Approaches to measuring the effects of human disturbance on birds

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Human recreational activities are often considered as potential threats to biodiversity, by restricting animals' access to resources that otherwise would be exploited. Because access to wildlife areas is one major means of increasing their public value, and hence the pressure to conserve them, it is clearly critical to be able to identify accurately when human presence is a threat to conservation and when it is not. A wide range of methods have been used to assess the impacts of human disturbance on wildlife and these methods are summarized here. The type of method used depends principally on whether the disturbance issue relates to a particular site, a particular group of individuals or whole populations. Within these categories, both comparative and experimental approaches have been used to assess behavioural, distributional, demographic and population responses to human presence. Examples of each approach are given here, together with an assessment of the information each method provides.

Human disturbance of wildlife is frequently mentioned as one of the principal issues of concern in biodiversity conservation, yet the information required to assess the extent of this threat is rarely available. The issue presents a potential dilemma for conservationists because human access to wildlife areas is a critical element of generating public support for maintaining areas for biodiversity conservation. Providing access to wildlife areas is also a key element of educating and influencing the public and the next generation of conservationists. In this context, it is clearly extremely important for researchers to identify accurately cases where human presence is adversely impacting on wildlife, and to be able to quantify this effect in relation to the potential benefits of access.

The principal way in which human presence can impact on wildlife is by altering the ability of animals to exploit important resources. This can operate either through directly restricting access to resources such as food supplies, nesting sites or roosting sites, or by altering the actual or perceived quality of these sites. Direct restriction of access to resources can occur through animals avoiding areas where humans are present. Changes in the quality of sites as a result of human presence could occur, for example, if predators

were attracted to areas with humans, or if the presence of humans reduced the presence of prey species. The threat of human presence leading to restricted access to resources has led to a very large number of studies of a wide range of taxa. A variety of approaches have been taken by different researchers (Hill *et al.* 1997) and different methods are appropriate for different questions and circumstances (Table 1).

RESEARCH PERSPECTIVES AND APPROACHES

The majority of studies of the impact of disturbance on patterns of resource use by species have broadly taken one of three perspectives: a site-based perspective focused on the impact of disturbance on numbers of animals using particular sites, a demographic perspective focused on quantifying the costs of disturbance in terms of reductions in survival or breeding success, or a population perspective focused on measuring the density-dependent consequences of shifts in distribution resulting from disturbance.

Within these three perspectives, both comparative and experimental approaches are commonly adopted. Experimental approaches clearly have the benefit of controlling for many of the other factors that will influence responses to disturbance, but comparative approaches are also of great value, particularly where

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Table 1. Examples of typical measures of four different types of effect of human disturbance on animal populations, and the information that each measure provides.

Effect of disturbance	Information provided
Change in distribution	
• Long-term avoidance of areas with high levels of human activity	Site-based issues, e.g. reduced numbers on a site designated for a species
• Short-term movement in response to human presence	Could indicate a site-based effect if movement is repeated or prolonged
Change in behaviour	
• Flight response	Could indicate *either* potential demographic costs or that individuals are
• Increased vigilance	responding because they can afford to, rather than because they are vulnerable
• Altered incubation pattern	
Change in demography	
• Reduced fecundity in disturbed areas	Reduced fitness of a particular group of individuals, e.g. may be important for
• Reduced survival in disturbed areas	species of conservation concern
Change in population size	
• Severe demographic changes causing population decline	Effect of disturbance on population status – may be most relevant for small populations
• Population decline as a result of density-dependent changes to mortality or fecundity following redistribution in response to disturbance	Effect of disturbance on population size and status Ability to predict population-scale responses to altered disturbance regimes

they allow a wide range of sites or circumstances to be included within studies.

Site-based perspective

In some cases, the issue of concern may be whether the numbers of animals at a particular site are constrained because of human presence. This is often the case when management of a site is targeted towards particular species, or where a site has received a national or international designation requiring numbers of particular species to be maintained at that site.

