

The effects of human disturbance on
breeding and foraging birds

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Declaration

I declare that this thesis is my own work and no part of the work submitted here has been submitted as part of any previous examination. Supervision by P. Monaghan has helped develop ideas throughout the thesis.

A handwritten signature in black ink, appearing to read "Chris Pash". The signature is written in a cursive style with a large initial 'C'.

Abstract

The appropriate management of visitors to nature reserves is an important conservation concern. In this thesis I briefly review the current literature describing the effects of disturbance on wildlife, concentrating mainly on birds (Chapter 1). Recent literature has provided worrying critiques of the practical and theoretical bases upon which management practice is based. Here, I address a number of questions that seek to clarify the impacts of human disturbance on birds. I started by asking whether behavioural measures of disturbance are accurate indices of the negative effects of disturbance. Through an experimental test of a theoretical model, I showed that animals that respond most to disturbance may in fact be those individuals that face the lowest cost associated with such disturbance (Chapter 2). Turnstones *Arenaria interpres* provided with extra food over three days showed stronger behavioural responses to a standardised disturbance stimulus than those without extra food. Behavioural measures are therefore not always a good index of disturbance effects. Consequently, the conclusions of some of the studies reviewed in Chapter 1 must be considered doubtful.

Although some large declines in breeding success of some species are caused by human disturbance, such effects are obvious, simple to remedy and appear to be rather rare. If human disturbance is a general concern it is therefore necessary to assess whether human disturbance has impacts on species that are not obviously sensitive. To investigate this, I modelled the impact of human disturbance on the nesting success of kittiwakes *Rissa tridactyla* and guillemots *Uria aalge* (Chapter 3). By directly measuring a range of nest site parameters as well as those parameters involving human disturbance, I was able to improve the power of the analysis to detect disturbance effects over those of previous, less detailed, studies. Both species, but particularly kittiwakes, are generally considered tolerant of people, as they show few obvious behavioural responses to human presence. However, I found that human disturbance parameters were the largest factors explaining nesting success in these species, suggesting again that superficial behavioural observations can be misleading. It is possible, therefore, that disturbance impacts are more widespread than is immediately obvious.

Since disturbance impacts of potential concern are shown by kittiwakes, it is interesting to ask whether behaviour could give a useful indication of these changes. I assessed this through observing the behaviour of kittiwakes nesting in areas with different exposure to human disturbance and on days with differing visitor numbers (Chapter 7). Although both these measures of human disturbance (daily visitor number and exposure to disturbance) are ostensibly similar, the relationships between them and chick neglect are opposite. Thus nests in areas of high exposure to humans showed high chick neglect, but chick neglect was lowest on days of high visitor numbers. These patterns are comprehensible in terms of the costs and benefits of chick neglect, but again show how hard it is to determine disturbance impacts from changes in behaviour.

As kittiwakes do show declines in breeding success associated with human disturbance it is important to determine the mechanisms that allow this decline (Chapter 6). I found that changes in behaviour associated with human presence were unlikely to be the mechanism that leads to nesting failure, but that heart-rate mediated effects were plausible. An incidental prediction of this mechanism is that chick neglect is likely to increase in nests with the greatest exposure to human disturbance, which I found to be the case (Chapter 7). The understanding of this mechanism is important, as it shows clearly that impacts of human disturbance on parameters of fundamental importance to conservation (breeding success) can be completely uncoupled from behavioural responses. Thus, not only is it possible that use of behavioural indices may incorrectly assess the fitness consequences of human disturbance (Chapter 3), but significant impacts may occur in the total absence of behavioural responses.

As well as an indication of a plausible mechanism linking human disturbance and nesting failure, I showed that it is useful to think of human disturbance as a form of perceived predation risk (Chapter 3). This understanding, and an understanding of a mechanism that can link human presence and breeding failure even in the absence of behavioural responses, allows assessment of current management protocols. I found that building a model of perceived predation risk suggested that taking account of visitor numbers was at least as important as establishment of set-back

distances (Chapter 3). After suitable testing in other colonies, I used these models to develop guidelines for optimal visitor distribution around nature reserves (Chapter 4). Examining the daily pattern of visitor numbers and failure rates showed that, for kittiwakes at least, failures were most common on days with peak visitor numbers, showing again the importance of visitor numbers irrespective of distance (Chapter 5). Patterns of chick neglect also showed that daily variation in visitor numbers affects birds, such that on busier days birds were less likely to neglect their chicks and consequently have less time for foraging (Chapter 7). These patterns, and the considerable individual variation in heart-rate responses at different distances (Chapters 7 & 8), suggest that the most effective form of access management may be the restriction of daily visitor numbers and provision of visitor free periods. Whilst imposing these restrictions, managers may be able to further reduce the impact of human disturbance by manipulating the distribution of visitors within the reserve. I conclude the thesis by summarising management guidelines and placing these ornithological findings in a wider conservation perspective.

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CHAPTER 1

General review and introduction

The effective management of visitor access to wildlife areas is an extremely important conservation issue, as ever more people opt to spend their free time in the countryside (Keirle 2002; Gray *et al.* 2003). It is recognised that the first-hand experience of wildlife gained by visitors to nature reserves is one of the best ways to inspire concern for conservation (Hendee 1972; Bogner 1998; Bogner 1999) and increases the importance and value of such areas in the eyes of the public (Adams 1997). However, poorly managed visitor access is widely perceived to lead to negative consequences for the wildlife that visitors come to see (Wauters *et al.* 1997; Higham 1998; Frid 2003; Stevens & Boness 2003; Taylor & Knight 2003). In the UK, recent legislative changes (in England the Countryside and Rights of Way (CROW) Act 2000, in Scotland the Scottish Land Reform Bill 2002) have greatly increased public access to open countryside, with corresponding concerns about the potential impact that this will have on wildlife (Anon 2003; Liley 2002). In recognition of these concerns, the same laws that give open access to the public provide conservation bodies with the possibility of restricting access to sensitive areas where such action can be justified (CROW Act 2000). If conservationists are to exercise these powers wisely, they must ensure that potential impacts are real and significant. It is clearly vital that all such decisions are therefore backed by good quality science.

The general picture of the effects of human presence on wildlife is a negative one, with many declines in breeding success or population size reported and attributed to the effect of disturbance (Pierce & Simons 1986; Sandvik & Barrett 2001; Fernández-Juricic *et al.* 2003). For example, in the UK Red Data Book, human disturbance is described as a contributory factor likely to be responsible for the threatened status of 76 of the 113 bird species listed (Batten *et al.* 1990). However, a more critical reading of the available literature suggests that perhaps these effects are exaggerated or based on insufficient primary data (Hill *et al.* 1997; Nisbet 2000). Here I start by reviewing the literature reporting the different types of effects of human disturbance on animals. Much of the published literature focuses exclusively on disturbance to birds and consequently ideas about disturbance effects are most well developed for this group. For this reason, I focus most of this introduction on the effects of human disturbance on birds, though, where available,

I also refer to other taxonomic groups. I summarise these findings and describe the management measures currently used to minimise the effects of human disturbance in conservation areas. I then draw together some general themes from these studies, to highlight the areas where the gaps in our knowledge are greatest.

The term “human disturbance” has been used to describe two somewhat different conservation problems. Firstly, “human disturbance” may refer to the indirect effects on animals caused by habitat modification due to changes in land use or management (e.g. Erwin 1980; Franco *et al.* 2000). As these effects may be understood in the context of habitat modification, they are different from the sort of human disturbance relevant to the management of access. Instead, I take this second definition for the following review: “any human activity that changes the contemporaneous behaviour or physiology of one or more individuals ...” (Nisbet 2000). From this definition it is clear that human disturbance necessarily produces a measurable effect on the animals in question, though not necessarily an impact on conservation or welfare: the effects of disturbance may be entirely trivial or even beneficial. It is therefore important to distinguish between disturbance effects, which need not be important, and disturbance impacts: those effects that have substantive negative impacts on conservation or welfare.

MEASURES OF DISTURBANCE

Behavioural responses to disturbance

Much of the human disturbance literature focuses on the effects of humans on the behaviour of wildlife: animals may stop feeding or flee approaching humans, for example (e.g. Nettleship 1972; Fortin & Andruskiew 2003). In general, it is accepted that the study of behaviour within a conservation context is to be encouraged, as ultimately most fitness consequences are mediated by behavioural decisions made by individual birds (Sutherland 1998a,b). However, if studies reporting behavioural effects of disturbance are to be useful in guiding management practices, the link between such behavioural changes and actual fitness costs must be clear (Gill *et al.* 1996; Hill *et al.* 1997; Nisbet 2000; Gill *et al.* 2001a).

Researchers have used a variety of ways to assess whether behavioural effects of disturbance affect a species' conservation status. Some focus on using behaviour as a sensitive index of the effects of human disturbance. They argue that if no behavioural change is apparent then there can be no fitness consequences or, conversely, species showing the greatest behavioural responses are believed to be the most sensitive (Tuite *et al.* 1984; Klein *et al.* 1995; Blumstein *et al.* 2003). Other studies focus on the costs of the changed behaviour itself: some show a behavioural change and simply assume that this must have a negative impact (Burger & Gochfeld 1983; Madsen 1998; Mann *et al.* 2002; Quan *et al.* 2002; Williams *et al.* 2002; Fernández-Juricic *et al.* 2004), whilst others attempt to link behavioural changes to putative energetic costs and argue that this will, in time, become a fitness cost (Bélanger & Bédard 1989; Keller 1991; Galicia & Baldassarre 1997; Lafferty 2001). Very few studies actually link behavioural changes to anything that can be directly shown to affect conservation status (Gill *et al.* 2001a; Hill *et al.* 1997).

It is clear, however, that if behavioural measures are not necessarily an indication of fitness effects, then the use of these to quantify the impacts of disturbance on conservation status is not justified. A recent paper by Gill *et al.* (2001a) suggests that a lack of behavioural response may not imply a lack of fitness consequence but may instead reflect a lack of choice. Gill *et al.* give the example of ducks using a lake and their response to shooting. Different species respond differently, with relatively more dabbling ducks leaving than diving ducks. This response is usually interpreted as showing that dabbling ducks are more affected by disturbance but may instead be related to the availability of alternative areas. There may be more ponds suitable for dabbling than for diving and therefore diving ducks appear to “choose” to stay where they face a shooting risk when in fact they have no alternative. In this case, a lack of behavioural response results in decreases of fitness; the opposite effect to that generally assumed. This process is directly analogous to the decisions made by birds feeding in areas of high predation risk, where evidence suggests that individuals expose themselves to more risks when environmental conditions are harsh and the bird's condition poor (Hilton *et al.* 1999). As Gill *et al.* (2001a) note, this pattern is not restricted to movements of

birds but also relates to other behavioural responses. Moreover, the same reasoning can be applied to intra-specific differences in sensitivity depending on each individual's current state.

Not only does this finding question the assumption that behavioural changes are necessarily linked to fitness consequences via energetic consequences associated with the behaviour; it also questions the use of behaviour as a sensitive index of other costs. It is quite possible, therefore, that significant behavioural changes can be realised without any fitness cost whatsoever. Moreover, there is an increasing number of studies that provide initial evidence for potentially damaging responses to human presence even in the absence of behavioural responses, to which I shall return later (e.g. Nimon *et al.* 1995; Fowler 1999).

It should be noted, however, that whilst based on sound theoretical models, Gill *et al.*'s results have received little empirical testing. Some limited evidence may be found in an earlier study of wintering pink-footed geese *Anser brachyrhynchus* (Gill *et al.* 1996). Geese are generally believed to be at risk from disturbance (Madsen 1985; Ebbinge 1991) yet no biologically important impacts were identified by Gill *et al.* (1996), suggesting that traditional threat assessment may be faulty. Further evidence may be found in the literature relating to bird scaring, where the birds that are most difficult to move are immatures, which are likely to be in a poorer condition than adults (Aubin 1990). Fernández-Juricic *et al.* (2003) also provide experimental evidence suggesting that responses by House Sparrows *Passer domesticus* to humans can be non-linear. They suggest this provides incidental evidence for the type of context-dependent decisions Gill *et al.* (2001a) predict. However, whilst showing that responses to humans may be more complex than initially expected, their results are not a direct test of Gill *et al.*'s (2001a) model.

Resource-use based models

Although not widely applied, human disturbance has been studied through the use of resource-use based models (Gill *et al.* 1996; Percival *et al.* 1998; Gill *et al.*

2001b; Fernández-Juricic *et al.* 2003). Such models develop a behaviour-based model to assess the impact of human disturbance, but do not rely on directly measuring the behavioural responses animals show to human presence. Instead, they assume that animals show behavioural responses to humans but suggest that if any significant fitness costs are associated with such responses, a critical, limiting resource will be under-used. Therefore, patterns of resource use are determined instead of measuring behaviour directly. If resources are under-utilised in areas where disturbance is high, human disturbance is regarded as having an impact of conservation concern. For example, Gill *et al.* (2001b) report a study of the effect of disturbance on the Black-tailed Godwit. They showed that, despite this species being perceived as sensitive to human disturbance (Batten *et al.* 1990), no under-use of food resources was detected. They therefore conclude that although these animals appear to avoid human presence, this does not reduce the number of animals supported by the estuaries they studied.

