Predicting the population consequences of human disturbance for Ringed Plovers *Charadrius hiaticula*: a game theory approach

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Human disturbance and its potential impacts upon bird populations are currently topical and contentious issues for conservationists. Although many studies have revealed a behavioural impact, or even direct effect on breeding success or survival, these cannot usually be extended to predict the impact on population size. Here we present a population model that allows predictions of the effect that changes in human numbers, visiting a 9-km-long section of the coastline, may have upon the size of a Ringed Plover *Charadrius hiaticula* population. Human disturbance affects Ringed Plovers in our study area through birds avoiding areas of high disturbance and, in addition, through the accidental trampling of a small number of nests by people walking on the beach. Using the level of human disturbance and habitat variables (which define territory quality) it is possible to predict which areas of beach are occupied and therefore the sites available to the population. Breeding success, for a given area of beach, can be predicted from habitat data. Incorporating known, density-independent, adult mortality allows the equilibrium population size to be predicted. This provides a model that predicts population size. This model is then used to predict the population that the site would support with different, hypothetical, levels of disturbance. If nest loss from human activity was prevented, for example by fencing nests, we predict the Plover population size would increase by 8%. A complete absence of human disturbance would cause a population increase of 85%. If the numbers of people were to double, we predict the population would decrease by 23%.

There is a large volume of published information on the effects of disturbance to birds (see reviews by Hockin *et al.* 1992, Carney & Sydeman 1999, Nisbet 2000, Woodfield & Langston 2004). Various studies have shown a wide range of effects such as taking flight, an increase in heart rate or accidental trampling of nests. Despite this volume of literature, there is little information as to when disturbance is a serious issue and what levels of disturbance might cause a problem.

Such information is particularly important where the species is of conservation concern, yet to our knowledge, apart from Mallord *et al.* (in press), no published study of a breeding bird species quantifies the population consequences of disturbance. This is despite the fact that disturbance has been implied as a factor causing population decline for a wide range of species (Birdlife International 2000).

Population regulation occurs through density-dependent, negative feedback mechanisms and the strength of the density-dependence will determine the extent of the regulation. Territorial behaviour can provide an obvious mechanism for density-dependence (see Sutherland & Norris 2002) and through an understanding of territorial behaviour it is then possible to predict how density-dependence may operate for a population. There are essentially three mechanisms by which density-dependence can arise through territorial behaviour: when population size increases territories may compress, poorer quality sites may be used and individuals may refrain from breeding (Sutherland 1996, 2006).

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Territory size is elastic (Krebs 1971) and smaller territories may occur at high densities. In Davies's (1992) study of the Dunnock *Prunella modularis*, complex mating and territorial behaviour is shown to relate to the spatial distribution of the population. Mating behaviour is determined by territory size and the degree of territory overlap.

A wide range of studies shows that breeding sites vary in quality, for example in their habitat structure (Korpimaki 1988, Catchpole & Phillips 1992, Ens *et al.* 1992, Olson & Rohwer 1998, Murison *et al.* 2006), predation risk (Möller 1988, Penloup *et al.* 1997), nest-site availability (Plissner & Gowaty 1995), prey abundance (Komdeur 1992) or ease of defence (Eason 1992). Where such variation in site quality occurs, it can act as a mechanism for population regulation if at higher population sizes there is greater use of poorer sites with lower productivity (Rodenhouse *et al.* 1997). For this mechanism to work, individuals must be able to distinguish between sites that differ in quality. There is strong evidence that this is the case (Rodenhouse *et al.* 1997). A number of studies have shown that individuals will switch to better quality sites as they become available (Krebs 1971, Petersen & Best 1987, Switzer 1993, Greenberg & Gradwohl 1997). Territories ranked by the permanency of occupation (Korpimaki 1988, Möller 1982, Baeyens 1981, Bunzel & Druke 1989, Newton 1989), order of settlement (Brooke 1979, Lanyon & Thompson 1986, Bensch & Hasselquist 1991) or age (Lanyon & Thompson 1986) usually show a correlation with such rank and breeding success. The mechanisms by which these correlations occur are usually assumed to involve individuals sampling many sites. However, if dispersal is reduced or survival is higher on good quality sites, the same relationship between occupancy and quality will result (Rodenhouse *et al.* 1997).

