

# The effects of disturbance on habitat use by black-tailed godwits *Limosa limosa*

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## Summary

1. Human disturbance of wildlife is widely considered to be a serious conservation problem. However, despite many qualitative studies, little attempt has been made to assess whether human presence limits the number of animals that sites can support. This can be quantified by incorporating measures both of human presence and of resource distribution into analyses of population distribution. The effects of disturbance can then be measured from any reduction in resource use at disturbed sites, which in turn indicates any reduction in the number of animals supported.

2. Shorebirds are often considered highly susceptible to disturbance because of their very obvious flight responses to humans and because they use areas that are generally subject to high levels of human recreational use.

3. This study addressed the effect of human presence on the distribution of black-tailed godwits *Limosa limosa islandica* on coastal areas in eastern England. We identified the prey types selected by godwits and related their depletion to different levels and types of human disturbance at a range of spatial scales.

4. Three methods of analysis are described: simple regressions of the effect of human activity on the number of godwits supported; multiple regression analyses of the effect of human presence and prey density on godwit numbers; and analyses of the effect of human presence on prey density at the end of the season. The latter method assumes that godwits are responsible for the majority of resource depletion. None of the analyses showed any effect of human presence on the number of godwits supported by the food supply at any of the spatial scales examined.

5. Many species may appear to avoid human presence but this may not reduce the number of animals supported in an area. Assessing the influence of disturbance on the relationship between animal distribution and resource distribution provides a means of assessing whether numbers are constrained by disturbance.

*Key-words:* bivalves, estuaries, human presence, prey selection, waders.

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## Introduction

The effect of human disturbance on animal distribution has received considerable attention in recent years (Owens 1977; Stalmaster & Newman 1978; Bélanger & Bédard 1989; Keller 1991; Stockwell, Bateman & Berger 1991; Pfister, Harrington & Lavine 1992; Reijnen *et al.* 1995; Madsen 1998). Assessing the severity of the effects of disturbance has important practical consequences; if it has serious impacts, conservationists are justified in

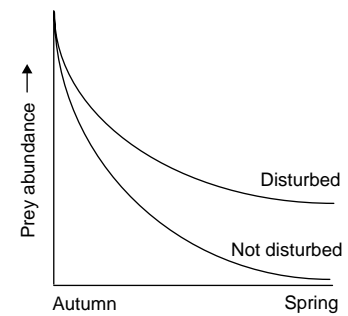
recommending that access to wildlife areas be limited (Burger 1981; Tuite, Hanson & Owen 1984; Klein, Humphrey & Percival 1995). However, if the impacts of disturbance are trivial, then such measures cannot be justified. Restricting human access to the countryside can be expensive and time-consuming but, more importantly, it goes against the increasing view that rural access should be increased. Moreover, access to areas of conservation value can be the best way to protect them, as it increases the value placed on them by society (Adams 1997). There is therefore a need to quantify the extent to which disturbance adversely affects animal populations, in the context of a wider debate of how much human access to wildlife areas should be sanctioned or discouraged.

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There are two components to the problem of disturbance: whether human presence causes animals to avoid areas that they would otherwise use, and whether this in turn affects mortality, reproductive success or population size (Gill & Sutherland 2000). The majority of studies of disturbance refer to the first component and use one of two approaches. The first compares animal distribution between sites with differing levels of disturbance (Tuite, Hanson & Owen 1984; Pfister, Harrington & Lavine 1992; Sutherland & Crockford 1993; Milsom *et al.* 2000; Suárez, Balbontín & Ferrer 2000). Interpreting such studies can be difficult because variations in disturbance are often confounded by factors such as prey density, competitor or predator density, or the locations of territories, nests or roost sites. Nevertheless, such information is necessary in order to demonstrate whether disturbed sites support fewer animals than the resources would potentially allow, and to quantify the extent to which the use of such sites could be increased if disturbance was absent. The second approach involves recording short-term behavioural responses to disturbance (Draulans & van Vessem 1985; Bélanger & Bédard 1989). It is, however, impossible to relate such short-term responses to the pattern of use of sites over a whole season. This is because animals may be displaced from disturbed sites in the short term but may return at a later date; over the course of a season the overall use of these sites may then be unaffected by disturbance. Studies of disturbance need, therefore, to identify the major factors related to the distribution and behaviour of the species in question and then to examine the role of disturbance in altering these relationships (Gill, Sutherland & Watkinson 1996).

Much of the concern about the effects of disturbance relates to coastal areas, because they sustain high levels of human recreational use (Davidson *et al.* 1991) and because they are important for wildlife (Smit & Piersma 1989; Piersma & Baker 2000). Such studies have often focused on shorebirds (Charadrii) as they frequently occur on areas subject to high human pressure and because their tendency to take flight in response to human presence suggests that they may be particularly susceptible (Burger 1981; Kirby, Clee & Seager 1993; Smit & Visser 1993). Sites with high levels of human activity often have lower densities of birds than sites with low levels (Burger 1981; Klein, Humphrey & Percival 1995). However, none of these studies has addressed whether disturbed sites could have supported more birds in the absence of human presence. While these studies may suggest an effect of disturbance on habitat use, it is clearly important to establish whether avoidance of human presence results in reduced use of the habitat over the course of a season or whether it is simply a short-term change in spatial distribution that will be reversed at a later date (Gill, Sutherland & Watkinson 1996).