The comparative approach to site-based issues is one of the commonest approaches adopted in studies of the impact of disturbance on biodiversity (e.g. Burton *et al*. 2002, Finney *et al*. 2005, Yasue 2005, Burton 2007). Comparisons of spatial or temporal variation in disturbance can yield information on the distribution of animals or their behavioural responsiveness to human presence. For example, Fernández-Juricic and Telleria (2000) made use of the numerous footpaths through parks in Madrid to show that the abundance of bird species adjacent to the paths decreased dramatically with increasing numbers of pedestrians. Similarly, many studies have compared the distribution or behaviour of animals before and after disturbance events (e.g. Bélanger & Bédard 1989, Finney *et al*. 2005). A limitation of these types of

approaches is that the numbers of animals that would use these sites in the absence of disturbance is generally not known. For example, if the sites with higher levels of disturbance also have lower levels of resource availability (e.g. food or nest-sites) or higher risk of predation, then removing the source of disturbance may have no effect on the numbers of animals in the area.

An alternative comparative approach that takes account of correlates of disturbance is known as the resource-use trade-off approach (Gill *et al*. 1996). This method can be used when the resources that are being used by animals within an area can be identified and quantified (e.g. the abundance and distribution of prey species in the case of foraging animals, or the availability of suitable nesting locations for breeding species). Resource-use trade-offs operate by quantifying levels of resource use in patches with varying levels of disturbance. For example, in a study of Pink-footed Geese *Anser brachyrhynchus* foraging on the harvested remains of sugar beet crops, Gill *et al*. (1996) showed that the proportion of the crop that was not consumed on individual fields decreased significantly with the distance of those fields from roads (Fig. 1). This approach allows calculation of the number of animals that the area could potentially support if disturbance levels were reduced. Similarly, in a study of Black-tailed Godwits *Limosa limosa*
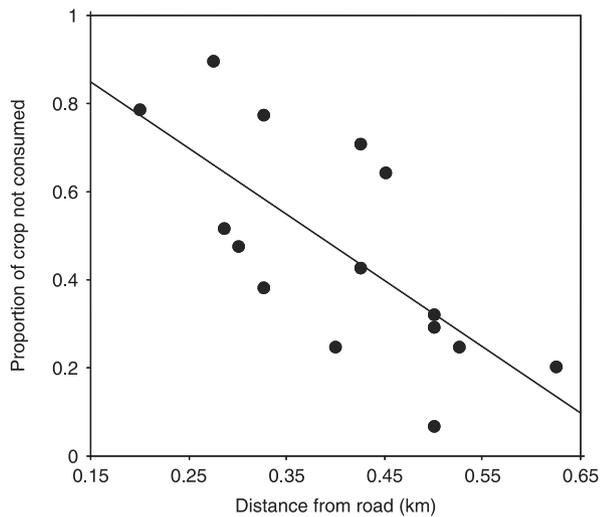
Figure 1. The relationship between the distance between foraging flocks of Pink-footed Goose and the nearest road and the proportion of sugar beet roots not consumed by the Geese, across 15 fields in Norfolk (from Gill *et al.* 1996).

islandica wintering on estuaries in southeast England, the resource-use trade-off approach showed that there was no difference in the proportion of available invertebrate prey consumed by the birds on sites with varying levels of disturbance (Gill *et al.* 2001a).

Experimental approaches to site-based concerns over disturbance impacts have also been employed. For example, concern over the impact of hunting disturbance on numbers of wildfowl using a major wetland site in Denmark resulted in hunting restrictions being imposed on different sections of the wetland over several years (Madsen 1998). This ambitious large-scale study showed a dramatic impact on species such as Eurasian Wigeon *Anas penelope* in which numbers in the protected areas increased greatly within just a few years. Stillman and Goss-Custard (2002) also carried out an experimental study of disturbance impacts but in this case they were able to incorporate these effects within their models of resource exploitation by Eurasian Oystercatchers *Haematopus ostralegus* foraging on mussel beds on the Exe estuary in England. This study clearly showed that the response of Oystercatchers to human presence depended greatly on foraging conditions, as the number of birds leaving disturbed mussel beds and their return time were both lower later in the winter, when more foraging time was necessary to meet their energy requirements.

Physiological responses to disturbance are also frequently explored within an experimental frame-work. Commonly measured physiological responses include changes in heart rate (e.g. Weimerskirch *et al.* 2002, Holmes *et al.* 2005) and the adrenocortical stress response, which results in an increase in corticosterone levels in birds (Walker *et al.* 2005). These comparisons have revealed stress responses to disturbance in birds constrained to areas such as nesting sites (e.g. Holmes *et al.* 2005), although habituation has been reported to reduce stress responses (Walker *et al.* 2006), and the fitness consequences and long-term impact of such stress responses are difficult to measure (Walker *et al.* 2005).

