Continental inland, 92000; Continental coastal, 66500. From Goss-Custard et al. (1995d). Density-independent variables were set at values given in Table 1.

Fig. 3. Frequency histogram of the densities of breeding territories found in studies of coastal salt-marshes and sand dunes and of inland sites. The data came from Greenhalgh (1969); Heppleston (1972); Vines (1979); Swennen & de Bruijn (1980); Fuller (1981); Martinez et al. (1983); Galbraith, Furness & Fuller (1984); Pienkowski et al. (1986); Ens et al. (1992); Stock, Leopold & Swennen (1987); U.N. Safriel, A.J. Mercer, K-M Exo and K.B. Briggs, unpublished data. Coastal territories exclude the size of the intertidal feeding territories.

where region-wide severe winter mortalities were assumed not to occur, fluctuated much less than the Continental population.

Habitat loss simulations were run for 1000 years, to ensure stability had been reached, and outputs averaged over the final 100. The wide fluctuations in the Continental population when chick mortality was density-independent meant that the final Continental population was somewhat affected by the particular random seed used to generate the occurrence and magnitude of the severe winter mortalities. To avoid this source of variation between simulations and so reduce the numbers needed, all winter habitat loss simulations used that same random number seed. The simulations thus explored the effect of winter habitat loss on populations subjected to an identical frequency, magnitude and ordering of severe winters. Tests showed that the population consequences of winter habitat loss with this one seed were identical in the Atlantic subpopulations and very similar in the Continental subpopulations to the means of eight runs with differing random seeds.
TEST OF THE BASIC MODEL

For this, it was only possible to compare with observed values the model’s predictions for the proportion of birds of all ages (i.e. including young birds) that do not breed. From Goss-Custard et al. (1995d), the total numbers of pairs, and thus individuals, breeding in each region was compared with the total numbers of birds of all ages recorded in the same region in autumn, before the winter mortality occurs (Table 2). Two estimates for observed values are given, corresponding to the maximum and minimum numbers thought to breed in each country. As the intensive study on the Wadden Sea island of Schiermonnikoog suggested that 46% of the total population do not breed (Ens 1992), the higher values in Table 2 may be the more realistic.

The basic model, with density dependence due only to competition for territories and winter mortality, predicts similar proportions of non-breeding birds across all simulations for the Atlantic population, irrespective of the values of $b_T$, $c_W$ and $b_W$ used and whether or not $b_T$ values were the same for inland and coastal sites. Model predictions for the Atlantic region compare well with the minimum observed estimates, but less well with the maximum estimates (Table 2). Varying the parameters for the more fluctuating Continental population gave predictions for the proportion not breeding that, across their range, matched the observed minimum and maximum field estimates quite well. Introducing density-dependent chick mortality to the basic model increased the predicted proportion not breeding by only a little. As there is some evidence that more females than males may die each year, perhaps especially during their immaturity (Durell & Goss-Custard 1995), the effect of adding a sex difference in the mortality rate outside the breeding season, either in young birds alone or in birds of all ages, was also explored. With a sex difference in mortality occurring at all ages,
the proportion non-breeding increased to levels that were generally similar to the maximum observed estimates. However, if the sex difference in mortality was only assumed to apply in immature birds, the model quite considerably over-predicted the proportion not breeding. Thus, over a variety of assumptions, the model predictions fell within the observed range, except when the sex difference in mortality rate was assumed only to occur in immature birds.

**Effect of winter habitat loss**

**The Basic Model**

Without winter density dependence, winter habitat loss would not affect winter mortality rates so the equilibrium population size would remain the same even if all coastal sites were removed. Clearly, this is absurd. Habitat loss simulations were therefore run with a winter density-dependent mortality function included and \( m_W \) set, for each age-class and subpopulation, at the mean observed winter mortality rates given in Table 1. As the real, region-wide values for \( b_W \) and \( c_W \) (Fig. 1a) are unknown, a range of probable values was used. The breeding season density-dependent function parameter \( b_T \) (Fig. 1b) has been estimated for one inland and one coastal site (Goss-Custard et al. 1995d). Along with the breeding population changes recorded in a variety of coastal and inland sites, these suggest that \( b_T \) is higher in coastal than inland sites. But as the evidence is limited, simulations were run either with the same value of \( b_T \) in all subpopulations or with a higher value in coastal subpopulations.