During winter, estuaries at northern latitudes are an extremely important source of food for many thousands of shorebirds. Studies of many species have demonstrated the overwhelming importance of the



**Fig. 1.** The potential influence of human disturbance on prey abundance in spring. If human presence influences animal distribution such that disturbed sites are used less, then levels of prey depletion will be reduced in disturbed sites, resulting in higher spring prey densities than in undisturbed sites.

invertebrate prey population of estuaries in determining the spatial and temporal distribution of the birds that consume them (Zwarts & Blomert 1992; Goss-Custard *et al.* 1995; Piersma *et al.* 1995). Thus, if human presence alters the distribution of these birds, the most important consequence is likely to be an alteration in use of the food supplies. Several studies of shorebirds have demonstrated the importance of quantifying the fraction of the prey populations that are both accessible to the birds and profitable to consume. For example, studies of predator-prey relationships frequently show that prey which can bury deeper in sediments are less accessible to predatory shorebirds (Myers, Williams & Pitelka 1980; Zwarts & Wanink 1984; Wanink & Zwarts 1985; Piersma *et al.* 1993; Zwarts & Wanink 1993). In addition, the size of prey can affect its availability to predators; prey may be too large to be consumed or too small to be profitable (Zwarts & Blomert 1992; Piersma *et al.* 1993; Zwarts & Wanink 1993). Assessing the impact of disturbance on the use of prey populations by shorebirds will therefore require measures of prey selection.

We aimed to assess the extent to which different types of human activity might reduce the number of shorebirds that can be supported by invertebrate food supplies at a range of spatial scales. We focused on the black-tailed godwit *Limosa limosa islandica* L., which winters on the estuaries of north-west Europe. Our study area included estuaries with some of the highest levels of recreational use in Britain (Davidson *et al.* 1991). Black-tailed godwits are a species considered to be at risk from disturbance in the wintering grounds (Batten *et al.* 1990).

The effect of disturbance on site use can be examined in two ways. If the species in question is food-limited and responsible for virtually all of the depletion of the available prey, levels of human activity can simply be related to the abundance of prey at the end of the season (Fig. 1). This method assumes that initial resource abundance is not related positively to levels of human activity. This method has been used successfully to identify the extent to which the use of sugar beet fields by pink-footed geese *Anser brachyrhynchus* was constrained by human disturbance (Gill 1996). The resource need not be food

supply, but must be the major cause of the occupation of the area by the species in question, for example breeding territories, nesting sites or roosting locations. The territory use and consequent productivity of ringed plovers *Charadrius hiaticula* has also been shown to be markedly affected by human disturbance, resulting in significant reductions in local population size (Liley 1999).

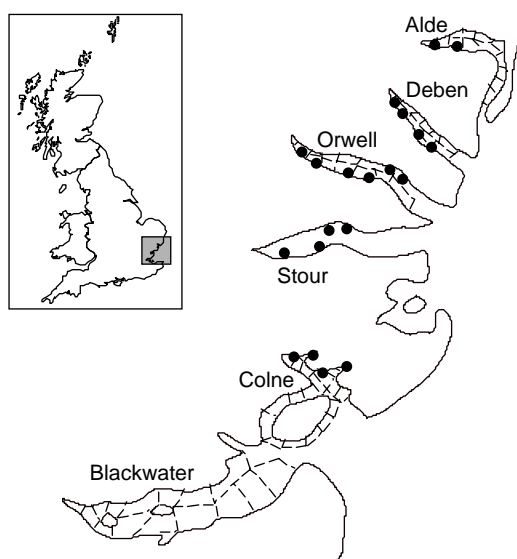
Alternatively, if the predator in question is not responsible for virtually all prey depletion, the effect of human activity can be included along with all other relevant variables in an analysis of the factors determining distribution.

In this study we adopted both techniques, although we have shown previously (Gill, Sutherland & Norris 2001b) that black-tailed godwits are the major cause of over-winter depletion of available prey in our study areas. Both techniques require accurate assessments of prey availability.

## Methods

### LARGE-SCALE RESOURCE USE

Invertebrate sampling was carried out between 13 September and 17 October 1994 on five estuaries on the east coast of England (the Alde, Deben, Orwell, Colne and Blackwater; Fig. 2) and between 4 and 8 October 1996 for one estuary, the Stour. These estuaries were selected in these winters in order to coincide with the British Trust for Ornithology (BTO) Low Tide Count Scheme (Waters *et al.* 1996), which took place on three of the estuaries during the study. Sampling sites within estuaries were selected by placing a  $1 \times 0.5$ -km grid on a 1 : 50 000 map of the estuary and sampling at each intersection (Alde:  $n = 17$ ; Deben:  $n = 15$ ; Orwell:  $n = 16$ ;



**Fig. 2.** Map of the study estuaries. Dashed lines show boundaries of area where human presence was measured, and dots mark the 20 patch-scale study areas. The shaded area within the inset indicates the location of the estuaries within Britain.