Demographic perspective

In many cases, the issue of concern over human disturbance is not constrained to a particular site but instead relates to the impact on a particular group of animals. Large numbers of studies have approached this issue by recording behavioural responses to disturbance, such as flight responses, reductions in nest incubation or changes in foraging behaviour (e.g. Rodgers & Smith 1995, Gutzwiller & Anderson 1999, Fernández-Juricic & Telleria 2000, Fernández-Juricic *et al.* 2001, Verhulst *et al.* 2001, Coleman *et al.* 2003, Burger *et al.* 2004, Rees *et al.* 2005, Webb & Blumstein 2005; Table 1). Most such studies assume that these changes in behaviour will have fitness consequences for the individuals involved but these assumptions are rarely tested and, in many cases, may not be justified (Gill *et al.* 2001b). Behavioural responses are always context-dependent and individual responses to human presence will therefore depend on the trade-offs experienced by those individuals. For example, the decision to stay or to leave an area in response to disturbance will be influenced by the quality of the area, the availability and relative quality of alternative areas, relative predation risk on current and alternative sites, and so on. Animals may remain in disturbed areas because the cost of moving to a new location is too great or because food resources are more abundant or predation risk is lower than in alternative sites. By contrast, animals that move readily in response to disturbance may do so because alternative locations are plentiful and/or because the costs of moving are small. In this context, it becomes impossible to distinguish between animals that do not respond to disturbance because they are unaffected by it and those that are constrained to stay in the area but may suffer severe costs (e.g. reduced foraging time or nest defence) as a result. Similarly, it is impossible to distinguish between animals that

move because the costs of moving are trivial and those that move because the impact of disturbance exceeds what may be considerable costs of moving (Gill *et al.* 2001b). A clear example of this problem is described by Beale and Monaghan (2004), in which Turnstone *Arenaria interpres* were experimentally provided with supplementary food and their response to disturbance was measured. The distances at which birds took flight in response to human presence was significantly greater for birds provided with supplementary food than for control birds. The traditional interpretation of such variation in flight distances would have been that the birds responding at greater distances were more 'vulnerable' to disturbance (e.g. Klein *et al.* 1995), implying that those individuals were suffering greater costs of disturbance than individuals that did not respond so rapidly. However, this experiment clearly shows that these birds were simply more able to respond earlier, either because they were in better condition to stop feeding earlier or because they perceived their general environment to be of better quality and were thus more willing to move to an alternative location.

Behavioural responsiveness to disturbance is thus not sufficient to determine vulnerability to human presence, as the same responses can result from directly opposing circumstances. Studies of vulnerability must therefore quantify the fitness consequences of responses to disturbance in order to avoid this problem. A few studies have quantified fitness under varying disturbance regimes. For example, Pink-footed Geese migrating to their breeding grounds in Svalbard use passage sites in Norway to refuel during migration. These Geese feed on grasslands where they can come into conflict with farmers concerned about loss of grass production (Tombre *et al.* 2005). Individual marking of these Geese has allowed both the locations of birds in the Norwegian staging sites to be monitored, and their subsequent breeding success to be recorded, as Geese travel in family parties on autumn migration. Madsen (1995) showed that those birds that had staged in areas where the farmers deliberately disturbed the Geese to scare them from the grasslands gained less body fat and returned with fewer offspring in the autumn than those that had staged in undisturbed areas. More recent work has indicated that scaring tends to be concentrated in the most productive grasslands (Tombre *et al.* 2005); thus, the effect of disturbance on breeding success may be even more marked than previously thought, if access to high-quality food on spring passage enhances condition for breeding.

Demographic costs of human presence were also demonstrated by Beale and Monaghan (2005), in their study of nesting failure rates of seabirds at a colony regularly visited by tourists. Of the two species studied, failure rates were weakly correlated with higher visitor numbers in the Black-legged Kittiwake *Rissa tridactyla* but not in the Common Guillemot *Uria aalge*. The authors conclude that limiting visitor numbers could improve Kittiwake breeding success but that these benefits have to be weighed against the costs in terms of reduced public education and awareness. Remarkably few studies take such a balanced view of the disturbance issue and acknowledge that the conservation benefits of public access can potentially over-ride direct demographic costs to individuals. Much of the research on this topic has focused on remote areas such as Antarctica, where visitor impacts on breeding bird colonies and appropriate visitor management strategies have been extensively studied (Yorio *et al.* 2001, Mason 2005). The differences between species reported in this study also highlight the fact that the impact of human presence is likely to be both species- and site-specific.

