

A method to quantify the effects of human disturbance on animal populations

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Summary

1. The extent and consequences of human disturbance on populations of vertebrates are contentious issues in conservation. As recreational and industrial uses of the countryside continue to expand, it is becoming increasingly important that the effects of such disturbance on wildlife are quantified.

2. This study describes a method of quantifying the effect of disturbance, based on measuring the trade-off between resource use and risk of disturbance. This approach is based on one used by ethologists to study the effects of predation risk on patch use.

3. Pink-footed geese, *Anser brachyrhynchus*, feeding on arable fields, are highly responsive to disturbance from surrounding roads. The extent to which these fields are exploited declines linearly with increasing risk of disturbance. The reduction in use of these feeding grounds caused by disturbance can be quantified by translating the biomass of food not exploited into the number of birds that this food could have supported.

4. This approach allows both quantification of the impact of disturbance on a population, and exploration of the potential consequences of changes in disturbance on the size of populations.

Key-words: pink-footed goose, trade-off, depletion, predation.

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Introduction

Controversy has arisen in recent years over the extent to which human uses of the countryside may have adverse effects on wildlife. Such uses include tourism (Schulz & Stock 1993), recreation (Batten 1977; Yalden 1992) and industrial development (Meire 1993). Consequently, there is considerable conservation interest in quantifying the effects of such disturbance upon animal populations (review in Hockin *et al.* 1992).

Disturbance is often implicated as having potentially damaging effects on wildlife (e.g. Hume 1976). However, in the field of conservation, the critical factor is whether disturbance results in lower population sizes. In some cases there is a clear link between the extent of disturbance and either the survival or reproductive success of individuals (e.g. Schulz & Stock 1993), but in many cases disturbance acts in a more subtle way, by reducing access to resources such as food supplies or nesting sites. Studies of such effects have generally been carried out in one of two ways; often the distribution of animals before and after inci-

dents of disturbance is recorded (e.g. Draulans & van Vessem 1985; Bélanger & Bédard 1989; Koolhas, Dekinga & Piersma 1993). However, recording the redistribution of animals after disturbance will not necessarily reflect a negative effect of disturbance, because the new distribution pattern may only be temporary; animals may return to their original distribution at a later date to exploit the remaining resources. For example, Owens (1977) found that disturbance caused brent geese, *Branta bernicla bernicla*, to avoid some sites early in the season, but these sites were eventually used when food on other, less disturbed sites had been depleted.

The second way in which disturbance effects have been studied has been to relate the numbers of animals to varying rates of disturbance across a number of sites or patches within sites (e.g. Tuite, Hanson & Owen 1984; Pfister, Harrington & Lavine 1992; Sutherland & Crockford 1992; Stock 1993). However, unless the numbers of animals that would use these sites in the absence of disturbance is known, it is still impossible to say whether or not the numbers using the site have been lowered as a result of disturbance.

The framework proposed in this paper is derived from that widely used to quantify the trade-off in the choice of foraging location between food density and the risk of predation (review in Lima & Dill 1990). In many ways, the effects of disturbance on animal foraging and choice of foraging sites mirror those of predation risk. For example, Milinski (1985) described such a trade-off in three-spined sticklebacks, *Gasterosteus aculeatus*. In this case, a smaller proportion of the available prey was consumed by the sticklebacks in the patches closer to an apparent predator, a cichlid fish.

In the context of disturbance studies, animals often perceive humans as potential predators. The response to disturbance can then be studied in the same way as the response to predation; by measuring the reduction in the use of a resource in response to disturbance. This methodology, therefore, differs from the disturbance studies described above by evaluating the trade-off that animals face between disturbance rates and the amount of a given resource available between patches. This resource could be food, nesting sites, roosting sites or any other potentially important variable. The resource we consider in this paper is food abundance.