A further aspect of territoriality is a phenomenon known as floating, whereby individuals present on the breeding grounds do not hold their own territories, even when such territories are available (Smith 1978, Smith & Arcese 1989). Following Ens *et al.* (1992), Komdeur (1992), Sutherland (1996) and Kokko and Sutherland (1998), we think of individuals as deciding not to breed rather than being prevented from doing so. Such individuals 'queue' for good quality territories rather than adopting a poor quality territory. In this way, the decision to adopt a territory or not is dependent on perceived territory quality, survival and the length of the queue.

With knowledge of the behavioural decisions that individuals make, density-dependent reproductive success can be determined, as at higher densities poorer quality sites may be adopted or, if all suitable sites are occupied, individuals may refrain from breeding. Equilibrium population size will occur when the mean lifetime reproductive success per individual is equal to 1. Thus, if mortality rates are known, it is possible to determine the density at which the population will reach equilibrium.

In this paper we illustrate the application of this approach and determine the consequences of human disturbance to the Ringed Plover *Charadrius hiaticula* population at a study site in Norfolk, England. Ringed Plovers provide an ideal species with which to explore the approach as they are associated with coastal areas which often receive high visitor pressure, especially during the summer, and there is evidence for a decline in the coastal breeding population of Ringed Plovers in the UK, with human disturbance having been implicated as a cause (e.g. Briggs 1983, Pienkowski 1984). The species is amber-listed as a species of conservation concern within the UK, owing to a moderate decline in the wintering population (Gregory *et al.* 2002). A number of other members of the genus are also threatened, and human disturbance is widely implicated as a cause, especially for species such as the globally threatened Piping Plover *C. melodus* (Birdlife International 2000).

METHODS

Habitat recording

Fieldwork was undertaken at Snettisham, Norfolk, England, on the eastern shore of the Wash (Fig. 1). The study site, stretching from Hunstanton in the north to the south end of the Snettisham Royal Society for the Protection of Birds (RSPB) reserve, consisted of a linear beach bordered on the inland side by an artificial sea-wall. The beach was divided, along the sea-wall, into 92 sections, each 120 m in length. The following variables were recorded in the centre of each section. Top of sea-wall: width and percentage vegetation cover; slope of sea-wall: width, percentage vegetation cover, angle of slope and percentage shingle; base of sea-wall to winter tideline (the strandline): width, percentage vegetation cover, number of ridges, percentage shingle and percentage cover of debris; tideline to edge of mudflat: percentage shingle and percentage cover of tideline debris.

Figure 1. Location map, showing location of study site. Stars mark the three car parks, providing vehicular access to the beach.

Disturbance

Forty-seven transects of the whole study site were walked at a consistent pace between February and August in 1996 and 1997. Direction, day of the week and time of day were varied. All persons, vehicles or dogs seen on the sea-wall or beach were mapped, allowing a figure for the total number of people recorded from all transects within each section to be calculated and used as an index of disturbance.

Trapping and colour-marking

Adults and pulli Ringed Plovers were individually marked using plastic colour rings. The majority of adults were trapped on the nest, using either a spring trap or a walk-in cage trap. Nest trapping was always conducted at least 10 days after the last egg was found, and only in good weather, with the trap over the nest for a maximum of 30 min. No nests were deserted after trapping and no eggs were damaged in the course of the ringing. Small numbers of adults were caught using spring traps and cannon and 'whoosh' nets were used outside the breeding season.

Adults in the hand were aged (see Prater *et al.* (1977) for ageing criteria). Sex could sometimes be determined if both members of the pair had been seen during trapping, through the behaviour or contrast in plumage between the two individuals. In the hand, the presence of a bright yellow or orange orbital ring was taken as indicative of a male, but as some known males lacked this feature, it was not used to sex females positively.

Colour-ringed individuals at the site were monitored on regularly spaced transects conducted at high tide along the entire study site. All Ringed Plovers were mapped. Sightings of colour-ringed birds away from Snettisham were received from other observers submitted through the British Trust for Ornithology.