A typical simulation output is shown in Fig. 5, the density-dependent parameter values being shown in the legend. After winter habitat loss, the total population breeding in summer and arriving on the wintering areas in autumn reach new equilibria quite rapidly, even in the more fluctuating Continental population. In this case, a 60% winter habitat loss led to a 60% reduction in autumn population size but to a 69% reduction in breeders. The latter illustrates the potential non-linear relationship between the proportional loss of winter habitat and its population consequences.

To simulate the effect of habitat loss, the area available in winter was reduced in successive simulations, by steps of 10%, until 90% had been removed. The coefficients of the winter density-dependent mortality function were kept the same throughout. This means that, at each step, it was assumed that habitat of average quality was removed. If habitat of above- or below-average quality had been removed preferentially, the slope \( b_W \) of the winter density-dependent function would have increased at each successive step (Goss-Custard et al. 1995a,c). It is therefore important to note that the present simulations refer only to the removal of habitat of average quality.

The values of the density-dependent and density-independent parameters in summer were held constant over all steps of habitat loss. It was therefore assumed that removing intertidal feeding grounds did not affect the feeding space available to breeding birds. This assumption is reasonable over a wide range of values of habitat loss because, as Ens (1992) showed, most feeding in summer is concentrated along a narrow strip of intertidal ground adjacent to the nesting sites which, being on land, were assumed not to be affected by habitat loss. Nonetheless, more realism would be added to future versions of the model by allowing for any loss of intertidal feeding grounds on the reproductive success. In all simulations, the area of the wintering grounds was set initially such that bird density at the start of the winter stabilized around 1 oystercatcher per ha, approximating the average density of oystercatchers on British wintering grounds. Therefore, as Fig. 6 illustrates, the density at which the winter mortality became density-dependent, \( c_W \), simply determined the point at which habitat loss started to affect population size. This is most clearly illustrated in the
Atlantic combined population. With $cW$ set at 2 birds per ha, for example, equilibrium population size began to be affected by habitat loss only after 50% of the present wintering area had been removed. Importantly, habitat loss began to affect population size earlier in the more fluctuating Continental population that was subjected to quite frequent and large density-independent severe weather mortalities. This happened because, in such a population, winter densities must have repeatedly exceeded 2 birds per ha, for example, well before 50% of the habitat had been removed. Winter habitat loss would thus be expected to affect population size sooner in populations that fluctuate widely than in ones that do not.

Once enough habitat had been lost to affect population size, the magnitude of the impact then depended on the slope of the density-dependent winter mortality function, $bW$. In all these simulations, $cW$ was set at 1-0 bird per ha. The results showed that the effect of winter habitat loss varied between inland and coastal subpopulations in both regions, even though the strength of the summer competition for breeding territories was the same ($bT = 0.5$) in all four subpopulations (Fig. 7). Perhaps because of their greater clutch size and hatching success (Table 1), the inland subpopulations in both regions were initially less affected by winter habitat loss than were either of the two coastal subpopulations. However, in all subpopulations, the impact of habitat loss increased as $bW$ increased, especially over the lower range of values. Fig. 8 highlights this by plotting population size at a particular percentage reduction in winter area according to the value of $bW$. At any given amount of habitat loss, the equilibrium size of the Continental and Atlantic populations combined were little affected by increases in $bW$ above a value of 0-05.

The limited data available (Goss-Custard et al. 1995d) suggest that competition for territories is less intense inland than on the coast. To explore the possible effect of this on habitat loss predictions, $bT$ was set at 0-3 in both inland subpopulations and at 0-7 in both coastal subpopulations. In fact, extensive tests showed that, at any given strength, $bW$, of winter density dependence, the strength of the summer competition for territories over a wide range ($bT = 0.3–0.9$) had rather little influence on the predicted effect of winter habitat loss; the only difference occurred in the Continental population when the lowest values of $bW$ and $bT$ were used. Mostly however, the population consequences were virtually the same as when the intermediate value of 0.5 was used in all subpopulations.
Population consequences of habitat loss. II

Fig. 6. The effect of reductions in the winter habitat of up to 90% on the size in autumn of the population at equilibrium of the four subpopulations, separately and combined into regions. The different lines refer to different values of c\textsubscript{W}, the density at which the winter mortality becomes density-dependent: ●, c\textsubscript{W} = 1·0; ▲, c\textsubscript{W} = 1·25; *, c\textsubscript{W} = 1·5; ■, c\textsubscript{W} = 2·0. In all cases, b\textsubscript{T} = 0·5, and b\textsubscript{W} = 0·05. The density-independent variables were set at the values given in Table 1.