Population perspective

Fitness consequences of human disturbance are clearly important at the individual level, but whether these effects translate into population-scale impacts will depend on the scale at which disturbance occurs, and the extent of any secondary effects on animals in undisturbed areas. These secondary effects will depend on the strength of density dependence operating within populations. For example, in cases where animals respond to human presence by redistributing to new locations, the impact on the population will depend on whether the increased densities at these new sites result in reduced *per capita* survival or fecundity.

Sutherland (1998) described how density-dependent mortality and fecundity can combine to determine population-scale impacts of disturbance. This approach describes the change in the total population size (ΔN) that will result from a given level of disturbance within one site:

$$\Delta N = LM\gamma \, d'/(b' + d') \qquad (1)$$

where L is the area affected by the disturbance, M is the density within the site prior to disturbance, b' is the strength of *per capita* breeding output, d' is the *per capita* density-dependent mortality and γ is the
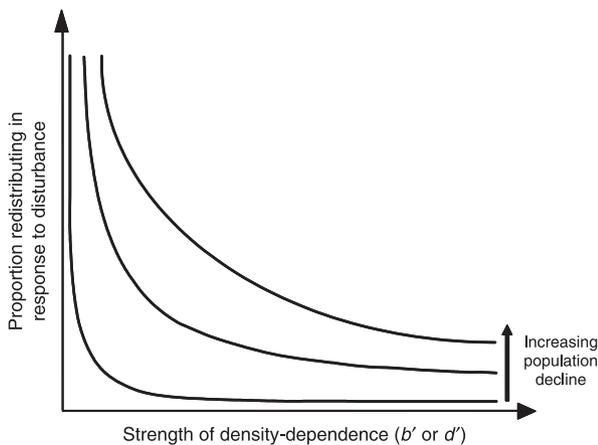
Figure 2. The effect of the strength of density-dependent fecundity (*b'*) or mortality (*d'*) on the overall population decline resulting from the redistribution in response to disturbance (γ) at one site (after Gill & Sutherland 1999).

proportional change in the number of animals in the site as a result of disturbance. Gill and Sutherland (1999) used this equation to demonstrate how the effect on population size of redistribution in response to disturbance is dependent upon the strength of density dependence, as illustrated in Figure 2. Populations in which density dependence is strong (i.e. increasing density results in higher overall mortality, for example through higher rates of prey depletion or increased predation rates) can suffer severe population declines from only small redistributions in response to disturbance. By contrast, populations with weak density dependence can experience extensive redistributions with minimal impacts on population size.

The detailed field studies necessary to quantify density-dependent impacts of disturbance have been carried out in only a small number of cases. For example, Liley (1999) demonstrated how quantifying territory quality for breeding Ringed Plovers *Charadrius hiaticula* allowed the construction of models predicting declines in *per capita* breeding success as the population fills progressively poorer quality territories. Breeding success of Ringed Plovers declines sharply with territory quality and thus restricting access to high-quality sites can significantly influence productivity and local population size. Ringed Plovers avoid breeding in areas of beach with high tourist presence, and these models were used to predict the population size that could result from changes in the numbers and distribution of tourists (Liley & Sutherland 2007). Similarly, recent work by Mallord (2005) and

Murison *et al.* (2007) have indicated the importance of density dependence in quantifying population-level impacts of disturbance on breeding populations of Woodlarks *Lullula arborea* and Dartford Warblers *Sylvia undata*. The clear message from all of these studies is that although disturbance may be the issue of concern to conservationists, at a population scale any declines in survival or fecundity will result from density-dependence and not directly through disturbance. Efforts to manage disturbance in order to maintain populations must therefore be based on an understanding of the density-dependent consequences of avoidance of disturbed areas.

SUMMARY

Conservation of wildlife areas and habitats depends on public interest and support. Actively encouraging public education and responsible access to the countryside is a crucial element of local conservation efforts, and of developing the interests of current and future generations. In this context, restricting public access should only be considered when the conservation impact of human presence is demonstrably severe. An array of methods of measuring disturbance impacts is available in the literature and different methods are appropriate to different circumstances. In issues of site conservation, simple approaches of measuring use of locations with different levels of human presence can be sufficient, particularly if the effect of disturbance on the use of key resources within those locations is also quantified. In issues of species conservation, there is a real need to go beyond behavioural studies and to explore the consequences of disturbance for demographic and population processes.

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