These studies of resource use have so far focussed on utilisation of food supplies (Gill *et al.* 1996; Gill *et al.* 2001b; Fernández-Juricic *et al.* 2003) and wintering habitat (Percival *et al.* 1998), but could also be used in relation to other resources, including breeding territories. However, such studies rely heavily on the correct identification of critical resources. If the effects of disturbance was measured on the use of the wrong resource, it would be possible to incorrectly conclude that human disturbance was not an important factor. It is possible, for example, that the utilisation of food resources is unaffected by human disturbance, but that roosting behaviour is negatively affected. Alternatively, it might be possible to wrongly identify human disturbance as limiting populations for the same reasons. For example, if some other external factor holds an animal's population artificially low and these animals show avoidance of humans, they may not make full use of resources in disturbed areas. However, it would be wrong to assume that this pattern of resource use provided evidence that disturbance was involved. If the population were to increase, birds might eventually decide to forage in the more disturbed areas.

Human disturbance and breeding success

Unlike behavioural effects, if human disturbance can be shown to affect breeding success, the link with conservation concerns may be much clearer. Consequently, many papers that seek to assess the impact of disturbance measure changes in breeding success (e.g. Pierce & Simons 1986; Blanco *et al.* 1999; Shealer & Haverland 2000).

One general criticism of avian studies using nesting success is the difficulty of finding controls (Nisbet 2000). As studies are often of colonies, control and experimental birds may be nearby and controls may suffer some of the disturbance experienced by experimental birds (e.g. Rodway *et al.* 1996; Shealer & Haverland 2000). Furthermore, the effects of disturbance are not necessarily incremental; the first few times a nest is visited may have disproportionate effects on the total disturbance experienced, making minimally visited nests poor controls.

Nisbet (2000) highlights another problem in using nesting success to evaluate the impact of human disturbance, noting that when one nesting attempt fails, birds may move elsewhere and try again. Furthermore, nesting success is often not a good measure of fitness and a better measure may be recruitment. For example, if disturbance results in lower productivity, then density dependent mortality may compensate, resulting in the same number of birds surviving to recruit. The effect of lowered productivity may therefore cause no decline in populations, an effect that is known from the limited success of population control methods such as culling (e.g. Olijnyk & Brown 1999; Frederiksen *et al.* 2001).

Furthermore, a distinction must be drawn between biological and statistical significance of the effects found. As breeding success is a simple binary measure of success or failure, the statistical detection of small changes in this parameter is difficult without very large sample sizes. Unless a change in breeding success caused by disturbance is very large, therefore, it is possible that small, but potentially important, changes in breeding success go unnoticed. To assess how important this is in published studies of the effects of disturbance on nesting

success, I reviewed 16 papers reporting on nesting success in a total of 44 comparisons between control and experimental groups. Using a method based on post-hoc power tests (Appendix 1) I calculated the maximum decline in nesting success that we can be 95% certain did not occur (Table 1). From this it is clear that 93% of analyses (41 of 44) using an experimental approach (and including a control) were not capable of detecting declines in nesting success smaller than 10% with 95% certainty. Indeed, one reports no change, but actually only a decline in nesting success greater than 84.8% would have had a 95% likelihood of being found. This problem of low statistical power is inherent within all studies assessing the impact of human disturbance on the nesting success of birds with small clutch sizes. Therefore, when very large sample sizes are impractical, nesting success will be of very limited use in assessing the impact of human disturbance on birds.

Other measures of disturbance

A minority of papers attempts to measure the effects of disturbance in ways that do not depend on behavioural or demographic parameters. Chosen measures are often physiological. Additionally, a few studies have attempted to quantify direct effects on mortality (Feare 1976) and on chick growth rates (Harris & Wanless 1984; Pierce & Simons 1986). Where mortality effects of disturbance have been measured, the impact on populations is obvious, whilst the suitability of other measures needs more justification.

For example, chick growth rate has been found to be slower in disturbed colonies of Guillemots (Harris & Wanless 1984) and Tufted Puffins (Pierce & Simons 1986). This is believed to result in lower fledging weights or later fledging and is assumed to be important in a conservation context, although it is hard to find supporting evidence. Where heart-rate or steroid levels are measured, the intention is often to measure a variable associated with stress. The typical vertebrate response to stress is activation of the hypothalamo-pituitary-adrenal (HP) axis (Siegel 1980; Romero 2004). This results in the release of glucocorticoids into the blood following a stressful event (after around three minutes (Kitaysky *et al.* 1999)). As adrenaline is known to increase heart-rate and forms part of the HP axis

(Rosenbruch *et al.* 1993), measurement of heart-rate is also considered to be a sensitive measurement of stress (Wilson & Culik 1995; Nimon *et al.* 1996). More direct measures have also been achieved by measurement of corticosterone (Fowler 1999; Müllner *et al.* 2004; but see also Romero 2004).

Some penguins are noted for their lack of behavioural responses to visitors, especially in areas where visitors are frequent (e.g. Nimon *et al.* 1995; Fowler 1999). This lack of response led to the suggestion that these birds are habituated, a claim also made for other species (Nisbet 2000). The first study using physiological measures of disturbance (Wilson *et al.* 1991) used heart-rate monitors to show that tourist presence caused significant increases in heart-rate even in the absence of behavioural response. Although this result was initially questioned (Nimon *et al.* 1995), further analysis has confirmed the finding in both the original and other penguin species (Wilson & Culik 1995).

Fowler (1999) took the study of penguin stress responses further by studying directly the hormonal and behavioural responses in areas of differing disturbance. Fowler showed no difference in physiological responses between birds in medium and low disturbance plots, but found a significantly decreased hormonal response in the high disturbance areas, indicative of habituation. These results are inconclusive, however, as variation was large in the control plots but small in the disturbed plots. This suggests that, rather than birds habituating, birds that showed high responses left the area. This is further suggested by the lower nesting density in the high disturbance plot (Fowler 1999). Fowler also showed that average strength of the behavioural responses in each plot decreased with visitor levels, but did not examine the relationship between an individual's hormonal and behavioural responses.

As described earlier, studies that show that disturbed birds suffer from stress even in the absence of behavioural responses are important as they provide evidence that human presence may have adverse impacts even where behavioural responses are minimal. Stress responses to disturbance are potentially of conservation concern as prolonged increases in corticosterone levels can have

physiological consequences (Sapolsky 1987; Romero 2004) and may lead to population decline (Lee & McDonald 1985). In addition, a raised heart-rate may itself have conservation consequences, as maintaining raised heart-rates requires increased metabolic costs which may, in turn, affect demographic parameters. Regel and Putz (1997), for example, measured the temperature of penguins as an index of metabolic rate and showed that disturbance caused by research procedures resulted in an increase in daily energy expenditure of 10%. They argue that much of this raised temperature is due to the raised heart-rate measured in other studies. Such studies, although still far from linking human disturbance directly to population declines, allow us to glimpse a mechanism perhaps capable of making this link even in the absence of behavioural changes.

Although there has been much research into the effects of disturbance on wildlife, many of the results are difficult to interpret. Where breeding success has been found to show clear declines, we can be certain that the level of human disturbance is indeed of conservation concern. However, the use of such measures is limited, both temporally to the breeding season and generally to studies where very large sample sizes are possible. Furthermore, the wisdom of using behavioural measures, either as an index of other assumed fitness costs or in an attempt to quantify the energetic costs associated with human disturbance, is questionable on theoretical grounds. Consequently, the current use of set-back distances as the primary management tool for protecting animals from the effects of human disturbance is also based on shaky foundations (see below). By contrast, the few studies of physiological or metabolic responses provide intriguing evidence of a mechanism with the potential to link human disturbance to breeding failure. However, these studies are still far from confirming this mechanism and they do not offer any insight into how general these mechanisms may be. The very few studies that used resource utilisation to measure disturbance effects offer one solution to these issues, but require correct identification of critical resources, which may not always be possible.

CURRENT MANAGEMENT PROTOCOLS

Where a problem of human disturbance exists (or is perceived to exist), there are three main ways to make practical management improvements. The distance between people and the sensitive wildlife can be increased; the number of visitors allowed into the area could be reduced, or the distribution of people within a reserve may be altered. Obviously, the three management options could also be combined. In practice, however, and short of totally closing areas to all human activity (as the case in core zones of UNESCO's Biosphere reserves (UNESCO 1974)), it seems as though most managers focus on a distance-based management procedure (Ikuta & Blumstein 2003). For example, many of the papers reviewed here seek to recommend fixed set-back distances, which are considered to provide a safe buffer between humans and the species in question (Rodgers & Smith 1995; Lafferty 2001; Lord *et al.* 2001; Fernández-Juricic 2004).

Appropriate set-back distances are usually determined by one or two researchers approaching animals and recording the distance at which they determine a response. This distance is then used to define a safe distance (usually by adding a further margin for safety) which is recommended as a minimum safe approach distance (e.g. Gander & Ingold 1997; Lord *et al.* 2001; Rodgers & Schwikert 2002; Fortin & Andruskiew 2003; Thomas *et al.* 2003). There are a number of important assumptions implicit within this management protocol (Blumstein *et al.* 2003). The most important assumption is clearly that behaviour is a reliable index of the conservation impact of human disturbance, which, as we have seen, is unlikely to be the case. Although the protocol can be extended to other, non-behavioural, measures such as a heart-rate response (Wilson *et al.* 1991), it seems unwise to define a distance based on one measure and then shortly after to have to revise this as ever more sensitive measures are developed (Fernández-Juricic *et al.* 2001). Firstly, beyond a certain distance it is questionable if visitors will feel that they have satisfactorily experienced the wildlife anyway. Secondly, and importantly, it is clear that at some point, although an effect may be measurable, the conservation impact may be insignificant. Moreover, it is also assumed that, at any one distance, the effects produced by one or two researchers

will be the same as those produced by a group of visitors, regardless of the number of groups, or number of people within each group: an assumption that seems doubtful (Frid & Dill 2002). Indeed, some declines have occurred even where visitor access has been carefully controlled and rigid distances maintained, throwing further doubt on the efficacy of the management by set-back distance alone (Higham 1998).

By contrast, although a few nature reserves aim to manage the total numbers of visitors present on the reserve (e.g. Harris & Wanless 1995), there seems to be relatively little research into the efficacy of this. I could find no papers that tested either the assumptions implicit in this approach (for example, that there is a positive relationship between visitor number and disturbance effect) or the practical outcome. Similarly, I found only one study that discusses, inconclusively, the potential of manipulating visitor distribution within a nature reserve (Fernández-Juricic *et al.* 2004). Fernández-Juricic *et al.* (2004) point out that enlarging visitor group size (by offering guided walks, for example) could result in lower overall incidence of disturbance, allowing animals to behave naturally for the majority of the time. They also suggest that for forest reserves, concentrating visitors into a small area of the reserve (allowing most of the reserve to be free from disturbance) may be more beneficial than spreading visitors thinly throughout the area. However, both these suggestions are very tentative recommendations based on a behavioural study, and as they are based solely on behavioural measures of disturbance must be treated as provisional.

If we are to make progress in understanding the effects of human disturbance on wildlife, we must focus on several areas. As an overriding concern significant not only in research into the effects of human disturbance, but also generally within the field of conservation biology, it is important that an experimental approach be used where possible. Much current work on disturbance is largely anecdotal in nature, or at best correlative, but such approaches are of limited use and can never confidently identify the causes underlying any changes observed (Nisbet 2000). With this in mind, the first steps towards improving the quality and utility of research on human disturbance must improve our understanding of methods for

measuring the effects of human disturbance. Once such methods are developed we must seek to understand the processes (be they behavioural or physiological) underlying these disturbance effects, before addressing anew applied questions concerning wise visitor management.

In chapter two I present an experimental test of the model of Gill *et al.* (2001a) that questions the use of behavioural measures of disturbance in the turnstone *Arenaria interpres*. In chapter three I seek to measure disturbance effects on breeding success of two species of seabird using new and more precise methodologies than previously and also ask whether, as Frid and Dill (2002) suggest, disturbance is best understood within a framework of predation risk. Building on the model of human disturbance effects developed in chapter three, I address questions of more direct management importance in chapter four. Here I ask what is the best distribution of visitors within a reserve? Is it best to concentrate visitors into small areas of the reserve, or spread them as thinly as possible throughout the area? Chapter five also deals with issues of visitor management by asking whether direct management of daily visitor numbers could provide good protection for wildlife.

At the same time as developing a better theoretical framework for thinking about human disturbance issues, it is important to assess directly the causal mechanisms linking human disturbance and breeding failure. If candidate mechanisms can be identified, further insights into how animals respond to human disturbance may be forthcoming. Consequently, chapter six assesses whether it is more likely that increases in energy expenditure due to raised heart-rates or behavioural changes associated with human disturbance underlie declines in kittiwake *Rissa tridactyla* nesting success. This is followed in chapter seven by the further assessment of an incidental prediction of the heart-rate mediated mechanism: that patterns of chick neglect may be affected by human disturbance. If such a mechanism does occur, it would clearly be advantageous to determine which individual birds show the largest increases in heart-rate without having to purchase costly equipment to measure this directly for each bird. Therefore, I finish in chapter eight by assessing the variability in the heart-rate response associated with

human disturbance in the shag *Phalacrocorax aristotelis*, and ask whether it is possible to identify correlates of strong heart-rate responses in this species.