The potential trade-off in patch choice between food abundance and disturbance for foraging animals is illustrated in Fig. 1. In this figure, a site contains 10 patches that vary in food biomass and disturbance. The location of each patch along the x-axis relates to its disturbance rate and this axis might therefore refer to the frequency with which humans use each patch or the distance of each patch from a source of disturbance. The y-axis is the biomass of food in each

patch. If the animals were limited by the amount of food on the site and were not affected by disturbance, then the theoretical expectation is that each patch should be depleted to the amount at which it is no longer profitable to feed there (Fig. 1a). However, if the animals avoid patches with high disturbance, then, as with the response to the risk of predation, the amount of resource not consumed will be greater in disturbed patches (Fig. 1b). It is then possible to determine the amount of resources left uneaten as a consequence of disturbance, and the number of animals that could have been sustained by these unexploited resources in the absence of disturbance.

In order to use this approach, four pieces of information are required: the amount of a given resource in each of a number of patches, the proportion of this resource exploited, the total number of individuals supported by this resource and a measure of disturbance on each patch. Each of these parameters was recorded for a population of pink-footed geese, *Anser brachyrhynchus* L., wintering in north Norfolk, England. Pink-footed geese spend the winter months feeding almost exclusively on agricultural land and in north Norfolk the major food source is the remains of harvested sugar beet, *Beta vulgaris* L. (Gill 1994). Pink-footed geese are known to be sensitive to disturbance (Madsen 1985) and this may be linked to the fact that they are heavily hunted by wildfowlers (Harradine 1991) and shot as an agricultural pest when feeding on pastures and cereals.

In this paper, data are presented which describe the trade-off between resource use by wintering pink-footed geese and the risk of disturbance. These data are then used to illustrate a method which allows quantification of the effects of disturbance on the number of animals that the feeding grounds can support. Predictions are then made of the change in numbers of animals that would be expected to result from changes in disturbance.

Methods

The pink-footed geese in this study roost on Scolt Head Island, north Norfolk, England (National Grid reference: TF 790466) and feed on farmland between 3 and 15 km immediately inland of the roost. Between October 1992 and February 1993, the geese used 15 sugar beet fields within an area of arable farmland of ≈ 4000 ha. The geese also used winter cereal and stubble fields within the study area and a small number of fields outside of the study area. The beet fields were generally used for several consecutive days, the flock then moved to a new field and rarely returned. During mid-winter, when the population was at its peak, two or three fields were used simultaneously. The number of geese was recorded daily on each field; when summed this gave the total number of goose-days on each field. In addition, all sugar beet root fragments in 40–100 quadrats, measuring 1 m \times 1 m, were weighed

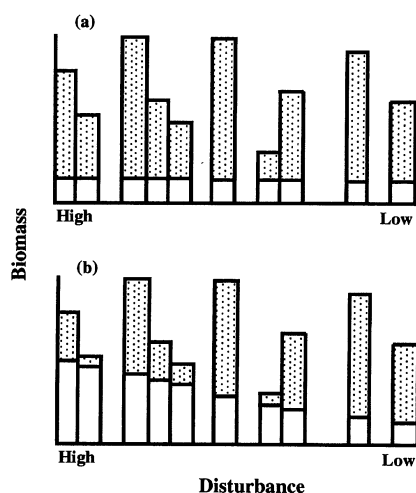


Fig. 1. Patch use in relation to disturbance. Each patch is represented by a bar and ranked according to disturbance. The height of each bar indicates the initial biomass in each patch. The dotted area represents the biomass removed by foraging animals. In (a) the foraging species is not sensitive to disturbance, while in (b) the species is sensitive to disturbance.

immediately after harvesting and immediately after the geese had abandoned the field. The quadrats were randomly located within the field, while the number of quadrats sampled depended upon the number of fields being measured on that day. The data from these quadrats enabled the amount of sugar beet consumed by the geese to be calculated, by subtracting the biomass of sugar beet on each field after the geese had left from the biomass immediately after harvest. A very small number of hares, *Lepus europeus* L., and pheasants, *Phasianus colchicus* L., feed on sugar beet remains but their effect is negligible in comparison to the thousands of geese using these fields. The effect of root dessication was measured on a set of control roots not accessible to the geese. Root mass declined significantly in the first 15–18 days after harvest and remained stable thereafter (Gill 1994). All repeat measures of biomass took place between 22 and 41 days after harvest and thus variation in the depletion between fields was not affected by root dessication.