Colne:  $n = 24$ ; Blackwater:  $n = 28$ , Stour:  $n = 15$ ). In cases where the intersection lay just adjacent to the mudflat, samples were taken from as near as possible to the intersection. At each sampling point, four replicate cores of 10 cm diameter and 15 cm depth (the maximum depth to which a godwit can reach) were collected. These were then transported to the laboratory and sieved in tap water through a 1-mm sieve (Piersma *et al.* 1993). All invertebrates were removed and preserved in alcohol within 4 days of collecting and usually on the day following collection. Within each sample, all invertebrates were identified and their maximum length was measured; for bivalves this was the maximum shell width and for polychaetes this was the maximum length when straightened. Within the bivalves, each species was separated into nine size categories (< 2.5, 2.6–3.9, 4.0–5.5, 5.6–9.5, 9.6–14.5, 14.6–19.5, 19.6–29.5, 29.6–39.5 and > 40 mm). These categories were selected in order to make the data comparable with previous studies. This sampling procedure was repeated in the following spring, between 21 February and 23 March 1995 and, on the Stour only, between 14 and 17 March 1997.

### HUMAN ACTIVITY

Levels of human activity were measured during the winter of 1994–95 on all estuaries except the Stour (Fig. 2). Each estuary was split into sections that could be observed from one position and were related to the invertebrate sampling sites. Each site was visited once during a weekday when weather conditions were good (dry and above freezing) and within 3 h of low tide. Each section was observed for 1 h, during which the number of four categories of human presence was recorded every 15 min (totalling five measurements per hour). The four categories were powered water craft (PWC), non-powered water craft (NPWC), aircraft (AIR) and walkers, dog-walkers and cyclists (WALKERS). The location of each source of disturbance was recorded, and its effect on the birds was recorded as whether the birds moved or took flight and how long the disturbance lasted. A mean of the five measurements per hour was then calculated and divided by the length of the section, to give a standardized index of human activity. Length was used because all shore-based and boating activity took place along linear axes of the sections, on the shoreline or on the water. Although each section was only visited once, 16 of the sections were included in the more intensive studies in which human activities were recorded every 2 weeks throughout the winter (see below). For these 16 sites, there was a significant, positive, correlation ( $r = 0.57$ ,  $P < 0.02$ ) between the single and multiple measures of human activity.

### BLACK-TAILED GODWIT SITE SELECTION AND USE

During the winter of 1995–96, detailed studies of 20 sites (mean area =  $7.5 \text{ ha} \pm 1.6 \text{ SE}$ ) on five estuaries

(Fig. 2) were carried out in order to identify the factors likely to determine which sites were selected by black-tailed godwits and the extent to which they were used. The 20 sites were chosen to represent a range of prey densities, sediment types, levels of human activity and godwit presence or absence.

Each site was visited once in every 2-week period between 16 October 1996 and 20 March 1997. At each visit, 1 h was spent at the site, during which disturbance was measured using the index method described above; the range of disturbance types and levels on these small sites was comparable to the range across mudflats and estuaries. Counts were made of all birds on the site, and the prey selection of any foraging black-tailed godwits was measured by observing individuals for the time taken for 10 paces whilst foraging. Within this time, the number of successful and unsuccessful pecks made was recorded, as was the identity of the prey (as bivalve or polychaete) where possible (prey could be identified in over 95% of observations). After each hour survey, the prey density was sampled within the site by taking six replicate cores of 6.4 cm diameter and 15 cm depth. Within these estuaries, black-tailed godwits consume bivalves and polychaetes. Of these, bivalves are the preferred prey and the three most common species, *Scrobicularia plana* (da Costa), *Macoma balthica* L. and *Mya arenaria* L., form the vast majority of the diet (Gill, Sutherland & Norris 2001b). In addition, the godwits select individual bivalves of size classes 3–6 (Gill, Sutherland & Norris 2001b). Hence in this study, the prey that were considered as 'available' to black-tailed godwits were *S. plana*, *Macoma balthica* and *Mya arenaria* of 4–19.5 mm shell length.

For each of the 20 sites, the distances to the nearest road and footpath were measured from 1 : 25 000 Ordnance Survey maps. The statistical significance of all relationships presented in tables is denoted by \* $P < 0.05$ , \*\* $P < 0.01$  and \*\*\* $P < 0.001$ . Analyses of these data are referred to as patch-scale analyses.

#### BLACK-TAILED GODWIT COUNTS

The number of waterfowl occurring on British estuaries is counted monthly by volunteers as part of the BTO Wetland Bird Survey (WeBS; Waters *et al.* 1996). These counts generally take place at high tide when birds are roosting. The counts can be used to give estimates of the total use made of an estuary by a given species by summing the number counted each month over the winter (October–March). These volunteer counts (or, in two cases, counts carried out by the authors) were used to calculate the total number of black-tailed godwit days on six estuaries, the Alde, Deben, Orwell, Colne and Blackwater in 1994–95 and the Stour in 1996–97 (the years in which the invertebrate surveys took place). These measures of godwit use were related to the mean index of human activity for each estuary. Analyses of these data are referred to as estuary-scale analyses.

The distribution of waterfowl on British estuaries is assessed monthly from November to February by volunteers as part of the BTO Low Tide Count Scheme (Waters *et al.* 1996). In this scheme, the distribution of birds is recorded by counting the number of foraging and roosting birds on individual mudflats. As the invertebrate sampling takes place from October to March, but low tide counts are only available from November to February, it was necessary to estimate the numbers of godwits present in October and March. This was done by assuming the number on each mudflat in October to be the same as that recorded in November and the number in March to be the same as that in February. Gill, Sutherland & Norris (2001b) show that this is a reasonable assumption. The summed counts from October to March thus gave estimates of the total number of black-tailed godwit days on individual mudflats. Analyses of these data are referred to as mudflat-scale analyses.