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Table 1. Papers describing the effects of experimental disturbance on nesting success. The effect measured by each study is included, as well as the decline measurable using the proposed mechanism. Where measured effect is not statistically significant this is indicated alongside the measured effect as NS. Papers are ordered by significance of results then alphabetically by author.

Paper	Species	Disturbance type	Measure	Measured effect	Measured statistics used	Decline measurable	Notes
Anderson & Keith 1980	Brown Pelican	colony entry (research)	nesting success	67% & 100%	comparison of confidence limits	6.94% & 50.0%	Two seasons
Blokpoel 1981	Caspian Tern	cannon netting in colony	nest/egg damage	14.2%	chi-test	12.0%	
Brubeck <i>et al.</i> 1981	Least Tern	trapping on nest and radio-tagging adults	egg-stage desertions	40%	chi-test	36.3%	
Cairns 1980	Black Guillemot	researcher activities	hatching success	48.9%	G-test	46.2%	Assuming G-test to have similar power to chi-square
Ellison & Cleary 1978	Double-crested Cormorant	ground nesting colony entry (research)	egg-stage desertions	41.6%	chi-test	32.0%	
Fetterolf 1983	Ring-billed Gull	colony entry (research)	hatching success	3.2% - 15.1%	chi-test	11.1% & 12.7%	Intermediate to high disturbance
	Ring-billed Gull	colony entry (research)	fledging success	18.9% - 40%	chi-test	13.7% & 15.5%	Intermediate to high disturbance

Paper	Species	Disturbance type	Measure	Measured effect	statistics used	Decline	Notes
Giese 1996	Adelie Penguin	tourist presence near small colonies	hatching	47%	chi-test	38.0%	measurable
	Adelie Penguin	researcher presence near small colonies	hatching	35%	chi-test	35.8%	
	Adelie Penguin	tourist presence near small colonies	nesting	80%	chi-test	55.5%	
	Adelie Penguin	researcher presence near small colonies	nesting	72%	chi-test	53.1%	
	Adelie Penguin	small colonies	success				
Hunt 1972	Herring Gull	colony entry (tourist)	hatching	55.8% &	Chi-test	47.0% &	
Piatt <i>et al.</i> 1990	Least Auklet	colony entry (research)	nesting	27.8%	chi-test	43.0%	Within colony, 45% decline between colonies
Pierce & Simons 1986	Tufted Puffin	colony entry (research)	nesting	80.9%	chi-test	50.0%	
			success				
Rodway <i>et al.</i> 1996	Atlantic Puffin	colony entry (research)	nesting	38%	chi-test	40%	
Blanco <i>et al.</i> 1999	South American Tern	colony entry (research)	hatching	0% NS	Z-test	3.8%	
			success				

Paper	Species	Disturbance type	Measure	Measured effect	statistics used	Decline measurable	Notes
Blokpoel 1981	Caspian Tern	cannon netting in colony	egg-stage desertion	5.4% NS	chi-test	12%	
Brown & Morris 1994	Ring-billed Gull	colony entry (research)	hatching success	0.9% & 12% NS	none	39.1% & 29.1%	assuming a t-test would have been used, differing visitor intensities
	Ring-billed Gull	colony entry around hatching (research)	fledging success	14.6% - 5.1% NS	Fisher's Exact	38.3% - 50.4%	Differing visitor intensities
Brubeck <i>et al.</i> 1981	Least Tern	trapping and marking adults off the nest	egg-stage desertions	7% & 12% NS	chi-test	45.2% & 48.6%	Different declines for different marks
Chairns 1980	Black Guillemot	researcher activities	fledging success	14.1% NS	NS G-test	43.7%	assuming G to have similar power to chi-square
Ellison & Cleary 1978	Double-crested Cormorant	ground nesting colony entry (research)	hatching success	1.3% & 0% NS	t-test	36.5% & 25.6%	Two seasons
	Double-crested Cormorant	ground nesting colony entry (research)	egg-stage desertions	0% NS	chi-test	29.8%	
	Double-crested Cormorant	tree nesting colony entry	fledging	0% &	t-test	29.8% &	Two seasons
	Double-crested Cormorant	(research)	success	2.6% NS		24.8%	
	Double-crested Cormorant	tree nesting colony entry	egg-stage	0% &	chi-test	35.8% &	Two seasons
	(research)	(research)	desertions	25% NS		25.1%	

Paper	Species	Disturbance type	Measure	Measured effect	statistics used	Decline measurable	Notes
Giese 1996	Adelie Penguin	tourist presence near large colonies	Hatching success	7.8% NS	chi-test	19%	
	Adelie Penguin	researcher activities near large colonies	hatching success	2.5% NS	chi-test	19%	
	Adelie Penguin	tourist presence near large colonies	nesting success	11% NS	chi-test	25%	
	Adelie Penguin	researcher activities near large colonies	nesting success	2% NS	chi-test	25%	
Hill & Talent 1990	Snowy Plover	trapping and marking adults off the nest	hatching success	0% NS	Z-test	4%	
	Least Tern	trapping and marking adults off the nest	hatching success	0% & 4.7% NS	Z-test	10% & 11.1%	Marking with rings and radio tagging
		Atlantic Puffin	colony entry (research) in previous year	nesting success	17% NS	chi-test	30.1%
Shealer & Haverland 2000	Black Tern	colony entry (research)	hatching success	Unstated NS	chi-test	84.8%	

Appendix 1. The use of power tests to assess the size of nesting success declines which would be detectable in published studies.

Population declines for species of conservation concern are typically mediated by small changes in demographic components (Siriwardena *et al.* 2000; Giese 1996). For example, the 49% decline in Lapwings in England and Wales between 1987 and 1998 is attributed to a change in clutch failure rates from 40% in 1968 to 49% in 1998 (Peach *et al.* 1994). However, small changes in breeding success are often difficult to detect using standard statistical procedures and, if such changes are not detectable, potentially biologically significant changes may be ignored (Giese 1996). This statistical problem has been identified and a solution based on measurement of confidence intervals proposed (Smith & Bates 1992; Hoenig & Heisey 2001). This solution works very well in new studies where data considerations can be incorporated into the project from the beginning. However, such a solution is often not possible when reviewing already published results. Instead, published results are more often amenable to analysis using a post-hoc power test to determine the change that it is 95% certain did not occur. This is a simple procedure and an example from published data is presented below, following Zar (1999).

Hill and Talent (1990) present data reporting no effect of capturing Least Terns on their nests. They caught birds from 10 nests and measured nest survival rate. These data were compared with results from 10 nests where birds were not caught. Calculation of the maximum change in nesting success that we can be 95% certain did not occur is presented below.

Survival in caught group (n = 10) = 0.9735 ± SD of 0.04143

$$\Rightarrow SS_1 = S^2 * v_1 = 0.04143^2 * 9 = 0.01545$$

Control clutch survival (n = 10) = 0.9503 ± SD of 0.07653

$$\Rightarrow SS_2 = S^2 * v_1 = 0.07653^2 * 9 = 0.05271$$

Chapter one

$$\text{Pooled variance} = s_p^2 = \frac{(SS_1 + SS_2)}{(v_1 + v_2)} = \frac{(0.01545 + 0.05271)}{(9 + 9)} = 0.003787$$

Detectable change =

$$\delta = \sqrt{\frac{2(s_p^2)}{n}}(t_{0.05(2),v} + t_{0.05(1),v}) = \sqrt{\frac{2(0.003787)}{10}}(2.101 + 1.734) = 0.1055$$

⇒ Percent decline undetectable in the current test = $100 * 0.1055 / 0.950 = 11.1\%$

Following this procedure, we are now 95% certain that a change in nest survival greater than or equal to 11.1% has not occurred. This means that a change in nesting success similar to that responsible for a 49% decline in a Lapwing population could not be detected or ruled out with 95% certainty in the study of Hill and Talent (1990).

CHAPTER 2

Behavioural responses to human disturbance: a matter of choice?

This chapter is in press in *Animal Behaviour* as a paper of the same title by:

COLIN M. BEALE & PAT MONAGHAN

ABSTRACT

Traditionally, how quickly animals respond to human presence is taken as an indication of their susceptibility to disturbance, with those species or individuals that take longest to respond being presumed to be the least vulnerable. However, it has recently been suggested that this may be based on an inadequate understanding of how the behavioural responses of individuals relate to their condition. If responsiveness is positively rather than, as such measures assume, negatively related to condition, erroneous conclusions may be drawn. Individuals showing no or little response may in fact be those with most to lose from changing their behaviour. We describe an experimental test of the link between individual state and responsiveness in birds. We manipulated state by supplementary feeding of turnstones *Arenaria interpres* on rocky shores. Birds in areas with extra food showed greater responsiveness to standardised human disturbance. These findings suggest that our current management of the impact of human disturbance may be based on inaccurate assessments of vulnerability, and we discuss the implications of this for refuge provision.

Behavioural change is often considered the most sensitive measure of the effects of human disturbance on animals, and behavioural responses have frequently been used as an index of disturbance effects (see Carney & Sydesman 1999 for a review). While the use of behavioural indexes in a conservation context is generally welcomed (Sutherland 1996), using behavioural measures as a crude index of disturbance effects has a number of potential limitations. In particular, there are fundamental questions concerning the decisions made by animals responding to humans. The 'state' of an animal represents its position in relation to a number of internal and external variables, thus encompassing its internal condition and environmental circumstances and perceptions of these (McNamara & Houston 1996). If animals make state-dependent decisions whether or not to respond to human presence, then the use of behavioural responsiveness as an index of the fitness consequences of a disturbance event is potentially flawed, since the nature of the response may vary amongst individuals.

In a recent paper, Gill *et al.* (2001) describe how the priorities that animals assign to different activities can affect the behavioural response they show to disturbance. They argue that, when animals have many options open to them (as they do when they are well fed and in good condition, or when there are good feeding areas close by), they may be more likely to change their behaviour than when they are more constrained by current requirements. When faced with a disturbance at a good feeding area, for example, individuals in good condition may be more capable of bearing the costs associated with suspending feeding or moving to other areas compared to individuals in poorer condition, for whom continuing feeding is a high priority. Individuals in good condition will therefore show a more marked behavioural response whereas individuals in poorer condition may have no option but to continue feeding for as long as possible. Similarly, animals feeding in particularly rich habitats may be more able to afford to interrupt feeding during disturbance than those in poor feeding areas where individuals must devote all their available time to feeding. Thus variation in individual state, both in relation to individual condition and perception of habitat quality, will influence behavioural responsiveness to disturbance; individuals appearing least responsive may be those

with most at stake. If this is the case, then current measures of sensitivity to disturbance are likely to be inaccurate and, consequently, the management procedures applied may be inappropriate.

We examined experimentally the link between behavioural responsiveness to disturbance and individual state in the turnstone *Arenaria interpres*. On the south-east coast of Scotland, the winter population of turnstones is in decline (Dott 1997) and it has been suggested that disturbance on feeding areas may be a contributory factor. As turnstones feed on a wide range of prey items (Gill 1986), they are a useful species for such experiments. In winter they show a clear preference for rocky shores and, where rocky outcrops interrupt sandy bays, turnstones flushed from one site will generally move to another area on the same outcrop (Metcalf 1989). Birds are known to use the same roost throughout the winter period and will forage in predictable nearby locations. Colour marking has shown that almost all birds roost within three kilometres of feeding sites (Metcalf & Furness 1985; Pearce-Higgins 2001). We manipulated individual state (encompassing both body condition and habitat quality) in foraging turnstones by the provision of supplementary food and examined the response to a standardised human disturbance. If Gill *et al.* are correct then, when approached, birds in better condition, feeding in the enhanced environments (and therefore with more options available to them) should respond most.

METHODS

Turnstones were studied at two sites on rocky areas on the East Lothian coast of Scotland. The sites were 6km apart, with sandy bays at least 1km long on both sides of each site. Turnstones were present at these sites at both high and low tide. Site separation and presence of both roosting and foraging birds at both sites made it extremely unlikely that there was any significant turnover or exchange of birds between the sites during the experimental period (Metcalf & Furness 1985; Pearce-Higgins 2001).