Breeding biology

Nest searching commenced in mid-April. By regular comparisons of maps of bird sightings (especially courting individuals) with nest locations it was possible to locate gaps where nests were missing or where a previous nest had failed but the continued presence of the adults suggested renesting would be

likely. Nests were found by searching with a telescope for incubating adults or by following adults back to the nest. Cold searches were also regularly conducted over all areas of the beach, particularly where the vegetation and topography hindered observation of adults. Nests were checked at approximately 2-day intervals.

Once sufficiently large, chicks were individually colour-marked and subsequent resightings enabled fledging success to be determined. Adult behaviour, such as broken wing displays and alarms calls, proved a reliable indicator of chick presence as they only occurred when chicks were present.

Modelling

In order to develop the model, the following stages were required:

(1) Prediction of breeding success from habitat data.

The mean number of chicks hatched per individual, per year, per section was chosen as the measure of actual breeding success. Many of the beach habitat variables would be expected to be correlated (for example, wider beaches would be expected to be shallower). Multiple regressions are difficult to interpret when the independent variables are highly correlated, and in such circumstances Principal Component Analysis (PCA) is a more appropriate approach (Freckleton *et al.* 1999). Each habitat variable was first tested singly against breeding success, using a standard linear regression. Different combinations of variables were then used within the PCA, and the factor scores were used as independent variables with which to predict breeding success. All combinations of variables were tried, and the combination which produced the best model (the most variance in breeding success explained using the fewest variables) was selected.

(2) Prediction of occupancy.

The probability of a territory being occupied or not was determined using binary logistic regression, using disturbance (total people) and habitat (the PCA factor score developed in 1) as independent variables.

(3) Predicting the number of pairs.

Sections of the beach with a probability of occupancy of 0.5 or above were predicted as ones which would be used by breeding pairs. As the sections differed in area (each section was the same length, but the width of the beach, from the sea-wall to mean high water (MHW) varied) the number of pairs within each section also varied. Beach width

measurements were therefore used to determine the number of breeding pairs that would be expected within each section. The sum of the number of pairs per section, for all sections where the probability of occupancy was above 0.5, gave the total number of breeding pairs.

(4) Determining equilibrium population size.

Pairs were assumed to settle sequentially, with the highest quality section (the section where breeding success would be highest) occupied first. Thus, mean breeding success declines as the population increases. The equilibrium population size occurs when mean *per capita* breeding success was at the level required to replace that individual within the population.

We assume that for the population in our study site winter mortality was density independent, as the winter distribution of adults and first winters was scattered over a wide range of localities. Whereas some individuals wintered on or near the breeding grounds, some, particularly first-winter birds, moved north with records as far north as Lothian, Scotland, and some individuals spent the winter in northern France. Although density-dependence is likely to occur on the wintering grounds due, for example to depletion and interference, the variation in the population size at Snettisham will have a trivial effect on the total population as these birds represent such a minute proportion of the total in their wintering area. We estimate mortality, immigration and emigration from ringing data and use this estimate to determine the level of breeding success at which an individual would replace itself within a population. We use this figure to determine equilibrium population size.

Eleven scenarios of different disturbance levels were chosen at which to explore the effect of disturbance on the equilibrium population size. The changes in disturbance levels used in these scenarios are perhaps unlikely at Snettisham as they were chosen in order to understand the role of disturbance on Ringed Plover population size. Although a change such as a doubling of disturbance levels across all sites is perhaps unlikely to occur, by considering such a level of change the models will demonstrate the full implications of disturbance on population size. The 11 scenarios chosen were:

(1) disturbance levels increased by 50% on all sections;

(2) disturbance levels increased by 100% on all sections;

(3) disturbance levels decreased by 50% on all sections;

(4) no disturbance on any sections and no direct nest loss from human activity;

Table 1. The effect of a range of beach habitat variables on the mean total number of chicks hatched per individual, per year, per section. Habitat variables used are those that describe the total beach area (total beach width) and those that describe the upper beach, where nesting occurs. Variables are listed in order of significance. In order to isolate the effects of habitat from disturbance, only those sections ($n = 28$) that have low disturbance levels are included, and all sections were settled in at least 2 years and with at least three nests found during the study.