**Extensions to the Basic Model**

Winter density dependence acts only on young birds

Birds in their first and second winters may be the most vulnerable to competition as overall density increases on the wintering grounds (Goss-Custard & Durell 1984). The effect on predictions of the effect of habitat loss on the total population size of restricting winter density dependence to just these young birds was therefore explored. In all four subpopulations, b\textsubscript{T} was set at 0·5 and a\textsubscript{W} and b\textsubscript{W} were varied as above. Compared with when birds of all ages were subject to winter density-dependent mortality (Fig. 7), the population size was less affected at the lower amounts of habitat loss, especially at low values of b\textsubscript{W} (Fig. 9).

Density-dependent fledging success

The effect of introducing density-dependent fledging success was explored in simulations in which b\textsubscript{T} was again set at 0·5 and b\textsubscript{W} at 0·05. In both coastal subpopulations, introducing density-dependent chick mortality substantially reduced the impact on population size of small amounts of habitat loss (compare solid circles with the dotted line in Fig. 10). This happened, of course, because elevated winter mortalities were compensated to some degree by greater fledging production at low breeding densities. The effect was much less marked in the two inland subpopulations where the density-independent chick production had, in any case, been relatively high. However, in all subpopulations, increasing winter habitat loss eventually caused the total population size to decrease sharply as the compensatory
increase in fledging success at low population densities no longer prevented a population decline from taking place.

Sex difference in mortality

The effect on the predictions of introducing a sex difference in mortality was explored in simulations in which $b_T$ was again set at 0.5 and $b_W$ at 0.05. Winter mortalities were set so that the population average equalled the previous values but the female rates were set 2% above the average while the male rates were set 2% below. Sex differences in mortality were introduced just for post-fledging young birds or for birds of all ages. Without also introducing density dependence in fledging success, all populations quickly went extinct because there were too few females available to produce enough young to sustain the population. With fledging success, however, density-dependent populations were sustained because of the increased production rate at low population sizes. In these circumstances, the effects on habitat loss predictions of introducing a sex difference into winter mortality of birds of all ages were generally small (compare dotted line with open triangles in Fig. 10). Introducing a sex difference in mortality in just the young birds made little difference to the consequences of habitat loss in the Continental population (compare open and closed triangles in Fig. 10). However, in the Atlantic coastal population, a sex difference in the mortality of just the young birds caused the predictions to return to the same base level where chick mortality was assumed to be density-independent (compare solid circles and solid triangles in Fig. 10).
Fig. 8. The effect of reductions in the winter habitat on the size in autumn of the population at equilibrium of the four subpopulations separately and combined into regions according to the strength of the winter density-dependent mortality \((bW)\). The different lines refer to different amounts of winter habitat loss; *, 10%; ●, 30%; ▲, 60%; ■, 90%. In all cases, \(bT = 0.5\) and \(cW = 1.0\). The density-independent variables were set at the values given in Table 1.

**Proportionate Habitat Loss and Population Size Reductions**

The practical task of predicting the population consequences of winter habitat loss would be quite straightforward if the reduction in population size was simply in proportion to the amount of habitat lost. This did occur approximately in a number of simulations, depending on the assumptions. Fig. 11 shows, for varying values of \(bW\) and for each subpopulation within each region singly and combined, the percentage reduction in population size following a given percentage reduction in the area of winter habitat. Irrespective of the value of \(bW\), the two percentages did not coincide closely in any of the subpopulations alone. However, they coincided more closely in the regional populations, but only at the higher values of \(bW\). A similar trend for the percentage reduction in population size to match the percentage reduction in wintering area more closely as the scale considered was increased was found in the other simulations detailed in this paper. However, the extent to which this occurred was sensitive to some model assumptions, although not all. Thus, at the scale of the total European population, the conclusion that matching occurred only at the higher values of \(bW\) was unaffected by the values given to \(bT\) in the inland and coastal breeding subpopulations (Fig. 12a and b). However, matching was not exact when density-dependent winter mortality was assumed only to affect young birds (Fig. 12c) and when chick mortality was assumed to be density-dependent and sex differences in winter mortality rate were assumed (Fig. 12d). Only in some circumstances will the proportionate reduction in population size match the proportion of the winter habitat that is lost.
Fig. 9. The effect of reductions in the winter habitat on the size in autumn of the population at equilibrium of the Continental and Atlantic populations when the winter density-dependent mortality affected birds only in their first and second years. The different lines refer to different values of $bW$, the strength of the winter density-dependent mortality: $\star$, $bW = 0.001$; $\star\star$, $bW = 0.01$; $\bullet$, $bW = 0.05$; $\blacktriangle$, $bW = 0.30$. In all cases, $bT = 0.5$ and $cW = 1.0$. The density-independent variables were set at the values given in Table 1.