We used supplementary feeding to manipulate the condition of birds and the environment experienced by them in the experimental site. In order to examine the effectiveness of the provision of food in doing this, we first measured the effect of provisioning with mealworms on pecking rates. At a third site in East Lothian separated from the main sites by at least 15kms, six 10x10m plots were defined low down on an extensive area of rocks exposed at low-tide. These plots were randomly assigned to three treatment and three control areas. Mealworms weighing on average $0.0935 \pm 0.0097\text{g}$ and containing approx. 63% water, 13% fat, 19% protein, and 2% carbohydrates by weight were bought from a specialist live bird food supplier (Wiggly Wigglers Ltd., Herefordshire, UK) with overnight delivery from source. Once delivered, mealworms were fed on bran to maintain their condition and all were used in experiments within 48 hours. For three days we scattered 450g of mealworms in the treatment areas at similar densities to those used in the main experiments described later. On each day, after waiting 15mins for the birds to return, we recorded turnstone feeding rates for 24 birds in the plots from a distance of around 50m, noting the frequency with which individuals pecked at prey items (calculating an average number of pecks per second). Observations continued for two hours, until the rising tide covered the plots. Throughout this period, observations were alternated between birds in treatment and control plots to eliminate systematic temporal bias. Through systematically observing birds from one side of the flock to the other, every attempt was made to ensure that each bird was only observed once, to avoid pseudoreplication. Each focal bird was observed foraging until hidden from sight and the duration of the focal period measured. Only birds observed for over one minute were used for analysis, with each bird being treated as an individual datapoint. Each instance of pecking was recorded throughout the observation period, and the frequency (in pecks per second) was calculated for each bird. We recorded the identity of every prey item over 2mm and the frequency with which these were eaten during the observation period. The frequency of pecking was compared between plots to examine the effect of the provision of supplementary food on intake rates. We also recorded the frequency with which other birds fed on the mealworms. To determine further what prey was

being taken naturally, we visited sites within roosts used only by turnstones after high tide and examined 20 faecal samples for prey remains.

In each round of the main experiments, the two sites were randomly assigned to either experimental or control treatment. For three consecutive days we visited experimental sites at low tide, located the foraging turnstones and scattered around 450g of mealworms on the nearby rocks, such that both density and total mass were the same as in the preliminary trials. As in the preliminary trials, supplemented areas were covered by the rising tide after approximately two hours. During the same low tide we visited the control site and provided a similar amount of disturbance to the birds there by locating and approaching the flocks in the same way as was done when spreading mealworms. On the fourth day no food was given, and on the rising tide a standard disturbance stimulus was used, consisting of one observer walking along the shore to the main flock of foraging birds. Experimental disturbance and response measurement were carried out sequentially at the two sites, the order of testing being determined at random.

We recorded three behavioural measures of disturbance typically used in other studies (e.g. Burger & Gochfeld 1983; Rodgers & Smith 1995; Fowler 1999). We first noted the distance from the observer at which birds flew off (flush distance, e.g. Lord *et al.* 2001) and the distance of the flight undertaken (e.g. Madsen 1998a). Flush distance was determined after the birds had flown by pacing from the point that the observer had reached when the birds flew to the location where the nearest flushed bird had been. Flight distance was determined by pacing from this point to the site where the flock first landed, once the birds moved away from the area of their own accord. Each datapoint was therefore the value for that site for the flock as a whole. For each bird present we then measured the length of two inter-scan intervals (the length of time the bird spends with its head down feeding between scans for predators e.g. Bélanger & Bédard 1989), and calculated the average for each bird. As with the feeding rate observations, the vigilance observations were made by studying birds systematically from one side of the flock to the other to ensure each bird was only observed once. We also recorded the number of birds

present, as it is known that this may affect the behavioural measures taken (Metcalf 1989; Burger & Gochfeld 1991).

After a break of three or four days during which no food was provided, we switched treatments so the control site became the experimental site and vice versa. A complete round of experiments consisted of both sites being used for both treatments. After another three or four day break, the cycle was repeated with treatment sequence assigned at random. Three treatment rounds were carried out in February and March 2002, resulting in six trials at each site, three being controls and three being experimental. Whilst weather conditions on testing days were effectively controlled by the paired nature of the experimental procedures, the number of birds found at each site on each day varied from 10 to 25 birds. There was, however, no consistent difference in the number in relation to either site or treatment (Site: $F_{1,8} = 1.066$, $p = 0.332$ n.s.; treatment: $F_{1,8} = 1.066$, $p = 0.332$ n.s.).

Data analysis was carried out in R v1.6.1 and follows Crawley (2002). For each of the three main behavioural parameters we built Generalised Linear Models (GLM) including the site, treatment and their interaction. All other tests are two-tailed, and errors (unless otherwise stated) are standard deviations

RESULTS

The data collected on the effect of mealworm provision in the preliminary trials showed that turnstones in areas with supplementary feeding had peck rates around 30% higher than birds in the control areas (Control: 0.389 ± 0.081 pecks/sec; experimental: 0.299 ± 0.0827 pecks/sec; $F_{1,24} = 5.61$, $p = 0.027$). During the observations, the only large items of prey observed being eaten were mealworms, with an average of 0.0108 ± 0.00878 mealworms per second in the supplemented areas. Birds fed in both control and treatment plots from the start of the experiments until the tide covered the areas approximately 2hrs later. In the control areas, prey items were too small to be identified and were never larger than 2mm in length. A few redshank *Tringa totanus* present in the area also fed on mealworms during the

observations, and a single curlew *Numenius arquata* fed for a brief period on one day. Other wader species present (mainly oystercatchers *Haematopus ostralegus*) were not observed feeding on mealworms. Analysis of prey remains suggested that prey taken in unprovisioned areas were mainly barnacles, mostly *Semibalanus balanoides* and other small crustaceans.

In all six trials in the main experiment, experimentally “enhanced” birds flushed at greater distance from the disturbance than control birds and scanned for predators more frequently than control birds (Figs. 1a & 2). The treatment effect was therefore significant, and there was no site effect or interaction between site and treatment (Table 1). Thus, the birds in better condition in the rich feeding areas responded sooner to disturbance and scanned for predators more frequently. On five of six trials, the distances flown by experimental birds were greater than those of control birds (Fig. 1b). There was a significant interaction between treatment and site with respect to distance flown, suggesting that the effect of the treatment varied with site, being stronger at one site than at the other.

DISCUSSION

The provision of supplementary food had a clear effect on the pecking rates of foraging turnstones for the period supplementary food was available. With average intake rates of 0.011 mealworms per second, and the manipulation lasting around 120mins, this represents an intake of 77.8 mealworms, or 7.3g, per bird, per day. From the nutritional value of the supplied mealworms, this gives an approximate energetic intake of 65.2kJ per bird per day. Average daily energy requirements are estimated for wintering turnstones as a maximum of 290kJ/day (Smart & Gill 2003). Our supplementary feeding can be expected to have provided 22% of the daily energy requirements for wintering turnstones. Gudmundsson *et al.* (1991) showed that turnstone condition can vary significantly over periods as short as 24hrs. Thus, particularly given that the birds in the study area are in decline and apparently short of undisturbed feeding areas (Dott 1997), following three days of manipulation the condition of birds foraging in the enriched treatment plots is likely

to have been substantially enhanced relative to those in control areas. It is also clear that our manipulations increased the quality of the feeding areas in the experimental sites.

Birds in experimental sites were likely to have more options open to them than control birds when faced with a disturbance: they were in better condition and probably also perceived their immediate environment to be richer so could afford to respond by flying away or stopping feeding sooner than birds in poorer condition. In line with Gill *et al.*'s hypotheses, we found that birds with more options open to them responded more to human presence; they showed an increase in the frequency with which they scanned for predators, took flight sooner and flew further away from an approaching human. Their behavioural responses to disturbance were changed such that those responding most were actually the least likely to suffer any fitness consequences associated with such disturbance: the opposite result from what is assumed when behaviour is used as an index of disturbance effects. These state-dependent behavioural responses to a standard disturbance are strong evidence in support of the theory of Gill *et al.* (2001), and further suggest that behavioural indexes of disturbance suffer from a fundamental flaw. We expect that the differing effect of the treatment on flight distance at the different sites was due to local topography, as the area of suitable rocky shore differed between sites.

Currently, flush distance is frequently used as a currency for measuring susceptibility to disturbance (e.g. Madsen 1985; Anderson 1988) and its species-specific properties are a key assumption of wildlife buffer zones (Blumstein *et al.* 2003). However, as demonstrated in this experiment, birds may change their response according to their individual state and the state of the environment they find themselves in, independently of the strength of the disturbance event. In fact, in our experiments, individuals that have most to lose from a reduction in feeding time showed the least behavioural response. Such effects may also apply between species. As we predicted, birds in manipulated areas were consistently more risk averse than control birds, acting as though they had more response options open to them. These findings are consistent with behavioural models developed and tested

in predator-prey systems such as the condition-dependent use by redshanks of feeding areas with varying predation risks (Hilton *et al.* 1999).

Our results suggest that a reserve manager relying only on behavioural measures of disturbance (such as flush distance) to determine which birds are at higher risk is likely to make inappropriate decisions. For example, in designating a nature reserve into zones with minimal human activity and areas where visitors are encouraged, we need to know where disturbance effects are greatest. Current practice involves measuring flush distances at various sites and determining in which area responses are greatest. Areas where responsiveness is high are considered more sensitive sites in need of greater protection (e.g. Madsen 1998b; Evans & Day 2001). By contrast, our results indicate that the high level of responsiveness at the site of greatest response may be due to the presence of birds in good condition or in particularly rich feeding areas, which do not necessarily need extra protection. If this is the case in the nature reserve in question, the designated zones would give inappropriate levels of protection to vulnerable groups.

Other factors may of course also influence the options animals have available to them. Animals that feed on a widespread and common resource, for example, may also have more options open to them compared to animals feeding on scarcer, localised resources, regardless of their condition. We would therefore expect that such generalists would also show greater behavioural responses to disturbance than would those relying on scarce resources. If this were so, then again protection levels based on the speed of response would be inappropriate.

Our experiments demonstrate that responses to human disturbance vary with the animal's state and context, in a way that differs from the assumptions that underpin current management practices. It cannot be assumed that the most responsive animals are the most vulnerable. Alternative measures such as measurement of stress levels (e.g. Nimon *et al.* 1996, Fowler 1999) or methods involving measurements of resource use (e.g. Goss Custard *et al.* 1995, Gill *et al.* 1996) are needed to allow more fundamental assessment of disturbance effects.

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Table 1. Results of Generalised Linear Models explaining the three measured disturbance activities: Inter-scan Interval, Flush Distance and Flight Length. Significance is indicated with asterisks

Measure	Parameter	F _{1,8}	Sig.
Inter-Scan Interval	Site	2.408	0.159
	Treatment	10.87	0.011*
	Site x Treatment Interaction	2.166	0.179
Flush Distance	Site	0.235	0.641
	Treatment	6.182	0.038*
	Site x Treatment Interaction	1.586	0.243
Flight Length	Site	2.564	0.148
	Treatment	2.564	0.148
	Site x Treatment Interaction	10.26	0.013*

FIGURE HEADINGS

Figure 1. Behavioural responses to a standardised disturbance regime by turnstones subject or not subject to supplementary feeding: (a) flock flush distance; (b) flock flight length. The data are combined for all trials in the same feeding treatment for illustrative purposes; the statistical analysis accounted for other sources of variation (see text and Table 1 for details). Errors are standard errors. Note that treatment has a significant effect on flush distance ($F_{1,8} = 6.182$, $P = 0.038$) and affects flight distance through an interaction with site ($F_{1,8} = 10.26$, $P = 0.013$).

Figure 2. Changes in inter-scan interval in response to a standardised disturbance regime by turnstones at two sites subject or not subject to supplementary feeding. Number of individual birds measured given in brackets. Filled markers indicate the site with supplementary feeding in each trial, shapes identify the individual site. Errors are standard errors. Experimental treatment has a significant effect ($F_{1,8} = 10.87$, $P = 0.011$).