Variable	Coefficient ± 1 se	P	r^2
% cover estimates (all arcsine transformed)			
% cover of tideline debris	7.45 ± 1.48	< 0.001	0.47
% vegetation on slope of sea-wall	0.94 ± 0.43	0.04	0.12
% vegetation at the base of sea-wall	−0.01 ± 0.01	0.32	< 0.01
% vegetation at the top of sea-wall	0.57 ± 0.58	0.34	0.04
% shingle from base of sea-wall to tideline	−0.05 ± 5.19	0.92	< 0.01
Width of top of sea-wall (m)	0.08 ± 0.04	0.06	0.10
Beach width measurements (log_{10})			
Total beach width (m)	1.39 ± 1.02	0.18	0.03
Width of slope of sea-wall (m)	−0.05 ± 0.04	0.23	0.02
Width of beach, sea-wall to tideline (m)	0.73 ± 0.37	0.58	0.01
Angle of slope of sea-wall	0.26 ± 0.71	0.72	0.005

(5) no disturbance on any sections but still nest loss through human activity (this allows the population consequences of direct nest loss from human activity to be determined);

(6) disturbance levels identical to those currently recorded, but no loss of nests to human activity;

(7) disturbance increased by 100% on the RSPB reserve (the southerly part of the study site, south of Snettisham Scalp);

(8) disturbance decreased by 100% on the RSPB reserve;

(9) disturbance increased by 100% on the ten widest sections of beach;

(10) disturbance decreased by 100% on the ten widest sections of beach; and

(11) new car park created at southern end of the RSPB reserve. The new car park is assumed to create disturbance levels identical to that for the car park at the end of beach road, and the six sections either side of the car-park location are changed accordingly.

The importance of different variables in determining the final estimate of equilibrium population size was used to determine the sensitivity of the model. The model was rerun with a single variable changed by ± 10% and the change in equilibrium population size used as an indication of the relative sensitivity of the model to that variable.

RESULTS

Predicting breeding success from habitat

Different habitat variables were tested singly to determine the effect of habitat on breeding success

Table 2. Results of the principal components analysis used to describe territory quality. The loading of each habitat variable on each component is shown.
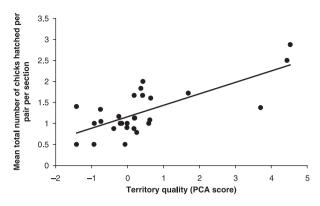
	Factor 1	Factor 2
% of variance	62%	21%
% cover of tideline debris in section	0.001	0.95
Width of beach, from tideline to sea-wall (m)	0.69	0.42
% vegetation cover, from sea-wall to tideline	0.89	−0.13
Total beach width (m)	0.78	0.17

(Table 1). The percentage cover of tideline debris per section was the most significant variable, describing 47% of the variance in hatching success. A better model was found by using a combination of tideline debris cover, beach width from the sea-wall to the tideline, total beach width and the percentage cover from sea-wall to tideline, within a PCA (Table 2). The factor 2 score from this PCA (Table 2) explained 53% of the variation in breeding success (Fig. 2).
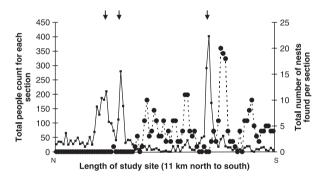
In total, 188 chicks were ringed between 1994 and 1996, usually at hatching or within a few days of hatching, of which 28 were resighted by 1998. The number of chicks hatched per individual was thus multiplied by 0.148 to convert the numbers of chicks produced to the number of surviving adults.