The impact of human presence on godwit use of these areas was examined in three ways. (i) The simple relationships between human activity and the number of godwit days on individual sites were examined at each of the patch, mudflat and estuary scales. (ii) The index of human activity and prey density were incorporated into multiple regression analyses of the factors affecting the number of godwit days at each spatial scale. These analyses could be illustrated by examining the effect of the index of human activity on the residual variance of the relationships between prey density and the number of godwit days at each scale. (iii) The relationship between the index of human activity and prey density at the end of the season was examined at each spatial scale to assess whether prey were exploited to a greater extent in sites with lower levels of human activity.

#### THE EFFECTS OF MARINAS AND FOOTPATHS ON RESOURCE USE

During the winter of 1995–96, a second survey of prey use was undertaken to compare sites with specific forms of disturbance. For this survey, two types of site were used, those with marinas (small ports for yachts and pleasure boats) and those with footpaths. These criteria were used because marinas and footpaths were the sites with the highest levels of human activity throughout the winter on these estuaries (mean index of human activity on sites with marinas:  $1.36 \pm 1.31$ ; sites with footpaths:  $1.29 \pm 1.76$ ; sites without marinas or footpaths:  $0.53 \pm 0.94$ ;  $F_{2,97} = 4.3$ ,  $P < 0.02$ ). For the marina survey, nine marinas were selected from five estuaries. Each marina was paired with a reference site that was close to the marina and contained similar sediment type and fauna but was far enough away (usually  $> 200$  m) to be unaffected by human activity at the marina (mean index of activity at marinas:  $1.42 \pm 0.45$ ; reference sites:  $0.29 \pm 0.17$ ;  $t_8 = 2.48$ ,  $P < 0.04$ ). For the footpath survey, three types of site were selected: those with high levels of human activity ( $> 20$  people  $\text{h}^{-1}$  as measured in the 1994–95 survey); those with low levels of human

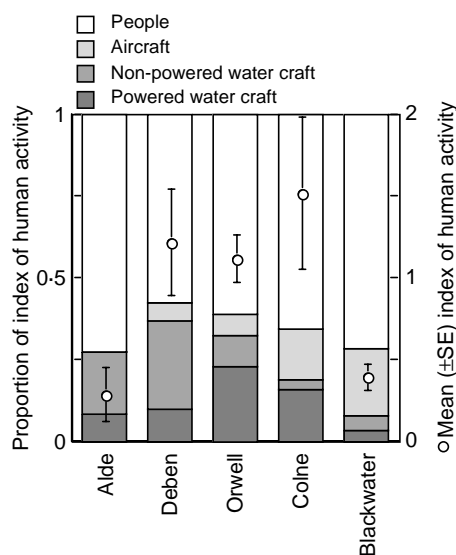
activity ( $< 10$  people  $\text{h}^{-1}$ ); and sites with no footpaths (mean index of activity at high use:  $1.19 \pm 0.13$ ; low use:  $0.45 \pm 0.09$ ; no footpath:  $0.31 \pm 0.14$ ;  $F_{2,15} = 14.78$ ,  $P < 0.001$ ). Each of the six estuaries in this survey had one of each of the three footpath categories. At each of the marina and footpath sites, prey samples were collected in the autumn (16 October–1 November 1995) and again in the spring (26 February–12 March 1996). The samples were collected from transects running out from the shoreline, with eight replicate cores of 6.4 cm diameter and 15 cm depth taken at 0 m (as close as possible to the shore), 20 m, 40 m, 60 m and 80 m, totalling a maximum of 40 replicates for each site [the width of some sites was less than 80 m, in which case transects were only run to 60 m (one marina + reference site and two footpaths) or 40 m (three marinas + reference sites and one footpath)]. This allowed disturbance to be examined both as a direct comparison of sites with and without a source of disturbance, and as an effect of distance away from the shoreline, where the majority of the human activity occurs.

## Results

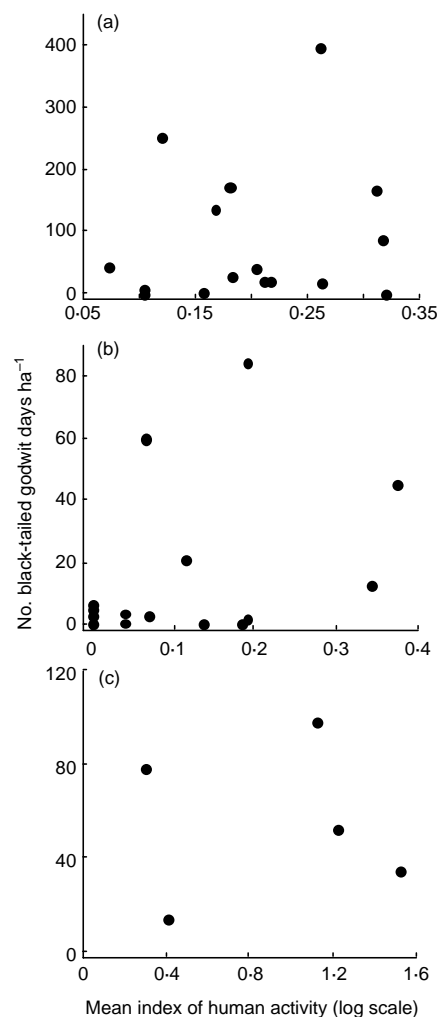
### LEVELS OF HUMAN ACTIVITY BETWEEN AND WITHIN ESTUARIES

Across the 20 small sites studied intensively in 1996–97, the level of disturbance on each site could be characterized by taking the mean value of the index of disturbance recorded every 2 weeks. This index varied significantly between sites ( $H_{19} = 165.6$ ,  $P < 0.0001$ ).