FIGURE 1

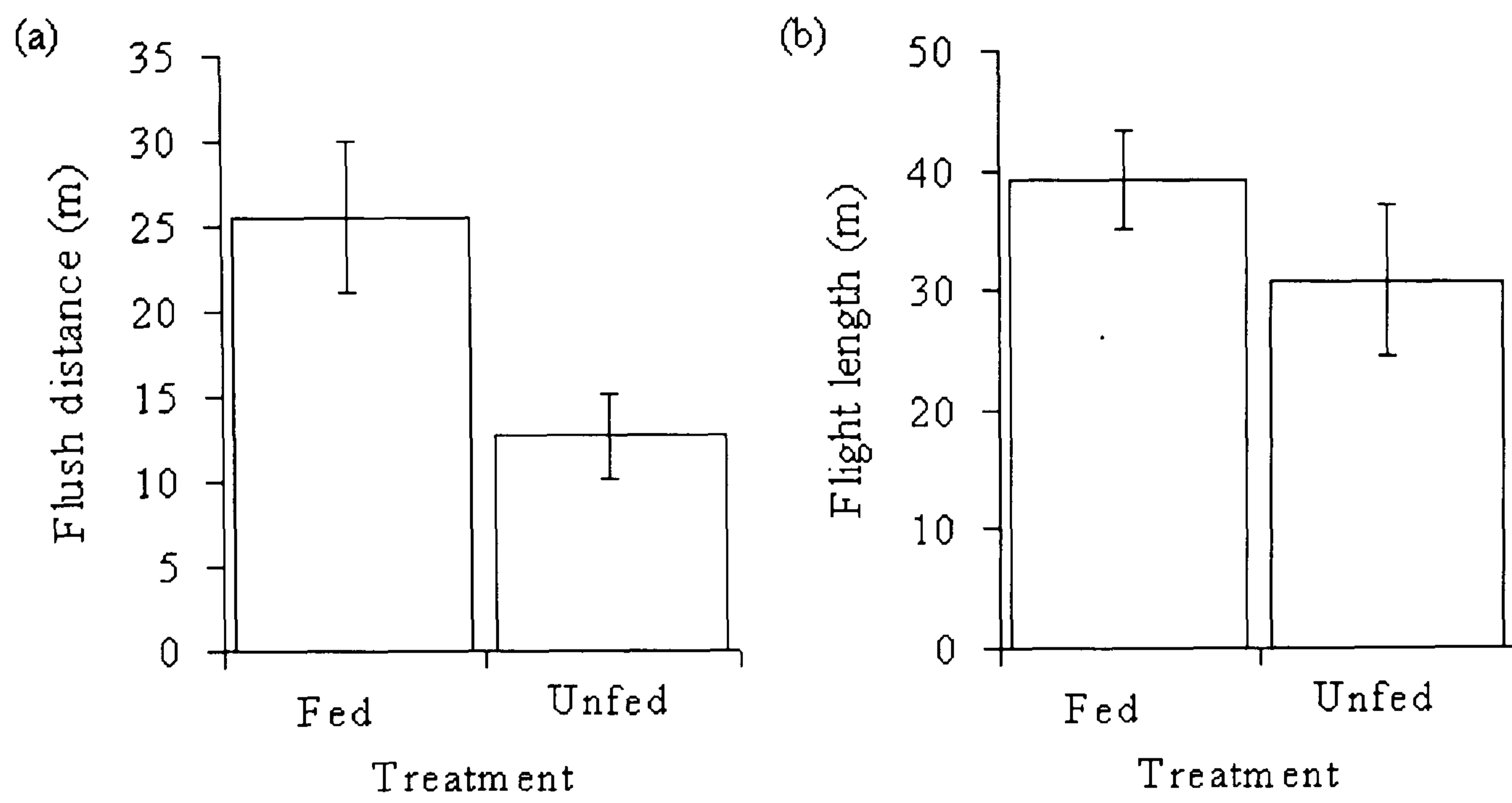
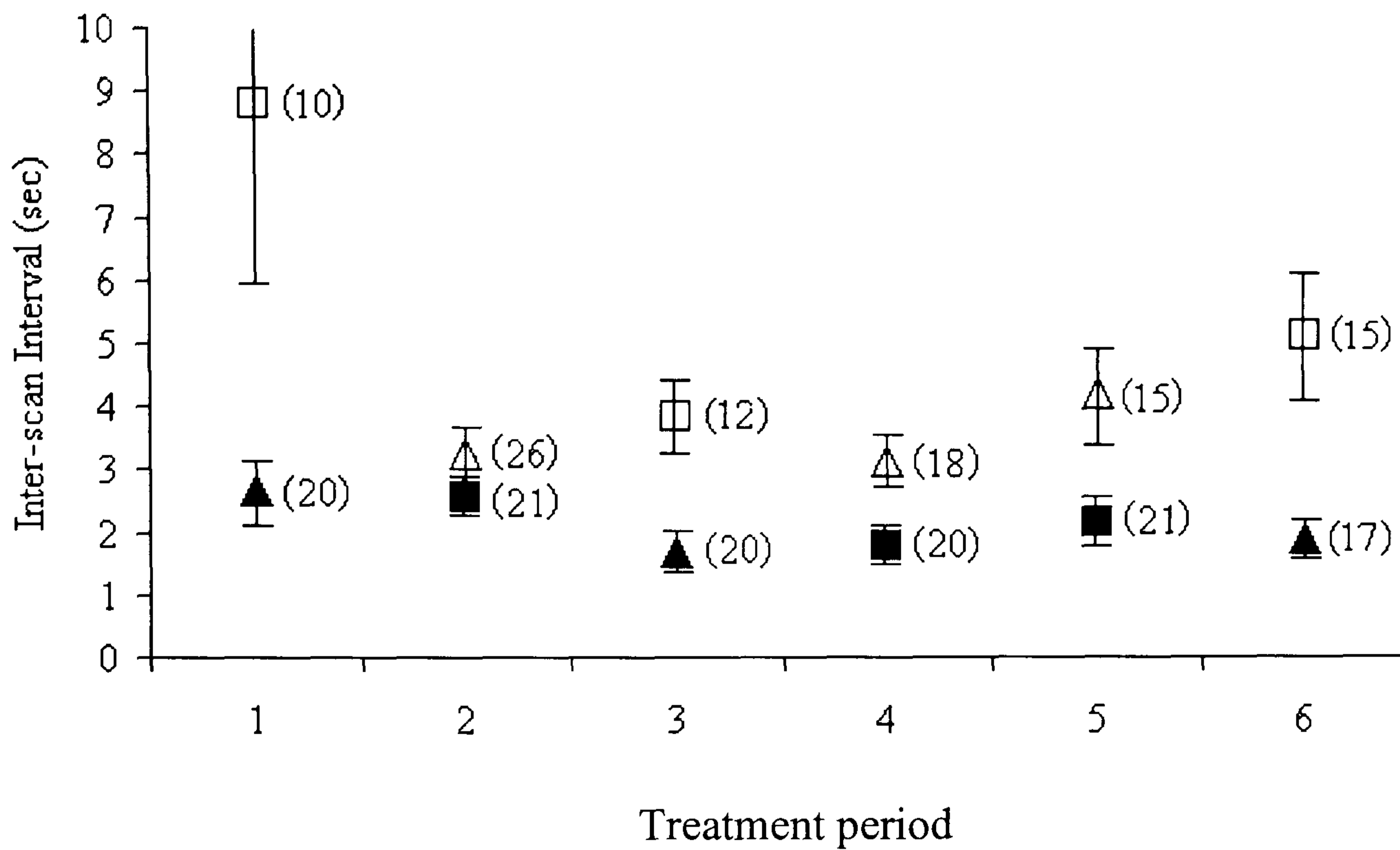


FIGURE 2.



CHAPTER 3

Human disturbance: people as predation free predators?

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COLIN M. BEALE & PAT MONAGHAN

Beale, C. M. and Monaghan. P. 2004. Human disturbance: people as predation free predators? *Journal of Applied Ecology* 41: 335-343.

SUMMARY

- 1.) Human disturbance has been associated with declines in breeding success in numerous species and is of general concern to conservationists. However, the current framework for predicting and minimising disturbance effects is weak and there is considerable uncertainty about why animals are disturbed by people in the first place.
- 2.) We developed a behavioural model of perceived predation risk as a framework for understanding the effects of disturbance on cliff nesting birds. This encompassed the concept that the effects of disturbance should increase with increasing numbers of visitors, and decrease with distance from the nest, an insight ignored in current conservation practice.
- 3.) The predictions of this model were tested using field data on nesting success in two species of seabird, kittiwakes *Rissa tridactyla* and guillemots *Uria aalge*. Statistical models of nesting success in both species suggested that perceived predation risk is a good predictor of the effects of disturbance.
- 4.) SYNTHESIS AND APPLICATIONS. Our findings suggest that fixed set-back distances and buffer zones are likely to be inappropriate conservation measures in situations where the numbers of visitors to wildlife areas fluctuates spatially and temporally, as is generally the case. In managing access to wildlife areas there is a need to ensure that larger parties of visitors are kept further away from the nesting areas of vulnerable species or that set-back distances are determined for the largest party likely to visit the site.

INTRODUCTION:

Conservationists have long been concerned about the effects of human disturbance on wildlife (Carney & Sydeman 1999). Among the numerous reported effects, it has been suggested that disturbance can prevent successful breeding (Giese 1996), scare animals away from preferred feeding areas (Sutherland & Crockford 1993; Gander & Ingold 1997) and even have a direct effect on mortality rates (Feare 1976; Wauters, Somers & Dhondt 1997). With increasing access to the countryside being widely encouraged in the UK, any effects of disturbance on wildlife are set to increase. Unfortunately, disturbance research has been of varying quality, and many conclusions are now in doubt (Hill *et al.* 1997; Nisbet 2000; Gill, Norris & Sutherland 2001). In order to balance visitor access and species protection we need to understand the nature and pattern of human disturbance. However, one of the main problems facing ecologists interested in the effects of human disturbance and access management is the lack of a general framework for thinking about these issues (Frid & Dill 2002). This is in part due to the disparate, and at times conflicting, findings of many studies (see Carney & Sydeman 1999; Nisbet 2000).

In studies of human disturbance effects, a prime focus of attention has been the effect on avian breeding success. Many studies have documented negative effects, but few have attempted to explore in detail the relationship between visitor pressure and reproductive success, and fewer still have so far attempted to understand why humans affect birds in the first place. Mortality and egg losses as a direct consequence of humans are widespread (Madsen & Fox 1995), but most recreational activities do not involve such direct costs. It is therefore unclear why disturbed birds suffer a decline in breeding success. Most researchers who attempt to explain these declines do so in terms of desertion and predation of exposed nest contents (Götmark 1992; Bolduc & Guillemette 2003), but do not ask why nest desertion occurs in the first place. For species that are, or were until recently, hunted by humans the question may appear trivial; but several species apparently show little or no behavioural response to human disturbance and yet still suffer poorer breeding success (Carney & Sydeman 1999). Understanding why birds

respond to disturbance may give insights into how conservation managers may minimise the impact of visitor access provision to wildlife sites.

The most obvious reason why animals respond to humans is because they perceive humans as potential predators and respond accordingly (Frid & Dill 2002). Even for individuals showing no behavioural effects, physiological responses may be triggered before behavioural differences are observed (Wilson & Culik 1995; Fowler 1999). If this is so, the effects of human disturbance on individual nesting success should follow patterns that are best explained by a model of relative predation risk, even though we know that, for humans, this risk is not generally realised.

The simplest general model of perceived predation risk involves two parameters: distance (D), and number of predators (N). The further away a potential predator is from an individual, the lower the chances are of that individual being attacked and the greater the chance of survival [$P(s)$]. The more predators present in that group, the lower the probability of survival (Abrams 1993). This can be modelled simply as:

$$P(s) = (1 - 1/D)^N.$$

And now the perceived predation risk is:

$$\text{risk} = 1 - (1 - 1/D)^N.$$

This shows relative changes that approximate very closely to N/D . It is therefore clear that if the number of predators and the distance from the nest increase in direct proportion, the probability of an individual nest surviving is approximately constant. For example, a lone predator at 25 units distance gives a nest survival probability of 0.96. Double the numbers of predators but move them twice as far away gives a nest survival probability of 0.9604, very similar to the previous value. If humans really are perceived as predators, then N/D rather than either parameter alone should best model the effects of disturbance. This is in contrast to

assumptions implicit in fixed buffer zones and set-back distances, which rely on disturbance being related simply to the distance between people and wildlife.

This paper reports the results of experiments carried out at St. Abbs Head National Nature Reserve (NNR), Scotland, to examine the variation in nesting success as a function of different disturbance regimes, and thereby to test whether human disturbance effects are best explained by assuming humans are perceived as predators. St. Abbs Head holds one of the largest mainland seabird colonies in Britain and receives up to 50 000 visitors per year (National Trust for Scotland, unpublished statistics). Such high visitor numbers and the presence of large numbers of breeding seabirds present an ideal situation for the study of human disturbance. The two most numerous species nesting on the headland are kittiwakes *Rissa tridactyla* and guillemots *Uria aalge*. These unrelated species have been widely studied and many parameters affecting breeding success have already been identified (Harris *et al.* 1997; Massaro, Chardine & Jones 2001). Behavioural responses to disturbance at the distances visitors are from nesting birds are minimal, although effects have been postulated and researcher effects are known for kittiwakes (Harris & Wanless 1995; Sandvick & Barret 2001).

METHODS:

Data were collected in the seabird colony of St. Abbs Head NNR, south-east Scotland, during the 2002 breeding season. During the nest-building period, photographs of the whole colony were taken from the mainland. Target nests were selected throughout the colony using a grid of points marked on an acetate that was laid over the photographs: wherever a point fell on a nest this was selected for study. Totals of 106 kittiwake nests and 241 guillemot nests were selected in this manner, representing independent data points. Each nest was observed daily from a nearby cliff top, and the nest contents were recorded whenever possible. Using this protocol, laying dates were determined to within 2 days accuracy and hatching and fledging success were recorded for each nest. By modelling the effects of all parameters affecting nesting success, we expected to maximise the sensitivity of the analysis to additional effects pertaining to human disturbance. Taking as our guide

the literature concerning nesting success of these two species, we measured all the parameters previously identified as potentially significant in these species. Studies reviewed for the purposes of identification of potential parameters were Maccarone (1992); Falk & Møller (1997); Regehr, Rodway, & Montevecchi (1998) and Massaro, Chardine & Jones (2001) for kittiwakes; and Birkhead & Nettleship (1987); Wanless & Harris (1988); Olsthoorn & Nelson (1990); Hatchwell (1991); Murphy & Schauer (1994); and Harris *et al.* (1997) for guillemots. For both species this process identified a number of purely physical parameters which may affect nesting success, as well as some social parameters important to such colonial species, and also temporal parameters (Table 1). We assumed that between them these studies had identified all the main parameters affecting nesting success; in addition to these mainly physical parameters, we measured variables relating to human disturbance.