Pink-footed geese tend not to feed near to roads when on the wintering grounds (Madsen 1985; Keller 1991). This reaction to roads may be in response to the rate of disturbance, i.e. geese feeding close to roads may be disturbed more often than those far from roads. It is also possible that roads are perceived by the geese as potential sources of disturbance and will thus be avoided regardless of the actual disturbance. In the latter case, an indirect measure of disturbance such as field area or the distance of feeding flocks from roads may be the more accurate measure of risk of disturbance; this is also significantly easier for biologists to quantify than actual disturbance. Both direct and indirect measures of disturbance were examined in this study.

Throughout the winter of 1992–93, a total of 62 h of observations on the geese were carried out on 10 of the 15 sugar beet fields. These were detailed observations of the foraging behaviour and antagonistic interactions of the geese feeding on harvested sugar beet remains, and involved periods of observation lasting for between 15 min and 6 h. During these observation periods, the number and cause of all disturbance events were recorded; a disturbance event was defined as any event that caused the geese to take flight. From these data, a rate of disturbance was calculated for each field, as the number of disturbance events per minute of observation. Measures of indirect disturbance included field area, distance from the centre of the field to the nearest road and to the nearest building, the proportion of the field surrounded by road and by hedge, and the distance from the flock to the nearest road when the geese first landed on the field.

Results

Twenty-seven disturbance events were witnessed during the 62 hours of observation of foraging geese. This

Table 1. The relative importance of different forms of disturbance on foraging pink-footed geese, measured as the proportion of disturbance events recorded during behavioural observations. A disturbance event was defined as anything causing the geese to take flight

Cause of disturbance	Proportion of observed disturbance events ($n = 27$)
Farming activities	31.8
Birdwatchers	13.6
Jet aircraft	13.6
Pheasant shoots	13.6
Slow aircraft	9.1
Cyclists/Horseriders	9.1
Wildfowling	4.6
Grey heron	4.6

translates into a mean disturbance rate of one every 2 h 33 min; the fields ranged from no disturbance events recorded to one every 62 min. The rate at which disturbance events were recorded did not vary significantly between weeks over the season (Kruskal–Wallis Test: $H_{10} = 3.73$, NS). Farming activities accounted for one-third of all disturbance events with birdwatchers, aircraft and pheasant shoots accounting for $\approx 40\%$ of disturbances (Table 1). In order to find out whether the variance in the rate at which the geese were disturbed on different fields affected the degree of use of those fields, the relationship between disturbance rate and the number of goose-days spent on each field was examined. Figure 2 shows the significant negative relationship between the number of goose-days on each field and disturbance rate. Thus, those fields on which the geese were frequently put to flight were used significantly less often than fields on which the geese were rarely disturbed.

Of the several potential indirect measures of the risk of disturbance (field area, distances from roads and buildings, and the amount of hedge and road around the fields), only the distance from the flock at first

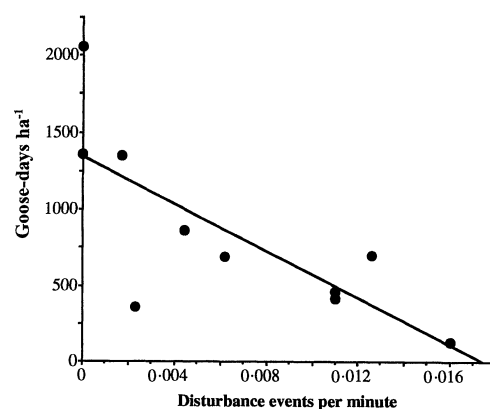


Fig. 2. The effect of the rate of disturbance events on the number of goose-days per hectare supported by each field ($y = -76767x + 1337$, $r^2 = 0.56$, $n = 10$, $P < 0.01$).