Discussion

The sensitivity of equilibrium population size in shorebirds to the parameter values of the density-dependent functions in both summer and winter and to the values of the density-independent mortalities has already been shown (Goss-Custard 1980, 1981, 1993; Goss-Custard & Durell 1984, 1990). The present results for oystercatchers confirm these earlier findings, as the response of overall population size to $bT$, the strength of the competition for territories in summer, illustrated. This is to be expected, given the results of general theory on the sensitivity of population size to quite small shifts in parameter values, even when all the relationships in the model are quite simple and deterministic (May 1981).

This paper, however, is concerned with the sensitivity to parameter values of the predictions of the effect on overall population size of varying amounts of winter habitat loss. As could be deduced without modelling, the density at which mortality became density-dependent in winter ($cW$) simply determined the point at which winter habitat loss began to affect population size. However, modelling drew attention to the point that habitat loss would begin to affect population size earlier in the more fluctuating Continental population. This happened because $cW$ was exceeded regularly in years when numbers, and hence densities, were high. Winter habitat loss would therefore be expected to affect population size sooner as habitat is lost in populations that fluctuate widely more than in ones that do not.

Another important conclusion from the model was that the value given to the slope of the winter density-dependent mortality function ($bW$) had a large influence on the predicted effects of habitat loss, but only at low values. Once $bW$ reached 0.05, when the mortality rate increases by 5% per 1 bird per ha increase in bird density, the predicted effect of habitat loss on the global population size was rather little affected by the value of $bW$, especially when large amounts of habitat were removed. This conclusion was robust across the probable range of values of $bT$, the strength of the summer competition for breeding territories, and unaffected by whether or not different values of $bT$ were used for inland and coastal breeding birds, and whether the sexes experienced different mortality rates outside the breeding season.

These findings have important consequences for research into the effects of winter habitat loss in shorebirds and in other taxa. They imply that, once winter mortality has begun to be affected by competition for food, the predicted effects of habitat loss will be greatly affected by the available estimates of $bW$, but only at low values. Field studies should therefore focus first on testing the hypothesis that some birds are in poor condition and die because of competition for food; in other words, that density dependence may be involved. It is thus important to estimate $bW$ to determine whether the probable value lies within the range where predictions are sensitive or insensitive to the precise value. If the latter applies, then predictions can be made with some confidence even if the estimate of $bW$ is only provisional and error-prone.

This sequence of analysis has so far only been applied extensively to oystercatchers. It is clear from the review in Goss-Custard et al. (1995d) that oystercatchers do die of starvation in winter and that competition may be involved. It is thus important to estimate $bW$. This is difficult to do directly by relating winter mortality rates to population density; mortality rates are hard to estimate in shorebirds and density changes rather slowly in this particular long-lived bird. However, $bW$ has been preliminarily estimated from simulations with a game theory.
Population consequences of habitat loss. II

Fig. 10. The effect of winter habitat loss on the size in autumn of the population at equilibrium of the four subpopulations separately and combined into regions when fledging success was assumed to be density-independent (●) or density-dependent (*) and when a 4% sex difference in winter mortality was introduced in either the young birds (▲) or all birds (△). In all cases, \( b_T = 0.5, b_W = 0.5 \) and \( c_W = 1.0 \). The density-independent variables were set at the values given in Table 1.