Human pressure

People visiting St. Abbs Head were counted automatically using an electronic counter as they started their walk around the reserve. A number of people who returned on the same path were counted twice, so the actual number of visitors passing was calculated using a correction factor based on survey results from the National Trust for Scotland. Most (90%) of visitors were present between 10:00 and 18:00 hours. Peak visitor numbers were recorded on sunny, calm days and at such times the distribution of people about the reserve was studied.

A total of 19 viewpoints was identified, where people stopped to observe the breeding colony. These viewpoints consisted of areas that people visited on their own initiative and areas where the numbers of people visiting each site were manipulated. Manipulation consisted of allowing people to use generally inaccessible areas (such as sites enclosed by fencing) or increasing the numbers of people visiting viewpoints where people gathered anyway. These extra people were mostly volunteers brought to the reserve for this purpose, who would observe the birds and behave as typical responsible tourists to St. Abbs Head. Such manipulations changed the number of people present at each site on average by

11%, with a range from 0 to 100% manipulation, daily throughout the breeding season.

On 14 warm sunny days (average number of visitors \pm S.D. = 370 ± 61.5) we recorded the number of people present at each viewpoint by counting the people present at the instant the researcher appeared within sight of each viewpoint, a process that usually took less than 1 min. This allowed the probability of humans being present at a viewpoint to be estimated, and also allowed the average group size to be calculated when people were present. Multiplication of the probability of human presence by 60 allowed the average number of minutes when people were present to be estimated, and multiplication of this by the average group size at each viewpoint generated a parameter measuring the average people minutes per hour for each viewpoint on busy days. This was taken as an index of human disturbance for that viewpoint.

Most nests were visible from only two viewpoints, so for each nest the nearest two viewpoints with a direct line of sight were located, and the average people minutes per hour over these two viewpoints was calculated. This parameter is referred to as the average number and similar measurements are common in disturbance research (Lafferty 2001). This parameter would have equal values for a site where low visitor numbers were regularly present and where large numbers of visitors visited occasionally, potentially ignoring important variability. However, none of the sites identified at St Abbs Head exhibited such variation in visitor patterns: sites with large numbers of people also had a high probability of presence, and sites with lower numbers had consistently low probabilities of presence. Another variable, the average manipulation was calculated from the proportion of the average number derived from the manipulation and was recorded as a separate variable for both species. If habituation or previously determined nest occupancy patterns (e.g. young birds being forced into traditionally disturbed areas) are important, the degree of manipulation will form a part of the models and should highlight such effects.

The distance between nests and the two nearest viewpoints visible from the nest was calculated by triangulation from measurements of a 1:5000 Ordnance Survey (OS) map of the area. The average distance to the two viewpoints was calculated and is referred to as the average distance. Finally, and again taking the two closest viewpoints in line of sight with the nest, the number of people minutes per hour at each viewpoint was divided by the distance to this viewpoint, and the average of these two values was calculated. This parameter, called the people load, takes a value that is similar in magnitude when large numbers of people are at a distant site and when small numbers are present nearby, and closely approximates to the relative perceived predation risk, if humans are perceived as predators.

Statistical analysis

Statistical analysis follows procedures and recommendations from Crawley (1993, 2002). Programmes for multiple model fitting and simplification were written in the statistical language S and implemented in R v1.6.1. Minimum adequate models to predict nesting success were built using a logit-link. Each nest was taken as a data-point, and the nest selection procedures excluded the possibility of pseudoreplication. In order to keep the number of effects fitted in any one model to an appropriate maximum for the number of data points (a ratio of > 5 data points to each effect), a simple backward-stepping algorithm was not possible and a five-stage simplification strategy was used instead. This process objectively thins the large number of potentially interesting main effects and interactions (with 13 main effects there are a potential 78 two-way interactions and 286 three-way interactions) to a number of terms that can then be used to identify a minimum adequate model using a standard backward-stepping procedure. This thinning was achieved by firstly removing variables of negligible explanatory power, then highlighting from the remaining effects those with the greatest explanatory power.

The first step was to remove variables with negligible explanatory power. These were removed by fitting all possible combinations of four variables with all three-way and lower interactions and then simplifying to a minimal adequate model on the basis of Akaike Information Criterion (AIC). We calculated the frequency with

which each variable was dropped from the model, and the main effect dropped most frequently was removed from consideration. This process was repeated until no remaining main effect was dropped from more than 75% of the models. This process allowed objective selection between highly correlated main effects, such as the distance of the nest from the water level (from water) and the total cliff height, and made the total number of variables more manageable. For both kittiwakes and guillemots this resulted in only eight (of an initial 13) main effects being used in the next stages.

The second step also sought to eliminate terms (both main effects and interaction terms) with minimal explanatory power, when tested simultaneously against all the main effects previously identified. To do this, all possible models containing all the remaining main effects, up to five three-way interactions and all the necessary component two-way interactions were fitted. In each case a minimal adequate model was derived on the basis of AIC. Again we recorded the frequency with which each term was dropped, and plotted a frequency distribution for the percentage of times each term was dropped. This formed largely bimodal distributions (at one end, effects dropped from over 55% of models, and at the other, effects dropped from less than 50% of models); only the peak of rarely dropped effects was used in the next stages. This eliminated many of the possible two- and three-way interactions from further consideration.

Having eliminated terms with negligible explanatory power, we then, as the third step, selected from the remaining terms those with the greatest power. We started this process by identifying the most important three-way interactions: to do this, all pairs of three-way interactions (and the necessary component two-way interactions and main effects) were fitted. These models were simplified as before using AIC, and we recorded the frequency with which each three-way interaction was dropped from the model. The three-way interaction dropped the greatest proportion of the time was removed from further consideration and the process was repeated until all remaining terms were retained in 50% or more of the models in which they were used. Models containing the remaining three-way interactions were then reduced to

minimum adequate models using the 5% significance level. This left a maximum of three three-way interactions to proceed to the final stage.

In exactly the same way, in the fourth step we sought to identify the most important of the remaining two-way interactions. These were selected by fitting models containing all the main effects and all possible combinations of five two-way interactions. Models were again simplified on the basis of AIC and the frequency with which two-way interactions were retained in the minimal adequate model was recorded. The two-way interaction dropped most frequently from the models was removed from consideration, and the process repeated until all remaining two-way interactions were retained in more than 50% of models in which they were fitted..

The fifth and final stage of the model selection procedure consisted of a standard backward-stepping algorithm identifying terms significant at the 5% level from among the terms identified as potentially significant by the preceding stages. This final model was fitted using the remaining main effects and the two and three-way interactions that were selected in stages three and four. This was simplified to the minimal adequate model by sequentially removing the least significant effect not required by a higher order interaction and not itself significant at the 5% level.

RESULTS

Kittiwakes

The minimum adequate model predicting nesting success for kittiwakes gave a mean deviance of 0.89, suggesting a good fit with some limited underdispersion of data (Table 2). Overall, 42.5% of nests successfully fledged one or more chicks during the study period, with most (59%) of the failures occurring during the chick-rearing stage. Nesting success was significantly correlated with six main effects and eight interactions (involving a total of eight main effects). All variables associated with people except average manipulation were related to nesting success. The physical nest site characteristics that were identified included the number of walls surrounding the nest, the total height of the cliff and the vertical height above the water. The nest locations associated with highest nesting success had few walls and

were situated low down a tall cliff. Interactions with laying date affected the importance of such features, and for nests laid late in the season it was more important to nest on an offshore crag rather than on the mainland. Overall, the presence of people was strongly related to poor nesting success, through the effect of people load. Increasing the visitor numbers by 8.5% resulted in a decline in nesting success to 29.4%, a 22% increase in failure rate, whilst halving the visitor levels results in a nesting success of 95.6% (Fig. 1). When people load was kept constant, however, the average number of people minutes per hour was positively correlated with nesting success and the distance these people were from the nests was negatively correlated with nesting success. Parameters reflecting human disturbance interacted among themselves and with the distance above the water level, such that the importance of people and people load both increased with increasing distance from water and the importance of people load also increased with increasing numbers of people.

Guillemots

Simple correlation analysis showed significant positive relationships between nesting success and both the number of walls and the number of neighbours. Significant negative relationships were identified between nesting success and both ledge slope and nest site slope.

Minimum adequate models for predicting guillemot nesting success were constructed (Table 3). Mean deviance for the main model is 0.86, suggesting a good fit with some limited underdispersion of data. Total nesting success was 70.1% with most (62%) failures during the egg stage. Eight main effects and 10 interactions formed the final model of nesting success. Nesting success was significantly correlated with both people load and average distance. Physical features associated with nesting success were the number of walls around the nest, the location of the nest on the mainland or a stack, the number of neighbours, the slope of the nest site and the distance of the nest above the water. These relationships were such that the sites with the highest nesting success were situated in a level site with several walls (a niche), high on a mainland cliff and with few neighbours. Nesting success

showed a small positive relationship with laying date, which was also involved in a suite of interactions with physical features, such that the importance of the various features changed as the season progresses. Overall, the presence of people had a strong negative effect on nesting success through the effect of people load.

Increasing the visitor numbers by 8.5% resulted in a decline in nesting success to 66.2%, a 13.0% increase in failure rate, whilst halving the visitor levels resulted in a new nesting success of 87.2% (Fig. 1). When people load was kept constant, however, the nesting success was negatively correlated with average distances people were from the nests. Parameters reflecting human disturbance interacted among themselves, such that the importance of people load increased with increasing distance from the nest.

DISCUSSION

Before exploring fully the effect of human disturbance on the nesting success of kittiwakes and guillemots, we must first satisfy ourselves that the modelling procedure was adequate. We approached this in two ways: by assessing the adequacy of the error model through consideration of the size of the mean deviance, and by comparing the results of these models with the previous studies of these species initially used to identify non-anthropogenic parameters affecting nesting success. If both statistical fits were good, and the effects of the non-anthropogenic parameters similar to other studies, we can have a good deal of confidence in our modelling approach, and therefore in the novel elements of this study that relate to the effect of human disturbance.

The models of kittiwake nesting success have low mean deviance and explain a reasonable degree of variation, with unexplained variation likely to be due to factors not examined in this study, such as the distribution of the tick *Ixodes uriae* (Boulinier & Danchin 1996) and parent quality (Coulson & Porter 1985). With respect to the effect of the non-anthropogenic attributes of the nest site on breeding success, there is good agreement between the findings of this study and those of previous studies. Significant parameters are all likely to affect the risk of the nests being predated, probably the main source of chick and egg mortality (Maccarone

1992; Regehr, Rodway, & Montevecchi 1998; Massaro, Chardine & Jones 2001). Predation pressure varies seasonally, presumably leading to the interactions that were observed in this study, which showed that the importance of certain parameters varied with date. Other interactions were mainly connected with human disturbance such that the importance of being lower down the cliff increased with increasing human pressure. The lack of significance of neighbour density confirms the findings of Falk & Møller (1997), whilst the other two studies (Regehr, Rodway, & Montevecchi 1998; Massaro, Chardine & Jones 2001) reported significant but opposite relationships from each other.

Previous studies of non-anthropogenic factors affecting guillemot nesting success report disparate, and often conflicting results, making it hard to identify what is consistently important in determining nesting success in this species (Birkhead & Nettleship 1987; Wanless & Harris 1988; Olsthoorn & Nelson 1990; Hatchwell 1991; Murphy & Schauer 1994; Murphy & Schauer 1996; Harris *et al.* 1997). Our models identify the same relationships for all parameters where previous studies are in agreement, with the exception of the height of the nest above the water, which contrasts with the opposite finding by Harris *et al.* (1997) and Parrish (1995). As both Harris *et al.* (1997) and Parrish (1995) suggest that the lower nesting success of guillemots near the top of the cliff is due to disturbance effects, explicit measurement of human disturbance in the current study is likely to explain this apparent difference: once variation caused by disturbance is accounted for, there remains a small but significant benefit to guillemots of nesting higher up the cliffs. Significant physical parameters are all likely to affect the predation risk, exposure risk and the likelihood of nest contents falling off the ledge. Interactions involving date again suggest that the ideal nest site changes as the season progresses (perhaps as weather or predation pressure differ), while the importance of nest slope also varied with other physical parameters, presumably also affecting the probability of eggs or chicks falling from the cliff. Overall, the model fits the data well (mean deviance of 0.86) and the overall fit is better than in other published studies (e.g. mean deviance of 2.53; Harris *et al.* 1997).

Human disturbance had a significant negative effect on the nesting success in both species, and it is clear that kittiwakes were more sensitive to human disturbance than guillemots at St Abbs Head, perhaps because kittiwakes were on average in closer proximity to viewpoints than guillemots. The proportion of the number of visitors present that was due to experimental manipulation was not a significant predictor in either model, suggesting that the effect of humans on breeding success is a direct consequence of disturbance. It is therefore clear that while there may be no behavioural response in these species, true habituation effects are small and there is no evidence that poor quality or young birds are forced to nest in sites traditionally subject to visitor disturbance.