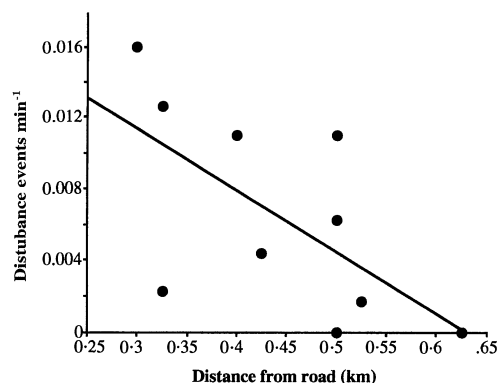


Fig. 3. The relationship between the distance from the goose flock to the nearest road at first landing and the disturbance rate ($y = -0.03x + 0.02$, $r^2 = 0.4$, $n = 10$, $P < 0.05$).

landing to the nearest road was significantly related to the actual disturbance rate (Fig. 3). None of the other field measurements showed any relationship with disturbance rate (field area: $r^2 = 0.02$, $n = 10$, NS; proportion of the field surrounded by road: $r^2 = 0.18$, $n = 10$, NS; proportion of the field surrounded by road and hedges: $r^2 = 0.03$, $n = 10$, NS; distance from the centre of the field to the nearest road: $r^2 = 0.22$, $n = 10$, NS; distance from the centre of the field to the nearest building: $r^2 = 0.09$, $n = 10$, NS). The distance from the flock at first landing to the nearest road also showed a very strong relationship with the number of goose-days recorded on each field (Fig. 4).

The reduction in the number of goose-days recorded on fields with a high risk of disturbance can also be measured in terms of the reduction in the amount of food consumed by those geese. The distance from the flock to the road was significantly and negatively related to the proportion of the crop in each field that was not consumed (Fig. 5). Thus, fields on which the geese are forced to feed close to roads

support significantly fewer goose-days and have a significantly smaller proportion of the crop consumed than fields where the geese can feed far from roads. Distance from the flock to the road was not significantly related to the absolute amount of food remaining on each field after goose grazing ($r^2 = 0.19$, $P < 0.11$).

The density of roots on these fields varies from 62 to 350 g m^{-2} . Although a proportion of the roots are of a size which is less preferred by the geese (Gill, Watkinson & Sutherland 1996), this proportion does not vary significantly between fields ($H_{14} = 21.15$, NS).

Discussion

Animals respond to disturbance from humans in the same way as they respond to the risk of predation, by avoiding areas of high risk, either completely or by using them for limited periods. The resources in such sites are therefore not exploited to their full potential and the animals are faced with a trade-off between exploiting these resources or feeding in less disturbed patches. This trade-off can be quantified by measuring the amount of resources not used under disturbed conditions. Pink-footed geese deplete the food supplies in sugar beet fields according to the risk of disturbance associated with those fields. Thus, fields subject to high disturbance rates have a greater proportion of food left on them than less disturbed fields (Fig. 5). The effect of disturbance on each field is thus defined by the equation of Fig. 5:

$$F = -1.51D + 1.08 \quad \text{eqn 1}$$

where F is the proportion of food not consumed and D is the distance to the nearest road, measured in kilometres.

In order to calculate the number of animals that this site could support in the absence of disturbance

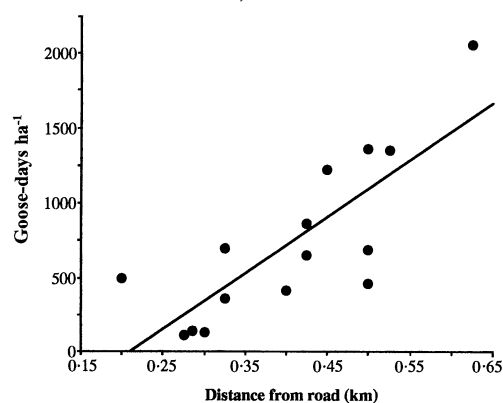


Fig. 4. The effect of the distance from the goose flock at first landing to the nearest road on the total number of goose-days per hectare on each field ($y = 3799x - 788$, $r^2 = 0.63$, $n = 15$, $P < 0.0004$).