Predicting occupancy

Those sections which were occupied during the study (i.e. at least one nest was found within the section during the period 1996–98) were those with
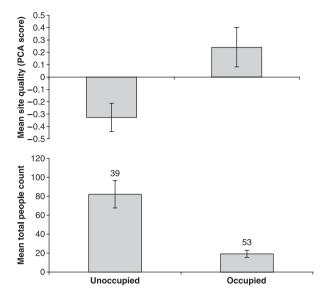
Figure 2. Relationship between breeding success (mean total number of chicks hatched per pair, per year, per section) and beach habitat, as described by the PCA factor 2. Data are for all sections occupied in at least 2 years (1996–98) and with at least three nesting attempts recorded in total over 3 years ($n = 28$ sections). For explanation of PCA, see Table 2. $y = 0.545x + 2.315$, $r^2 = 0.531$.

Figure 3. Number of nests (dotted line) and disturbance levels (solid line) across the whole study site. The disturbance data are total number of people recorded for each section from transect data in 1996 and 1997. The peaks in the disturbance levels correspond with car parks, symbolized by arrows above the graph. Nest data are the total number of nests found per section, 1996–98.

Figure 4. Mean disturbance levels (total people recorded per section) and site quality (PCA score, Factor 2) for sections occupied and unoccupied. 'Occupied' is defined as at least one nesting attempt occurring within the section between 1996 and 1998. Error bars show ± 1 se, sample sizes are given. For disturbance, $t = 4.80$, $P < 0.01$; for the PCA score, $t = -2.70$, $P < 0.01$.

Table 3. Contingency table comparing predictions of occupancy with actual occupancy. Those sections predicted as occupied are those with a probability, from the logistic regression in Table 4, > 0.5.

	Predicted		
Actual	Occupied	Not	Total
Occupied all years of the study	23	3	26
Occupied some years of the study	20	7	27
Never occupied during the study	8	31	39
Total	51	41	92

Table 4. Results of a logistic regression relating the probability of a section being occupied by breeding Ringed Plovers to habitat quality and disturbance levels per section. Habitat quality is the PCA score (Factor 2) described in Table 2, and disturbance levels are total number of people recorded per section. Data from 92 sections.

Variable	Parameter estimate (logit transformed)	Wald	P
Habitat quality	0.77 ± 0.39	3.86	0.04
Total people	−3.44 ± 0.78	19.74	< 0.001
Intercept	5.17 ± 1.14	20.75	< 0.001

the best habitat (PCA score) but there was also a clear impact of disturbance, with unoccupied sections having higher people counts (Fig. 3). As Figure 4 clearly shows, both disturbance and habitat determine which sections were used by breeding pairs.

Site quality and total people counts were used as independent variables in the logistic regression to predict the probability of a section being occupied and together correctly predicted occupancy ('occupied' territories being those with a probability of occupancy > 0.5) for 80% of sections (Table 3). The parameter estimates and regression statistics are summarized in Table 4. The logistic regression was

also repeated, including an interaction term for the two independent variables (i.e. disturbance × site quality). The interaction term was not significant (Wald = 0.173, $P > 0.677$), suggesting that highly disturbed sites would not be settled, regardless of the site quality.
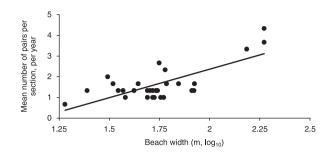
Using the parameter estimates in Table 4, the probability of a section being occupied can be calculated by the inverse logit of 5.17 + (0.77 × PCA score) + (−3.44 × total people).

Predicting the number of pairs within each section

Total beach width, as measured from the sea-wall to the edge of the mudflats, described the amount of space available within each section and was a significant predictor of the number of pairs within each section, explaining 32% of the variation in the number of pairs per section (Fig. 5).

Perception of site quality

The habitat variables used to predict breeding success in the PCA analysis are all fundamental aspects of the beach habitat and only the percentage vegetation cover changes within the breeding season. Figure 4 suggests that individuals are able to differentiate between good and poor quality sites and settle accordingly. Further measures of how individuals perceive site quality are variables such as the age of individuals within a section, male arrival date and

Figure 5. The relationship between the mean number of pairs per 120-m-long section and total beach width. Total beach width, measured at 90° to the sea-wall, determines the area of the section and thus the space available. Data shown from all sections 1996–98, where breeding occurred in at least one year of the study. $y = 2.591x - 3.314$, $r^2 = 0.318$.
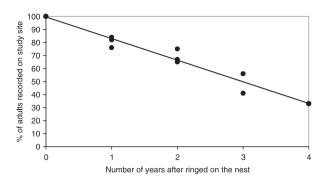
the mean lay date of first attempts within a section. Many such variables do correlate with territory quality (Table 5).