As the GLM appear adequate and the physical parameters identified here are broadly in agreement with the literature, we can be fairly confident that our modelling approach is adequate and that the novel findings concerning human disturbance are well founded. As predicted, the negative effect of disturbance in both species is entirely due to the combination parameter, people load, that includes both the number of visitors and their distance from the nest. However, if visitor numbers to St Abbs Head should increase dramatically, the additional effect on nesting success is, perhaps, unlikely to be as extreme as suggested in Fig 1, as such serious declines in reproductive success would clearly provide strong selection pressures in favour of birds that did not respond to humans.

The effect of people load on two unrelated species provides good evidence that even when humans represent no direct mortality risk to adult or young birds, they are perceived as predators by nesting birds. The birds respond in proportion to the degree of threat they perceive, though how this results in lower nesting success is unclear. Where behavioural responses to disturbance are absent or minimal it is hard to see how desertion and predation play a direct role in the lower nesting success of disturbed birds. Perhaps the most likely explanation is that nesting birds perceive people to be a potential predator and show appropriate anti-predator physiological responses. Physiological responses in the absence of behavioural changes have been recorded for a number of bird species (e.g. Nimon, Schroter, & Stonehouse 1995; Wilson & Culik 1995; Fowler 1999), and stress has been shown

to reduce breeding success in some birds (Silverin 1986). A mechanism leading to this reduction could be through an increased heart rate of disturbed birds (Nimon, Schroter, & Stonehouse 1995; Wilson & Culik 1995) resulting in increased metabolic requirements at a time of high demand (Thomson, Furness, & Monaghan 1998; Golet & Irons 1999; Golet, Irons & Costa 2000; Fyhn *et al.* 2001). This may cause disturbed birds to decline in condition faster than undisturbed individuals, which may in turn increase the likelihood of brood desertion (Coulson & Johnson 1993; Cadiou & Monnat 1996) and consequently increase predation on exposed nest contents. Such a mechanism would allow disturbed birds to show no behavioural differences compared with controls, except for the final desertion and failure, as the effects of disturbance would be cumulative throughout the breeding season. There is, however, much research that would be necessary before such a mechanism could be confirmed.

Although it is not yet possible to identify the proximate cause of failure in disturbed birds showing few behavioural responses, the current study does allow human disturbance to be identified as the cause of such losses. The identification of perceived predation risk as a likely mechanism of this response has a number of consequences for conservation managers. It is clear that increasing numbers of visitors to a nature reserve can be sustainable and need not result in increased failures, if viewpoints are moved further from the nests in line with visitor increases. In this example there would be no net effect on guillemot nesting success following a 10% increase in visitor numbers if visitors were moved a further 1.3 m away from the nests, or 3.9 m further away in the case of kittiwakes.

Of more concern to current conservation practice is the implication of these results for buffer zones or set-back distances. Conservation biologists are often interested in determining a 'safe' distance between humans and birds where the effects of disturbance are negligible (Carney & Sydeman 1999; Blumstein *et al.* 2003). This is typically attempted by one or two researchers approaching birds using a standardised disturbance regime and measuring the distance at which a bird shows a behavioural response (e.g. Rodgers & Smith 1995; Giese 1998; Lord *et al.* 2001). Implicit within this practice is the assumption that the numbers of people present do

not matter: it is assumed that the distance at which a bird responds to one or two researchers will also be the distance where effects are first manifest if larger groups of tourists are present. By contrast, the current results show that safe distances depend on the numbers of people visiting an area, and what may have little effect with one level of visitor numbers will certainly have more if visitor numbers increase. This understanding may help to explain why Higham (1998) found that the breeding success of a colony of northern royal albatrosses declined with increasing visitor numbers, despite provision of visitor facilities at a distance previously identified as 'safe'. Understanding that both numbers and distance matter in determining disturbance effects suggest that either set-back distances must be periodically re-assessed in the light of changing visitor numbers, or that visitor numbers should be strictly capped if effects are to be minimised.

In conclusion, this study provides good evidence from two unrelated species that human disturbance effects are related to perceived predation risk. This risk, and therefore disturbance effects, varies both with distance from humans and the number of humans present. This understanding has important implications for visitor management in nature reserves and the current use of set-back distances to minimise disturbance effects. If set-back distances are to be used as a management tool they must be measured and set for the greatest anticipated visitor numbers, and a strict cap must be maintained on visitor numbers at the site. The proximate cause of nest failures in species that show little or no behavioural response to humans is as yet unclear and worthy of further research, as this may suggest additional methods for mitigating the impact of human disturbance on animal populations.

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Table 1. Nest site characteristics measured in this study.

Parameter	Description	Kittiwake	Guillemot
Date	Date of clutch initiation (to within 2 days)	X	X
Mainland	Factor describing whether the nest was on the mainland or an offshore stack	X	X
Site Height	Total height of cliff at nest (from 1:5000 OS map)	X	X
From Top	Vertical distance from cliff top to nest (calculated from photographs scaled by reference to Site Height)	X	X
From Water	Vertical distance from nest to mean high water (calculated from photographs scaled by reference to Site Height)	X	X
Walls	Number of rock walls taller than incubating bird in contact with nest site	X	X
Roof	Factor describing presence or absence of overhang sheltering nest from above	X	
Neighbours	Number of neighbours nesting within a circle of radius 20cm (guillemots) or 2m (kittiwakes)	X	X
Distance to Neighbour	Distance to the nearest neighbour's nest	X	
Gradient	Gradient (to within 10°) of precise site where egg laid		X
Ledge Slope	Gradient (to within 10°) of the whole ledge, niche or platform containing nest site		X
Average Number	Index of average people minutes per hour at two nearest viewpoints	X	X
Average Manipulation	Proportion of Average Number explained by experimental manipulation	X	X
Average Distance	Average distance from nest to two nearest viewpoints	X	X
People Load	Average index of people minutes per hour divided by distance for the two nearest viewpoints	X	X

Table 2. Minimum adequate model predicting nesting success in kittiwakes.

	Nesting success		
Mean deviance	0.89		
MODELS	B	S.E.	P
Date(D)	0.000	0.000	0.063
Sides(S)	-82100	37600	0.029*
Mainland(M)	826700	428200	0.054
Site Height(SH)	4220	1830	0.021*
From Water(FW)	-0.185	0.094	0.049*
Average Number(AN)	0.326	0.134	0.015*
Average Distance(AD)	-0.001	0.000	0.047*
People Load(PL)	-48.66	18.28	0.008**
D * SH	-0.113	0.049	0.021*
D * S	2.196	1.005	0.029*
D * M	-22.11	11.45	0.054
M * SH	-14500	7100	0.041*
AN * FW	-0.004	0.002	0.038*
FW * PL	0.942	0.354	0.008**
AN * PL	0.232	0.092	0.012*
D * M * SH	0.389	0.190	0.041*
AN * FW * PL	-0.005	0.002	0.010**

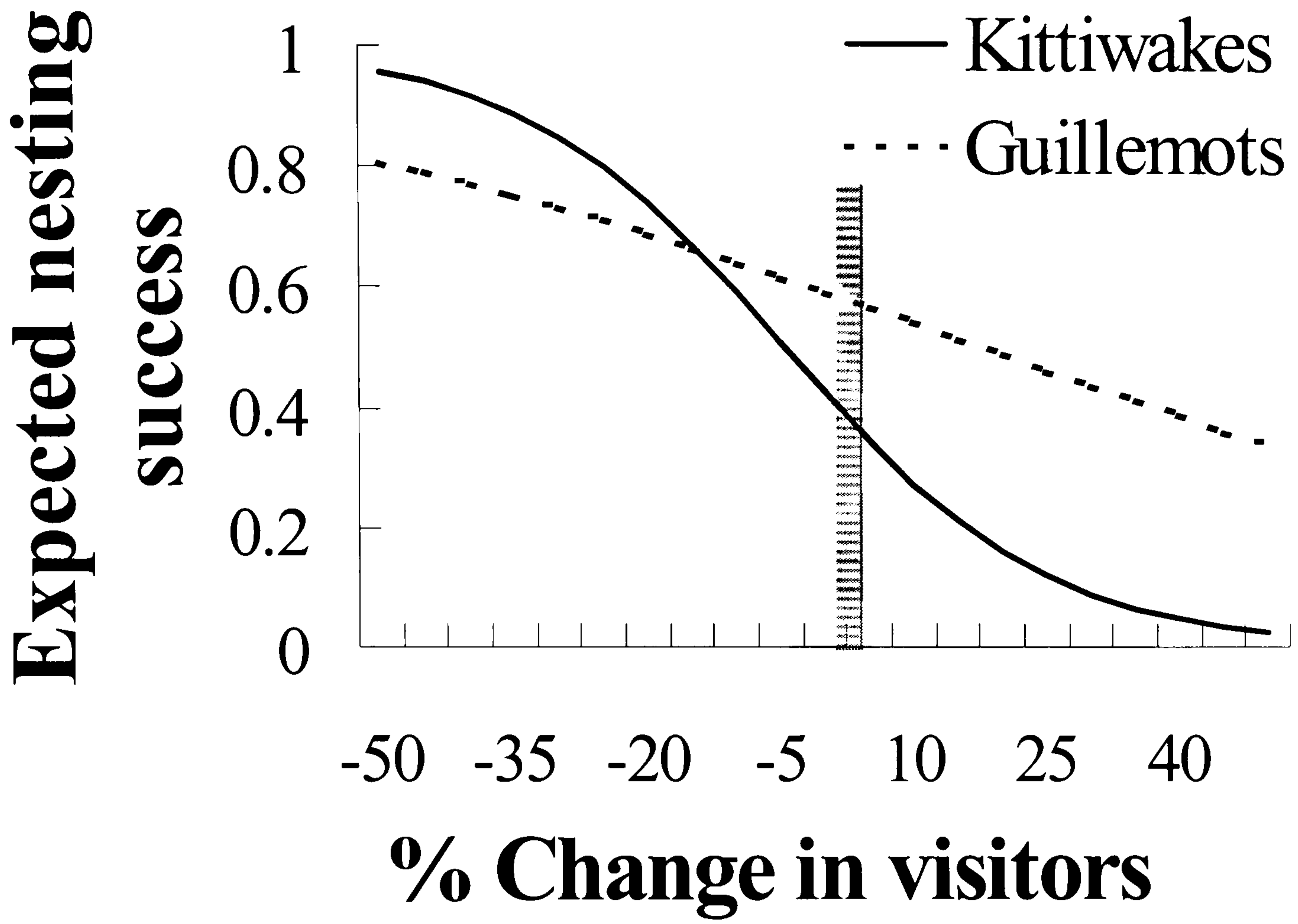
Table 3. Minimum adequate models predicting nesting success in guillemots

	Nesting success		
Mean deviance	0.86		
MODELS	B	S.E.	P
Date (D)	0.0003	0.000	0.004**
Walls (W)	1.005	0.347	0.004**
Mainland (M)	34100	11900	0.004**
Neighbours (N)	-17400	7170	0.016*
Gradient (G)	-18700	9060	0.039*
Site Height (SH)	-0.174	0.106	0.098
From Water (FW)	526	217	0.016*
Average Distance (AD)	-0.051	0.019	0.007**
People Load (PL)	-12.77	4.245	0.003**
AD * PL	0.175	0.050	0.001** *
D * M	-0.912	0.318	0.004**
D * G	0.501	0.242	0.039*
D * N	0.464	0.192	0.016*
D * FW	-0.014	0.006	0.015*
FW * SH	0.014	0.005	0.006**
SH * G	0.154	0.085	0.070
FW * G	0.520	0.179	0.004**
N * G	18400	7840	0.019*
FW * SH * G	-0.013	0.004	0.002**
D * N * G	-0.493	0.210	0.019*

FIGURE HEADINGS

Figure 1. The overall relationships identified between human disturbance and nesting success in kittiwakes and guillemots at St. Abbs Head National Nature Reserve, Scotland. Shaded bar represents current visitor numbers.

FIGURE 1.



CHAPTER 4

A method for assessing the optimal management of visitor distribution within a nature reserve

ABSTRACT

Managers of wildlife reserves have a range of tools available to them when considering the best way to provide visitor access while avoiding as many of the negative effects of human disturbance as possible. However, managers lack guidelines as to whether conservation interests are best met by spreading visitors thinly throughout a reserve or by aggregating them in a small area. Here I describe how relationships between nesting success and nest site characteristics can be used to address this issue. I show that a published equation predicting nesting success of Guillemots *Uria aalge* accurately predicts nesting success in colonies other than the one for which it was developed. I show how the equation can be used to generate general management guidelines on optimal visitor distributions. Optimal management for Guillemots depends on the number of people and the distance between the people and the birds. At high visitor numbers and close distances, management should aim to aggregate visitors in as small an area as possible, whereas, at lower visitor numbers and further distances, an even distribution of visitors is favoured.