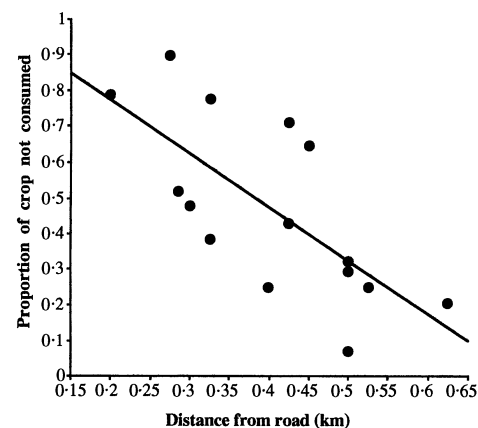


Fig. 5. The effect of the distance from the flock at first landing to the road on the proportion of the food that is not consumed on each field ($y = -1.51x + 1.08$, $r^2 = 0.50$, $n = 15$, $P < 0.003$).

it is important to know how much of the food supply can be exploited. It is unlikely that all of the resources present in a patch can be completely consumed; rather it is likely that there will be a threshold biomass of resources below which it is unprofitable for the consumers to continue foraging in that patch. This threshold biomass is often viewed as an absolute biomass of food (Sutherland & Anderson 1993). However, this assumes that all prey items are equally available to the consumers. In most situations, there will be variation in the extent to which prey are accessible (e.g. Zwartz & Wanink 1993). In this case, patches differing in initial prey density will not be depleted to a constant density, as this would result in a higher proportion of inaccessible prey on sites with high initial densities (Sutherland 1996). Thus, whether the threshold density is best considered as a proportion or as an absolute amount depends on the extent of prey variability and variation in prey suitability. In this study, the geese tended to avoid intermediate sizes of roots (Gill *et al.* 1996) while the fraction of total biomass that this size range comprised was constant, despite a fivefold difference in the density of roots on the fields. In addition, the distance of the geese from the road was not significantly related to the absolute amount of food remaining, but was strongly related to the proportion of food remaining (Fig. 5). Consequently, the most appropriate measure of threshold density in this study is the proportion of the crop remaining after goose grazing. Thus, the minimum threshold biomass was defined as the lowest observed proportion of the initial crop remaining on any field, 7.6% (Fig. 5). Given this threshold and eqn 1, it can be concluded that eqn 1 will only apply where $D < 0.65$, and that above this value $F = 0.076$.

Once the total amount of resource actually available to the animals is known, the potential results of a change in the rate of disturbance can be calculated. Figure 6 shows the possible results of a change in disturbance in the system presented here. Line (a) represents eqn 1, derived from Fig. 5, and is truncated by the line $F = 0.076$ where $D > 0.65$, the threshold biomass. Line (b) indicates the potential results of, for example, an increase in numbers of birdwatchers which may cause the geese to spend even less time on the fields close to roads. Line (c) describes the response that might occur via, for example, a reduction in hunting pressure resulting in the geese being more tolerant of humans and thus feeding closer to roads. The gradients of these lines, m , thus refer to the change in resource use that would result from a change in disturbance. The general equation of each line can be derived from eqn 1 and is given by:

$$F = m(D - 0.65) + 0.076 \quad \text{eqn 2}$$

For the specific example presented here, a field with the distance between the geese and the nearest road of 0.3 km and the current gradient of -1.51 (line a, Fig. 6), would have $\approx 63\%$ of the crop left uneaten.

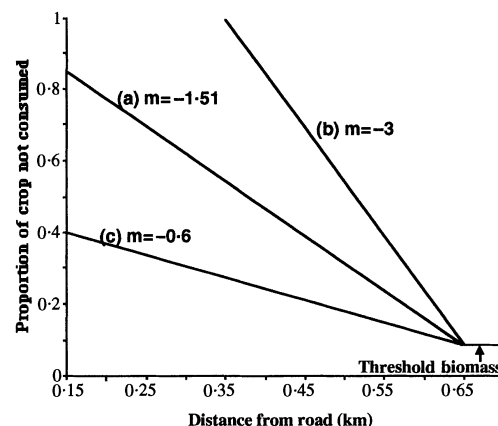


Fig. 6. The relationship between the proportion of food that is left on the fields, F , and the risk of disturbance, D , on the fields. Line (a) is the regression line, eqn 1, derived from Fig. 5; lines (b) and (c) show hypothetical changes in the susceptibility of the geese to disturbance, as reflected by changes in the gradient of the line, m . All of these lines are constrained to converge on the point $D = 0.65$, $F = 0.076$, the threshold biomass to which fields can be depleted. Where $D > 0.65$, then $F = 0.076$. See text for further details.