The mean disturbance indices also varied significantly across the five estuaries (Fig. 3). The Deben, Orwell and Colne estuaries had significantly higher levels of



**Fig. 3.** The mean index of human activity on each of the five estuaries studied in 1994–95 and the relative contribution of each of the four constituent components of the index, on each of the estuaries.



**Fig. 4.** The relationship between the mean level of human activity and the total number of black-tailed godwit days per hectare over the winter on (a) patches ( $r^2 = 0.02$ , NS); (b) mudflats ( $r^2 = 0.1$ , NS); (c) estuaries ( $r^2 = 0.001$ , NS).

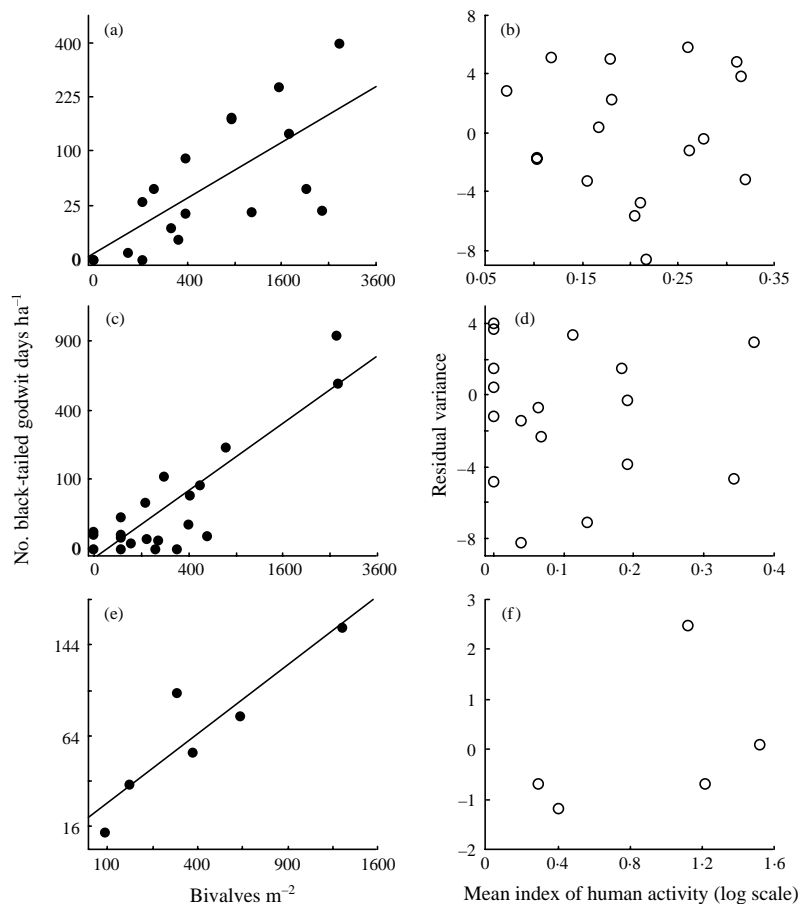
human activity than the Alde and the Blackwater (Kruskal–Wallis test:  $H_4 = 28.9$ ,  $P < 0.0001$ ). Figure 3 also shows the relative importance of each of the four constituent components of the index on each of the estuaries. The majority of human activity on each of the estuaries was due to shore-based activities. Water-based activities were more common on the Alde, Deben and Orwell than on the Colne and Blackwater.

### HUMAN ACTIVITY AND GODWIT NUMBERS

At none of the three scales was there a significant relationship between numbers of godwits and human activity (Fig. 4a–c).

### HUMAN ACTIVITY, BIRD NUMBERS AND RESOURCE ABUNDANCE

Over the 20 sites studied in 1996–97, black-tailed godwits showed a strong aggregative response, with the total density of godwits consuming bivalves (summed



**Fig. 5.** The relationships between the initial density of available bivalves in October and the total number of black-tailed godwit days feeding on bivalves on (a) patches of mudflat over the winter 1996–97 ( $y = 0.256x + 0.63$ ;  $r^2 = 0.46$ ,  $P < 0.003$ ); (c) whole mudflats over the winter 1994–95 ( $y = 0.49x - 1.60$ ;  $r^2 = 0.76$ ,  $P < 0.0001$ ); (e) estuaries over the winter 1994–95 ( $y = 0.36x - 1.03$ ;  $r^2 = 0.79$ ,  $P < 0.02$ ) (all axes were normalized by square-root transformation) and the relationships between the residual variance in these responses and the mean index of human activity on (b) patches, (d) mudflats and (f) estuaries (see text for analysis).

from counts every 2 weeks) over the winter increasing significantly with the initial density of available bivalves (Fig. 5a). Sites containing less than 150 bivalves  $m^{-2}$  in October were never used by godwits. When the mean index of human activity on these sites was included with initial bivalve density in a stepwise multiple regression analysis of the factors affecting total over-winter godwit density, the index of human activity was non-significant (partial correlation coefficient = 0.07,  $P < 0.79$ ) but available bivalve density was retained (coefficient =  $0.25 \pm 0.06$ ,  $r^2 = 0.53$ ,  $P < 0.0001$ ). This could be illustrated by relating the residual variance of the patch-scale aggregative response presented in Fig. 5a to the index of human activity (Fig. 5b). This indicated that human activity had no effect on the number of godwits supported on these sites.