Despite the insensitivity of the impact of winter habitat loss to the value of \( b_T \) in the summer, the simulations have shown that the shape, as distinct from the slope, of the density-dependent production function in summer may have an influence. In the basic model, the proportion of birds unable to acquire a territory, expressed as a \( k \)-value, increased linearly with increases in the logarithm of the total numbers of birds attempting to breed. In reality, it is more likely that the slope, \( b_T \), gradually increases as the competition intensifies (Klomp 1980; Goss-Custard 1993), but no way was found from present data to estimate that rate of change. But in terms of its influence on production, the same effect was achieved by adding density-dependent fledging success; compared with the basic model, per capita...
production was therefore greater at low population sizes but less at high population sizes. As the amount of winter habitat removed increased, the equilibrium population size settled initially at higher levels than with the basic model but, subsequently, decreased at a much faster rate. It is now important that attempts are made to determine the form of the density-dependent production function in a sample of areas of varying habitat quality in an attempt to generalize across the breeding range.

An interesting result from the modelling was the difference in response to winter habitat loss of the inland and coastal populations within both regions. As winter habitat was removed, the coastal breeding populations were initially most affected. In fact, in most simulations, the inland breeding populations maintained virtually their initial size until a high proportion of the winter habitat had been lost. Since this occurred when the value of $b_T$ in both breeding habitats was the same, the difference in response presumably reflects the difference in fledgling production per breeding pair in each habitat. Even though they intermingled on the wintering grounds and were subjected to the same competitive pressures, habitat loss initially most affected the slower breeding coastal subpopulations. Future papers will explore more closely how two or more breeding subpopulations, which have different fledgling production rates, are affected by the removal of their common wintering areas within which birds of different breeding origin compete on equal terms.

Clearly, the present version of the model is quite simple and further improvements are required to increase its realism. At present, the model uses single values for the density-independent functions across subpopulations or regions. Although a single overall value must exist, the real values will vary between areas, and not necessarily independently of...
Fig. 12. The percentage reduction in the size of the population at equilibrium associated with increasing percentage reductions in the area of winter habitat. All graphs refer to the whole European population. The diagonal dashed line, $x = y$, shows where the two percentages coincide exactly. (a) Varying values of $bW$, $bT = 0.5$ in all subpopulations. (b) Varying values of $bW$, but $bT = 0.3$ inland and 0.7 along the coast. (c) Varying values of $bW$ but affecting only the first- and second-winter birds. (d) With $bT$ and $bW$ constant at 0.5 and 0.05, respectively, but with fledging success either density-independent (▲) or density-dependent (*) and a 4% sex difference in mortality in young birds (●) or birds of all ages (■). In (a)–(c), ▲, $bW = 0.001$; *, $bW = 0.01$; ●, $bW = 0.05$; ■, $bW = 0.10$. The density-independent variables set at the values given in Table 1.

the risk of habitat loss occurring in the wintering grounds. The model also assumes a single density-dependent function across the subspecies range during both the breeding and wintering seasons. While such a function must again exist, using a single function in winter does imply that habitat of average quality only is removed. In reality, the losses may be concentrated on above- or below-average quality habitats. Simulations with our game theory distribution model show that the values of $cW$ and $bW$ are greatly affected by the relative quality of the habitat that is removed (Goss-Custard et al. 1995a). What is needed now is an exploration of how variations in habitat quality within both the wintering and breeding ranges influence the response of the whole population to winter habitat loss.

Despite its simplicity and limitations, the present model does attempt for the first time to quantify the effects on a migratory subspecies population of the removal of part of its wintering range. It shows that, even if habitat of average quality is removed, the reduction on population size is not necessarily linear. The simulations point to the need to determine more precisely the form and parameters of the density-dependent functions whose influence is so critical. Although often motivated by the need to predict the effects of habitat loss, much research on shorebirds has regrettably failed to focus on these all-important feedback processes (Goss-Custard 1980, 1993). Furthermore, studies of bird populations in general have focused on the factors and processes that determine local breeding density rather than the size of the total population, including non-breeders, across a subspecies or species’ range. Yet, as field studies on colonies of breeding gulls, Laridae (Coulson 1991), and the examples given in this paper demonstrate, the effects of habitat changes on population size must be viewed within the context of the greater population with which most local populations are a part. While technically difficult, attempts must be made with such mobile animals as migratory birds to make predictions at the large scale at which many of the determining processes occur (Goss-Custard 1993) even though, as this paper has shown, some simplifying assumptions may, at our present level of knowledge, have to be made.

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