Adult survival and movement

The proportion of adults present in subsequent years appears to decline in a linear fashion (Fig. 6). If the population is to remain stable, the mean breeding success per individual required is 0.165 chicks per year (calculated from the regression equation from Fig. 6). If the population proved to be a source or a sink (Pulliam & Danielson 1991) then this would confound any predictions. However, estimates of immigration and emigration rates showed them to be similar (Liley 1999).

Table 5. Correlation coefficients and significance for measures of perceived quality and actual site quality, as defined by the PCA Factor 2 score (see Table 2). Where perceived variable is a date, it is expressed as days from 1 January. Male arrival date is the earliest arrival date per section. Behaviour variables are from behavioural observations recorded during mapping of colour-ringed birds, and give the mean percentage sightings of individual breeding males per section involved in the behaviour. Ages are from 1998 only and expressed as years if the individual is less than 5 years old and if 5 years or older, or if ringed as an adult in 1994, it is aged as 5; where more than two ageable birds were present in any section, the minimum age was used. Maximum number of years present is calculated as the maximum number of consecutive years an individual was recorded breeding in a section.
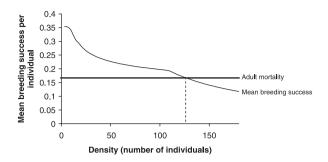
Perceived quality variable (per section)	Pearson correlation coefficient	*n* (no. of sections)	*P*
Mean no. of nests per pair (1996–98)	0.39	52	< 0.01
Mean lay date per section (first attempts only)	−0.26	50	0.07
Male arrival date (in 1997)	−0.25	28	0.21
% sightings of male involved in butterfly display	0.37	36	0.03
% sightings of male involved in aggressive encounter	0.20	36	0.24
Female age	0.14	34	0.45
Male age	0.46	27	0.01
Female, maximum no. of years present on section	0.40	34	0.01
Male, maximum no. of years present on section	0.36	27	0.07

Figure 6. Proportion of adults ringed in one year and present at the study site in future years. Only adults at least 2 years old or more are considered and sample is from those trapped on the nest – thus only birds known to have bred at least once. Sample sizes are 52 birds (1994), 17 birds (1995), 33 birds (1996) and 15 birds (1997). $y = -16.533x + 19.427$, $r^2 = 0.955$.

Figure 7. Density-dependent breeding success for Ringed Plovers, using current habitat and disturbance levels. Mean breeding success per individual is the number of young produced that return to the population in subsequent years. Density is the number of individuals within the population. Breeding success is predicted using habitat data; sections are predicted as occupied or not using logistic regression of disturbance and habitat data (Table 4) and sections assumed to be settled in order of quality. Once all occupiable sites are fully occupied then floating occurs.

Estimate of equilibrium population size

Figure 7 shows the density-dependent function that would result from the above analyses, using the current habitat and disturbance data at Snettisham. The predicted population size and breeding success values are given in Table 6, where they are compared with field data from 1996–1998. Table 6 shows that the predicted values represent the current situation, with only a slight underestimation of the number of pairs breeding and slight over-estimation of the number of chicks hatched. The number of floating individuals is impossible to measure in the field due to the presence of migrant and unringed birds, but there is evidence of floating occurring. In 1998, 22 colour-ringed individuals were present that did not breed on the site, 11 of these had bred in previous years and no nesting attempt was recorded for them within that year. The remaining 11 individuals were colour-ringed as chicks in previous years and had never been recorded breeding.

The density-dependent function (Fig. 7) shows a marked kink in breeding success near the end, as a point is reached at which no more sites are available. In Figure 6 this occurs at a population size of 109 individuals and at a mean breeding success of 0.192, just above the adult mortality rate of 0.165.