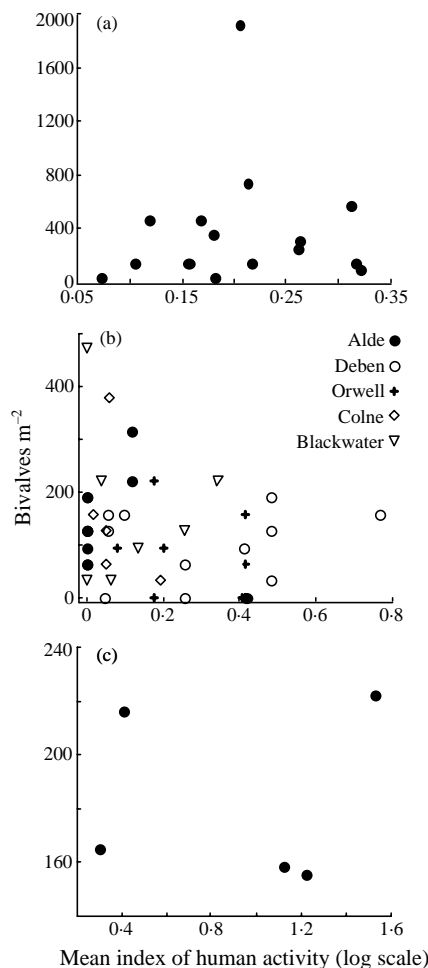
The distribution of black-tailed godwits was also strongly related to available bivalve density across larger mudflats (Fig. 5c). In a stepwise multiple regression analysis of the effect of bivalve density and human activity on total over-winter godwit density across mudflats, the index of human activity was again non-significant (partial correlation coefficient = 0.3,  $P < 0.7$ ) and bivalve density was retained (coefficient =  $0.36 \pm 0.09$ ,

$r^2 = 0.79$ ,  $P < 0.017$ ). There was therefore no relationship between human activity and the residual variance of the mudflat-scale aggregative response (Fig. 5d).

At the whole estuary scale, the total number of godwits over a winter was again significantly related to the initial bivalve density (Fig. 5e). The index of human activity was again rejected in a stepwise multiple regression analysis (partial correlation coefficient = 0.16,  $P < 0.83$ ), whereas bivalve density significantly affected godwit density at this scale (coefficient =  $0.80 \pm 0.11$ ,  $r^2 = 0.93$ ,  $P < 0.002$ ). There was therefore no relationship between human activity and the residual variance of the estuary-scale aggregative response (Fig. 5f).

#### HUMAN ACTIVITY AND RESOURCE ABUNDANCE

As bivalve populations on these estuaries undergo severe over-winter depletion, and as black-tailed godwits are the major cause of depletion of the available bivalves (Gill, Sutherland & Norris 2001b), it was possible to examine the relationship between levels of human activity and the abundance of bivalves remaining at the end



**Fig. 6.** The relationship between the mean index of human activity and the density of available bivalves in spring on (a) small patches of mudflat ( $r^2 = 0.02$ , NS); (b) mudflats across five estuaries (see Table 1 for analysis); (c) whole estuaries ( $r^2 = 0.004$ , NS). Only sites with more than 150 bivalves  $m^{-2}$  in autumn are included.

of the season. This method assumes that initial prey density at the start of the season is not related to levels of disturbance. At the 20 sites in which levels of human activity and prey abundance were recorded every 2 weeks throughout the winter of 1996–97, the prey abundance at which the godwits stopped consuming bivalves at each site was therefore known. On sites with available bivalve

**Table 1.** Summary of two-way analyses of variance of the effect of the index of disturbance on the density of available bivalves (*Scrobicularia plana*, *Macoma balthica* and *Mya arenaria* of less than 20 mm length) on five different estuaries in autumn and spring. Only sites with more than 150 bivalves  $m^{-2}$  in autumn are included

Source	d.f.	Autumn <i>F</i>	Spring <i>F</i>
(a) Index of human activity	1	1.81	2.08
(b) Estuary	4	0.69	2.49
a × b	4	0.56	0.58
Error	33		

densities high enough to attract godwits ( $> 150 m^{-2}$ ; Fig. 5a), the initial density of available bivalves was not related to the mean index of human activity ( $r^2 = 0.00001$ ,  $P < 0.99$ ). There was no relationship between the mean index of human activity and the abundance of bivalves after godwits had stopped using the sites (Fig. 6a). The level of human activity also had no effect on the abundance of bivalves at the end of the season at either the larger mudflat-scale (Fig. 6b; Table 1) or the whole estuary scale (Fig. 6c).