An increase in the susceptibility to disturbance to -3 (line b) would result in the field being completely avoided, whereas a decrease in susceptibility to disturbance to -0.6 (line c) would result in only 32% of the food not being eaten. No field can have more than 92.4% of the resource consumed as this is the threshold biomass.

The proportion of food not consumed can then be converted into numbers of goose-days that could have been supported by that food (P') simply by dividing the amount of resource currently used (C) by the number of goose-days supported (P), and multiplying this by the amount of resource that could be used (C') under different disturbance levels:

$$P' = (C/P) \times C' \quad \text{eqn 3}$$

During 1992–93, the area studied contained 15 fields which supported 170 955 goose-days. The analysis described above for one field can be carried out for each of these fields in turn, and the total population size can then be calculated. Thus, an increase in the susceptibility to disturbance to -3 (line b) would result in between 20 and 100% of the food on those 15 fields not being consumed, and a reduction in the number of goose-days that could be supported in the area to 66 830. On the other hand, a decrease in the susceptibility to -0.6 (line c) would result in only between 13 and 40% of the food on each field not being consumed and an increase in the number of goose-days to $\approx 242 090$. The critical feature in this analysis is the change in resource use in relation to the change in disturbance levels. Whilst the response in this study was linear, a similar approach could be used for non-linear responses. It should be noted that a number of fields within the study area were avoided completely,

possibly as a result of high risks of disturbance. These fields could therefore be used should the risk of disturbance decline, further increasing the number of goose-days that could be supported within the area.

There are two initial assumptions behind this approach which require further exploration. First, it is assumed that goose tolerance of disturbance will remain constant despite changes in other parameters. It is possible that an increase in, for example, the size of the wintering population may force the geese to tolerate disturbance to a greater degree. The number of geese wintering in Norfolk is currently increasing dramatically (Gill, Watkinson & Sutherland, in press). At present, the increasing population of geese is using a larger number of fields outside the core area of the study, and they are consequently moving further from the roost. At some point it is likely that the maximum distance from the roost that the geese are prepared to travel will be reached. At this point, the geese will have the choice of tolerating disturbed fields to a greater degree or moving to a new roost site. In the winter of 1993–94, with the population size in Norfolk reaching its highest ever peak at 68 560, there were a number of indications of potential new roost sites being formed in the region. Thus, the geese appear currently to be unwilling to increase their tolerance of disturbance risks on these fields.

A second assumption is that the threshold biomass of 7.6% that was observed during this study is the absolute minimum to which the geese will deplete the fields. It is possible that the geese could deplete the fields to an even lower food density. In the complete absence of disturbance (i.e. where the gradient of the line in Fig. 6 equals zero, and 92.4% of the food on all fields is consumed), the site would be expected to support 270 000 goose-days. In the unlikely scenario that the geese were capable of depleting 100% of the food on every field, the site could support 292 300 goose-days, an 8% increase on population size. Thus, alterations to this assumption would only have a relatively small effect on the predicted population sizes.

The approach described here is applicable to many animal species and many forms of disturbance, as the effect of disturbance is viewed as a trade-off in resource use in response to disturbance. Measuring this trade-off allows estimation of the number of animals that could be supported in the absence of disturbance. The value of this approach is firstly that it clarifies whether or not disturbance is having an effect on the distribution of a population at a given site, and secondly, that it allows quantification of the effect of disturbance in terms of the numbers of animals. In the case of conservation issues this is ultimately the measure which policy-makers require.

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