The effect of changing disturbance levels on equilibrium population size

The current equilibrium population size predicted by the model is 126 individuals (Fig. 7). It is possible to manipulate parameters within the model in order to determine the effects of changes in disturbance levels on the population size. The main effect of disturbance is through sections of the beach being unoccupied where disturbance levels are high. Any change in disturbance will alter the probability of a

Table 6. Predicted population size and breeding success at Snettisham from the density-dependent function (Fig. 7) compared with actual data. Actual data are the mean (± 1 se) from 1996 to 1998, except for the number of young recruited where the data are from 1996 only to allow 2 years before all returned young are present.

	Actual	Predicted
Number of sections occupied	39.0 ± 2.1	51
Total number of young hatched	124.7 ± 6.2	142.5
Number of young returning in future years	17	21.1
Number of individuals breeding	125.3 ± 3.2	109.5
Number of individuals floating	?	16.8
Equilibrium population size (number of individuals)	?	126.3

section being occupied, according to the logistic regression given in Table 4.

A further effect of disturbance is through direct loss of nests. Although only the sections with low disturbance levels are used by breeding pairs, 8.5% of eggs are still lost through human activity. There is no clear relationship, within these low disturbance levels, between the proportion of nests lost to trampling and the number of people recorded for that section. This is likely to be because other factors, such as nest location within the section, are important. If disturbance levels are changed, it is still only sections with low disturbance levels that will be occupied. In order to include nest loss through trampling within the model it is therefore necessary to assume that, at low disturbance levels, nest loss to human activity is equal across all sites. In total, 883 eggs were found over the 3-year study period. Of these, 75 were lost to human activity, while 409 hatched. Therefore, with current disturbance levels, hatching success is 46.3% and if there was no disturbance, hatching success would 50.6%.

The changes in disturbance levels described for each of the above scenarios were applied to the model. The results for all 11 scenarios are shown in Table 7 and Figure 8 shows three of the scenarios.

Sensitivity of the model to particular variables

The sensitivity of the model to the accuracy of parameter estimates was tested by changing each parameter value by 10% and examining the resulting change in equilibrium population size (Table 8). With the exception of total beach width, the equilibrium population size is not changed disproportionately for any of the variables. The model is especially sensitive to changes in total beach width.

DISCUSSION

Field data, theory and a modelling approach have been dovetailed in order to consider behavioural responses at a population scale. The model has been shown to represent the actual population, and allows floating to be considered in relation to density-dependence. The model is then extended to allow changes in human disturbance levels to be considered in a population context.

Disturbance clearly has a major impact on Ringed Plover population size. The provision and management of access to sites require careful planning and

the results presented allow such planning to be made in relation to maintaining or enhancing Ringed Plover population size. Sites that are highly disturbed are not used by breeding birds, and therefore any increase in disturbance levels on these sites will not alter population size. By contrast, large increases in disturbance levels to previously undisturbed sites would adversely affect population size, as these sites would no longer be used by breeding pairs. Areas of wide beach support higher densities of breeding birds, per metre of sea-wall, than narrow beaches. Thus, managing disturbance levels so that the widest sections are away from access points is likely to result in the largest population size possible per length of coastline.

Using the logistic regression equation it is possible to suggest the disturbance level above which the site would not be occupied. If the mean site quality value for all sections is used, in order to gain a probability of greater than 0.50 that a section will be occupied, the total people value is 30.90. This value is a total from all 47 transects (February–August 1996–98) and equates to an encounter rate of approximately 0.37 people per minute at average walking pace or an average of 0.005 people per metre of sea-wall per transect.

Assumptions used in the framework

The importance of perception

There are a number of alternative indicators of perceived quality. These include age, breeding chronology (such as arrival date or laying date), permanency of occupancy and various behaviours (see Table 5). These gave reasonably consistent indications of the importance of beach width and lack of disturbance.
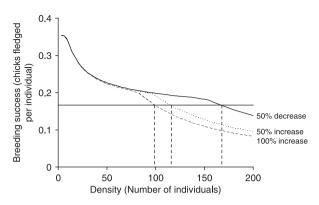
The density-dependence is produced by the model from the process of individuals selecting territories that have higher reproductive output. Of course, the presence of ecological traps, in which there are areas that are selected but are actually of poor quality (see Orians & Wittenberger 1991; Székely 1992) will greatly effect the shape of the density-dependent curve (Kokko & Sutherland 2001). The evidence from this study was that preference was related to breeding output.