At the patch-scale, the index of human activity could also be broken into its constituent components, but none was significantly related to the over-winter depletion of the available bivalves on these sites (Table 2). Disturbance could also be estimated from factors such as the distance to the nearest road or footpath, but again neither affected over-winter depletion of the available bivalves on these sites (Table 2). Human activity may not have affected the overall use made of the sites but may have affected the temporal pattern of use by the godwits. If the godwits used undisturbed sites preferentially, rates of prey depletion should have been higher in these sites than in undisturbed sites. However, the index of human activity had no significant effect on the rates of depletion of available bivalves ( $y = 0.04x - 0.14$ ,  $r^2 = 0.03$ ,  $P < 0.6$ ).

At all of these scales, almost all of the sites were depleted from a wide range of initial densities down to approximately 100–500 bivalves  $m^{-2}$  (Fig. 6). If human activity was restricting the use made of this food supply by the godwits, it would be unlikely that the spring densities would be so consistent.

**Table 2.** Summary of linear regression analyses of the effect of seven disturbance variables on the density of available bivalves on patches of mudflat in autumn and spring. Only sites with more than 150 bivalves  $m^{-2}$  in autumn are included

Disturbance variable	Autumn		Spring	
	Slope	$r^2$	Slope	$r^2$
Mean number of people $h^{-1}$	–ve	0.03	+ve	0.08
Mean number of PWC $h^{-1}$	–ve	0.10	–ve	0.03
Mean number of NPWC $h^{-1}$	–ve	0.08	–ve	0.11
Mean number of aircraft $h^{-1}$	–ve	0.07	+ve	0.01
Distance to road (m)	–ve	0.041	–ve	0.01
Distance to footpath (from shore edge) (m)	–ve	0.20	–ve	0.14
Distance to footpath (from centre of mudflat) (m)	+ve	0.10	+ve	0.10

**Table 3.** Summary of analyses of variance of the effect of marina presence and distance out from the shoreline on the density of available bivalves (*Scrobicularia plana*, *Macoma balthica* and *Mya arenaria* of less than 20 mm length) in autumn and spring. Only sites with more than 150 bivalves m<sup>-2</sup> in autumn are included

Source	d.f.	Autumn <i>F</i>	Spring <i>F</i>
(a) Marina or reference	1	0.69	0.03
(b) Distance from shore	1	0.68	0.06
(c) Site pairs	3	3.70	1.77
a × b	1	0.04	1.10
Error	10		

#### THE EFFECT OF MARINAS ON BLACK-TAILED GODWIT PREY USE

Sites that contained marinas did not differ from reference sites without marinas in the density of available bivalves in autumn or in spring (Table 3 and Fig. 7a). In addition, distance from the shoreline did not affect the spring density of available bivalves, nor were there any significant interactions between the presence of a marina and the distance from the shoreline (Table 3).

**Table 4.** Summary of analyses of variance of the effect of footpath presence and degree of use, and distance out from the shoreline, on the density of available bivalves (*Scrobicularia plana*, *Macoma balthica* and *Mya arenaria* of less than 20 mm length) in autumn and spring. Only sites with more than 150 bivalves m<sup>-2</sup> in autumn are included

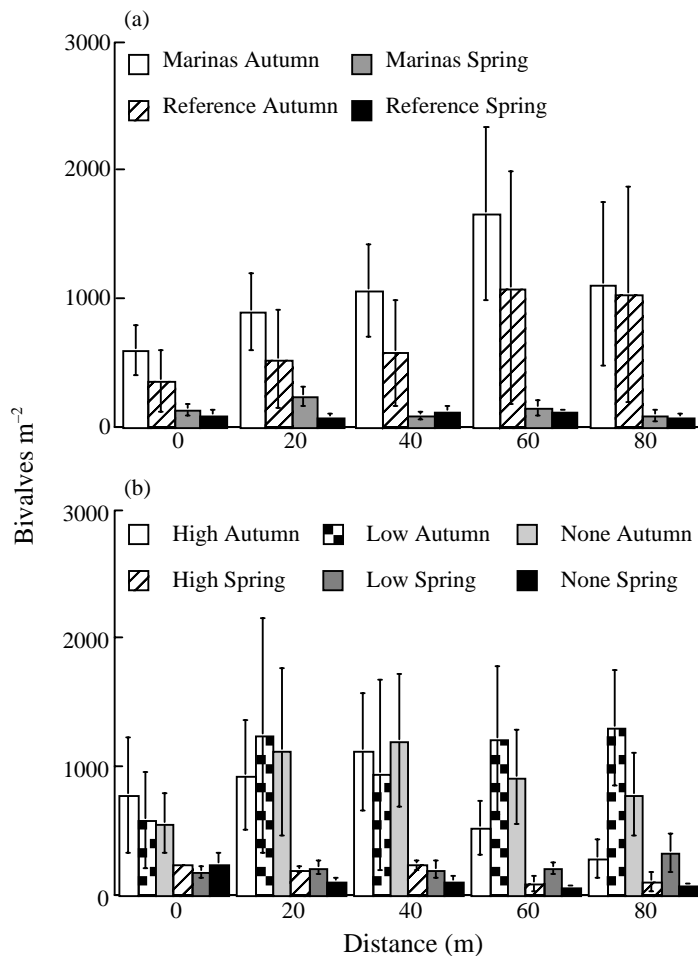
Source	d.f.	Autumn <i>F</i>	Spring <i>F</i>
(a) Footpath use	2	0.19	0.50
(b) Distance from shore	1	0.10	1.46
(c) Estuary	5	2.55*	1.87
a × b	2	0.03	1.86
Error	40		

\**P* < 0.05.

Counts of black-tailed godwits at these sites were not sufficient to produce accurate aggregative responses and thus could not be used.

#### THE EFFECT OF FOOTPATHS ON BLACK-TAILED GODWIT PREY USE

The presence of a footpath adjacent to a mudflat did not affect the density of available bivalves in autumn or in spring (Table 4 and Fig. 7b), and there were no



**Fig. 7.** The mean ( $\pm$  SE) density of available bivalves in autumn and spring at different distances out onto the mudflats of (a) sites adjacent and not adjacent to marinas and (b) sites adjacent to footpaths with high or low levels of use or sites with no footpath (see Tables 3 and 4 for analyses).



significant interactions with distance from the shoreline (Table 4). Counts of black-tailed godwits at these sites were also not sufficient to produce accurate aggregative responses.

## Discussion

Shorebirds often show strong avoidance of humans (Burger 1981; Kirby, Clee & Seager 1993; Smit & Visser 1993) and some studies have shown their numbers to be lower in disturbed than undisturbed sites (Klein, Humphrey & Percival 1995). However, we found no evidence that human presence reduced the number of black-tailed godwits that were supported on coastal sites at a range of spatial scales. The study took place on estuaries that varied widely in both the level and type of human activity, but neither had any influence on godwit distribution or abundance. There was also no effect of the presence of marinas or footpaths on the number of godwits supported on the adjacent mudflats.

The prey types involved in this study, estuarine bivalves, are relatively sedentary once they have settled in the sediment. It may seem intuitively obvious that using depletion as a measure of the effect of disturbance will not work if the prey are mobile. However, avoidance of disturbed sites only matters if it reduces the amount of prey that is available to be consumed. Consider the example of a predator that avoids disturbed sites and only feeds in undisturbed areas. In the absence of prey movement, only the prey in the undisturbed sites will be available to the predator and the increased depletion in these sites may impact on the fitness of the predator. However, in the case of prey that can move between sites, all prey will be available to the predator during the periods when they occur in the undisturbed sites. Levels of prey depletion will therefore be equal across all sites and the intake of the predator will be unaffected by disturbance, even though disturbance has restricted predator distribution. In such cases, the traditional method of comparing predator densities in disturbed and undisturbed sites will show an effect of disturbance on distribution but only measuring depletion will identify whether or not there are associated costs.

The advantage of the approaches used in this study over examining either behavioural responses to disturbance or relating numbers of animals across sites to disturbance levels, is that they identify whether sites could support more animals in the absence of disturbance. If disturbance constrains numbers of animals using sites, it also allows calculation of the increased numbers of animals that could use the site in the absence of disturbance (Gill 1996).

In the case of wintering black-tailed godwits, current levels of human activity did not influence distribution or habitat use in our study. The level of sampling of both predators and prey was sufficient to produce clear relationships between godwit and bivalve abundance; if human presence was important in determining current godwit distribution, it is likely that these

relationships would be much less clear. However, this does not mean that there are not other circumstances under which human presence could be a significant conservation problem, either for this or similar species, or on these or similar sites. For example, during periods of severe weather when wading birds are often under extreme stress (Dugan *et al.* 1981; Davidson & Evans 1982), any additional effects of human disturbance may be extremely important. Shorebirds are also present on coastal areas during the late summer when food may not be limiting but they are experiencing the stress of moult. At these times, high levels of recreational activity may be important.

A major factor likely to influence whether or not species respond to humans by avoiding specific areas is the risk of mortality associated with human presence. Thus, species that are hunted by humans might be expected to avoid humans more than species that are not hunted (Gill & Sutherland 2000; Gill, Norris & Sutherland 2001a). Although these estuaries are amongst the most heavily used for human recreation in England (Davidson *et al.* 1991), black-tailed godwits are not hunted in Britain, nor are they hunted on their Icelandic breeding grounds. This may therefore be one reason for the lack of a detectable response to human presence by this species.

## IMPLICATIONS FOR CONSERVATION

It may appear that a study showing that human presence has no impact on the species in question is relatively unimportant in conservation terms. However, a common problem in conservation science and policy is the failure to distinguish critically important conservation issues from trivial ones (Caughley 1994; Sutherland 2000). The consequences of this may be a dissipation of effort and a failure to use resources in the most cost-effective manner. Thus, of the 113 red data book bird species in the UK, 76 have disturbance included under 'Threats to survival' alongside factors such as habitat loss, poisoning and persecution (Batten *et al.* 1990), although the impact of disturbance has not been examined in any detail for any of these species. The protection of sites and conservation of the species inhabiting them is likely to be easier to achieve if other interested parties have access to the sites without diminishing their conservation importance (Adams 1997). It is thus clearly important to be able to distinguish cases where human presence results in significant changes in habitat use (as in the pink-footed goose and ringed plover examples above) from cases where it does not.

Quantifying the effect of human presence on habitat use is, however, only the first step, as altering the distribution and habitat use of individuals need not have any consequences for the population as a whole (Gill, Norris & Sutherland 2001a). Understanding the population consequences will require information on levels of density-dependent mortality and fecundity in a population and how these are affected by changes in distribution in response to human presence (Sutherland

1998; Stillman *et al.* 2000). Thus, while the role of human presence in constraining numbers of animals on particular sites can be assessed using the methods described here, quantifying the population consequences of these constraints will be far more complex.

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