Density-independent survival

In order to predict equilibrium population size in the future it is necessary to make some assumptions about survival. For Ringed Plovers at Snettisham we

Table 7. Population estimates for 11 different scenarios of differing disturbance levels. Scenarios are described in the text.

Scenario	Description	No. of sections occupied	Total young hatched	No. of young returning in future years	No. of pairs breeding	No. of individuals floating	Equilibrium pop. size (no. of individuals)	% change in pop. size
	Current disturbance levels	51	142.48	21.09	54.74	16.80	126.26	
1	50% increase, all sections	46	128.18	18.97	48.58	16.42	113.60	−10.14
2	100% increase, all sections	39	110.14	16.30	41.14	15.32	97.60	−22.78
3	50% decrease, all sections	70	187.17	27.70	77.02	11.84	165.99	31.37
4	No disturbance and no nest loss from human activity	92	263.45	38.99	104.04	25.38	233.46	84.90
5	No disturbance, nest loss from human activity	92	244.06	36.12	104.04	8.22	216.30	71.31
6	No loss of nests from human activity	51	153.79	22.76	54.74	26.81	136.30	7.95
7	Disturbance increased by 100% on RSPB Reserve	49	138.65	20.52	53.06	16.76	122.88	−2.78
8	Disturbance decreased by 100% on RSPB Reserve	51	144.467	21.38	54.74	18.54	128.02	1.40
9	Disturbance increased by 100% on 10 widest sections	51	142.48	21.09	54.74	16.78	126.26	0.00
10	Disturbance decreased by 100% on 10 widest sections	55	162.41	24.03	62.99	17.94	143.92	13.99
11	New car park created	44	129.80	19.21	48.98	17.06	131.40	−8.01

Figure 8. Assessment of equilibrium population size. The density-dependent function varies with three different hypothetical disturbance levels. Horizontal line represents adult mortality rate. The predicted equilibrium population sizes are at the intersections. Predicted population sizes for each scenario are given in Table 6.

assume winter survival to be independent of breeding density. This is because ringing recoveries of Ringed Plovers ringed at Snettisham and recorded during the winter (see Liley *et al.* 1999) clearly show that the Snettisham population winters across a very broad spread of sites, including northeast Britain, Ireland, southwest England and Brittany. Hence, we are focusing on a site supporting a local population which mixes with birds from other sites over the winter. Any factor affecting a single site will be unlikely to impact the winter population as a whole, and therefore density-independent winter survival is likely. This assumption would not apply for an analysis that affected the whole population, such as climate change.

To conclude, this paper demonstrates that it is possible to determine the impact of human dis-

turbance through an understanding of density-dependence. In terms of conservation it is at this level, the population context, that issues such as disturbance should be addressed. Human disturbance can be seen to have a major impact on Ringed Plover population size, and the estimated 85% increase in population size that would occur, were human access to be restricted, represents the impact of disturbance on the species. The framework utilized in this paper is flexible and potentially applicable to almost any aspect of environmental change or any species. The predictions presented here were obtained, in the main, over three breeding seasons. Whilst further years' data will provide them with greater strength, this paper illustrates that very long data sets are not necessarily essential to predict population-scale change.

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Table 8. Sensitivity of predicted equilibrium population size in response to changing individual parameters by 10%. Table gives the resulting equilibrium population size after increasing or decreasing the parameter value for each section by 10%. The percentage change describes the percentage change from the original estimate to the new.

Variable	Predicted equilibrium population size		Percentage change in equilibrium population size
	+10%	−10%	
% tideline cover	63.13	58.27	0–7.69
Base of sea-wall to tideline width (m)	64.00	63.13	1.38–0
Vegetation cover, base of sea-wall	63.13	62.33	0–1.27
Total beach width (m)	87.78	38.37	39.04–39.22
Total number of people per section	66.82	59.872	5.84–5.16
Adult mortality rate	57.40	70.16	9.22–11.08

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