INTRODUCTION

Human disturbance is recognised as an important concern in the conservation of many species (Nisbet 2000; de la Torre *et al.* 2000; Williams *et al.* 2002). It is recognised, however, that providing access to charismatic wildlife is often desirable, not only providing a potential source of conservation revenue (Gray *et al.* 2003) but also increasing the public appreciation of, and support for, conservation (Hendee 1972; Bogner 1998; Bogner 1999). This conflict can be managed in several ways. Most guidelines concentrate on managing the distance between wildlife and visitors (Galicia & Baldassarre 1997; Williams *et al.* 2002; Müllner *et al.* 2004), but the basis of such management has been questioned on theoretical and empirical grounds (Gill *et al.* 2001; Chapter 2). Other managers limit the number of visitors permitted to enter a reserve each day (e.g. Harris & Wanless 1995), though the effectiveness of this in minimising disturbance is unknown.

Instead of restricting access in these ways, Fernández-Juricic *et al.* (2004) discuss the possibility of manipulating the distribution of visitors within a reserve. This can be achieved relatively simply (e.g. by creating paths or placing information boards) and the use of such methods could result in the increased or decreased aggregation of visitors (Pearce-Higgins & Yalden 1997; Sutherland 2000). Aggregation into a small area is likely to result in locally increased disturbance impacts but allows the rest of the area to remain undisturbed (Pearce-Higgins & Yalden 1997), whilst an even spread of visitors ensures that birds in the area as a whole experience similar low exposure to people. However, whilst such management is relatively simple, Fernández-Juricic *et al.* (2004) reported no studies that dealt with this idea and did not themselves address the question of how to calculate the optimum visitor distribution for a particular species or reserve. With such a small scientific basis upon which to advise managers on visitor access, any additional tools offer important practical advances.

The management of visitor access is particularly important for colonial birds, where large numbers of people visit birds at their nesting grounds (Harris & Wanless 1995; Anderson 1988; Nisbet 2000). In such species, relationships

between physical nest-site parameters (including indices of human visitor pressure) and nesting success have been published (Beale & Monaghan 2004). If the parameters that affect nesting success are similar between colonies, published relationships may offer a basis for providing general management guidelines. Here, I show how an equation predicting Guillemot *Uria aalge* nesting success (Beale & Monaghan 2004) can be used to generate appropriate management guidelines for this species.

METHODS

If we understand the parameters that affect nesting success of any species well enough, it should be possible to predict how changes in these parameters will affect nesting success. It should, therefore, be possible to decide between management that aims to increase or decrease visitor aggregation by using equations predicting nesting success (that include human disturbance parameters) to simulate success under different management scenarios. By directly comparing the predictions of nesting success under the current management regime with those of alternative management options, it is possible to determine which management scenario is optimal. However, in order to do this, it is necessary to make a number of assumptions.

Firstly, current and future visitor distributions must be approximated. I was not interested in assessing management options that changed overall visitor numbers, as this is already known to be beneficial (Chapter 3). Instead, I focus here on the effects of changing visitor distribution alone. To keep calculations simple, I assumed that each nest in the simulated colony be subject to one of only two visitor levels. Visitors may be evenly spread through the colony, so all nests experience the same visitor levels, or there may be more visited and less visited parts of the colony. If visitors are not evenly spread, I assume that nests in more visited areas experienced 50% of the visitor pressure (measured in this example as people minutes per hour), with the remaining 50% spread evenly through the rest of the colony. Thus, in a situation where 50% of the visitor pressure is experienced by only 30% of nests in the colony and the overall average visitor pressure is 50

people minutes per hour, I estimated nesting success for a colony where 30% of nests experienced visitor pressure at 83 and 70% of nests had visitor pressure of 36. I assumed that changing the visitor distribution would change the area where 50% of the visitors could be found.

As an example of this process, I took the equation predicting Guillemot nesting success first developed at St Abbs Head National Nature Reserve, southern Scotland (Chapter 3). I predicted average nesting success for a number of possible initial management scenarios: an even distribution of visitor pressure; 50% of visitor pressure over 30% of the colony; or 50% of visitor pressure over 10% of the colony. As the value of any management depends on how clumped the visitor distribution will become, I then made the same predictions of nesting success for scenarios where management was anticipated to result in concentration of 50% of the visitor pressure into only 30%, 10%, 5% or 1% of the colony. For each scenario, I predicted nesting success using the mean values of the non-human parameters (from the original data) and combinations of visitor pressure (10 – 490 people minutes per hour) and mean distance between people and nests (5 – 100m). This resulted in a matrix of predicted nesting successes for each scenario, being highest at low visitor number and high distance, and lowest with high visitor numbers close to the birds. I then plotted areas where the current management scenario resulted in higher predicted nesting success than the future management scenarios over all likely ranges of people pressure and distances to nests (Fig.1). If increased visitor aggregation is not recommended by the guidelines, then decreasing the degree of clumping is preferred, and it is unnecessary to simulate separately the effect of decreasing visitor aggregation.

As in practice, visitor distribution is unlikely to be as above, it is necessary to assess the sensitivity of the guidelines produced to this simplification. This is possible by estimating nesting success where anticipated changes in visitor distribution results in a different distribution from the main scenarios, and assessing how sensitive the guidelines are to this change. This can be achieved by assessing the effect of total closure of portions of the reserve, a radically different distribution to the main simulations. For each management scenario, this involved setting

people pressure to zero for a proportion of the reserve and allowing all the visitor pressure to be experienced by the nests in the “open” portion (Fig. 2). Management guidelines derived from these distributions can then be compared with those where the management results only in a degree of visitor aggregation and the sensitivity to such different visitor distributions can be assessed. Comparing the guidelines generated with those for the main scenarios (Fig. 1) clearly shows that, in this example, threshold levels where management favours increasing or decreasing visitor aggregation are not sensitive to the assumed distribution. Furthermore, the threshold levels do not vary much over moderate degrees of visitor aggregation (the initial starting conditions), suggesting that only when there is a strongly aggregated distribution does the initial distribution matter.

As the equation predicting Guillemot nesting success used here involves both distance and number of visitors, we must also assume that the average distance between visitors and birds is fixed. In order to simplify the process, I also assumed that changing the visitor distribution will not alter the location of breeding sites. Making these assumptions means that the only parameter values that change between the simulated starting situation and the simulated situation under the new management regime are those that relate to visitor presence. As the non-human component of the model is therefore constant, the guidelines generated are independent of the values of the non-human parameters and can therefore be applied to any colony of the species in question. This is best understood through a mathematical representation of the process: our estimates of nesting success ($P(s)$) are a simple linear function ($f(x)$) of three components: the human parameters (H) that vary; the non-human components (NH) that do not change when changing visitor distribution, and a constant (c). Nesting success under the initial visitor distribution (H_1) is therefore estimated as:

$$P(s_1) = f(NH + H_1 + c)$$

and nesting success under the new visitor distribution (H_2) will be:

$$P(s_2) = f(NH + H_2 + c)$$

Subtracting the two predictions one from the other will indicate which visitor distribution is preferred, and it is clear that this only depends on the changes in the human components.

Finally, before the guidelines are adopted, it is necessary to check that the assumptions made during the simulation process hold and that the guidelines are robust to deviation from the simplifications made. A simple checklist of questions can achieve this:

1. Are the equation's predictions accurate in more colonies than simply where it was derived?
2. Are the guidelines produced when areas of the reserve are totally closed to visitors largely similar to those produced by the other simulations?
3. Is the species in question unlikely to change its nest sites in response to changes in the distribution of visitors?
4. Is the management unlikely to result in a change in the mean distance between people and nests?

If all these questions are answered positively, the guidelines generated are likely to be well supported, although it would be desirable to test the predictions experimentally. To determine this, I first assessed how generally applicable the published equation is by using it to predict nesting success in two different colonies in Orkney (Scotland): Mull Head (east Mainland) and Marwick Head (west Mainland). I measured nesting success of Guillemots in 2003 according to JNCC monitoring guidelines (Walsh *et al.* 1995). Using site visits and photographs of the monitoring plots, I estimated the parameters identified in Beale & Monaghan (2004; Chapter 3) as important in determining nesting success in each species based on data collected at St. Abbs Head, southern Scotland. In June 2004 I measured human visitor patterns in the same way as used to generate the original equation.

Assessment of visitor numbers was not possible during 2003, but the local recorder was confident that the distribution had varied little between years (D. Paice, pers. com.).

For both colonies, I calculated the average value of each parameter and used these means to estimate the mean nesting success for the monitoring plot. I further ranked the nests within each monitoring plot according to the people load (the most important human disturbance parameter, calculated from people minutes per hour divided by distance to the nest), and produced separate estimates of nesting success for the top and bottom thirds of the ranked list. Where the people load was the same for several nests and a division required, I selected nests from the tied rank at random. As there is considerable between year and site variation in Guillemot nesting success (Murphy & Schauer 1994), absolute values of the predictions offer a less stringent test of the equation than the relative changes in predicted and actual values. Consequently, I assessed equation accuracy by comparing both absolute precision and the magnitude and direction of changes within each colony.

Guillemot nesting success predicted by the equation sites was remarkably accurate at both Orkney sites, particularly for Marwick Head (Fig. 3). The equation successfully predicted the observed direction of change in nesting success at Marwick Head, despite nesting success increasing with people load. This contrary pattern is likely to be due to a negative correlation between human disturbance and the number of Guillemots neighbouring the nests, something not observed at Mull Head (Marwick $r^2 = -0.226$, $N = 115$, $P = 0.015$; Mull $r^2 = 0.149$, $N = 109$, $P = 0.123$). It seems, therefore, that the published equation is likely to be generally applicable. Had the predictions of the equation not been accurate, general guidelines would be impossible to generate, but should at least allow specific management guidelines to be developed for the site where the equation was originally built.

The assumptions that lead to questions 3 and 4 (concerning whether nest sites or distances between people and birds may change) are, in fact, not necessary for equations to be used in this way, but do simplify the process. Indeed, there is

evidence that many species probably do change their nest sites in response to humans (Higham 1998), though others (particularly some seabirds) do not (Nisbet 2000). Guillemots are very site faithful, but may change nest site if they fail in their nesting attempt (Harris *et al.* 1997). However, in a crowded colony where nest sites are at a premium, it is unusual for sites used once to subsequently be abandoned (Harris *et al.* 1997), so it seems likely that this condition is met in the current example. Similarly, management may result in visitors being concentrated in an area where there is a particularly close view, reducing the average distance between visitors and nests, although this is not necessarily the case. For Guillemots, all the questions concerning the assumptions may be answered positively and we can therefore conclude that the management guidelines developed from an equation predicting Guillemot nesting success at St Abbs Head (Beale & Monaghan 2004) are generally applicable. However, if these last assumptions are violated, guidelines may still be achievable if the changes in nest site or mean distances are themselves predictable. If such predictions are possible they may be substituted into the equation and management guidelines generated as above, though they will only be appropriate for the sites where the likely changes are known.

DISCUSSION

It is clear that if published relationships between physical parameters and nesting success measure human disturbance parameters, they can be used to develop useful guidelines for the management of visitor access. The process I describe provides guidelines to help determine whether the degree to which visitors are aggregated in portions of the reserve should be increased or decreased. Unfortunately, the number of studies currently published that provide an appropriate relationship between physical parameters and nesting success and includes human disturbance parameters is minimal. I demonstrated the processes involved in building and assessing these guidelines using an equation derived from St. Abbs Head to predict Guillemot breeding success (Beale and Monaghan 2004). As this is the first example of such management guidelines, it is interesting to examine what the guidelines actually recommend.

For all the main scenarios, the simulations suggest that optimal management strategies for Guillemots depend on both the number of people minutes per hour and the distance between people and birds (Fig. 1). Where visitor pressure is high and the distances between people and birds are low, the optimal strategy is to concentrate visitors into as small an area as possible. Where there are fewer visitors, or the distance between visitors and birds is high, the optimal management strategy is to spread visitors as evenly as possible.

For Guillemots, therefore, there is no generally applicable optimal management strategy. Indeed, the simulations suggest that, even within a reserve, if visitor numbers change, the advised management may also change. This can be seen by imagining a 20% increase in the average people pressure in a reserve where 50% of visitor pressure occurs in 30% of the reserve and the current average is 110 people minutes per hour with average distance 55m. A 20% increase will result in new visitor pressure of 132, so, whereas previously the guidelines advised decreasing aggregation, the guidelines now suggest that if 50% of visitors can be aggregated in 1% of the reserve, this is preferred. I do not think that the existence of such a threshold level where management should change from spreading visitors thinly around a reserve to, instead, increasing visitor aggregation has previously been identified.

The existence of this threshold means there is no general answer to how people should be distributed within a reserve. However, general answers may be possible for individual reserves. At St Abbs Head, the mean distance between visitors and Guillemots is 83m and 50% of visitor pressure occurs in approximately 30% of the Guillemot colony. Consequently, for this site at least, management should always aim at spreading visitors evenly. Using these starting conditions, if management resulted in an increased aggregation of 50% of visitors into only 1% of the colony, nesting success was predicted to decrease by 1%. If management resulted in an even distribution of people, nesting success was predicted to increase by 2%, which is unlikely to affect the population. At Mull Head, average people minutes per hour never exceeded 10, so at this site too, management should seek to spread visitors as thinly as possible. Only at Marwick Head, where average visitor

minutes per hour reached 63 and average distance was only 35m, did the guidelines suggest increased aggregation to be optimal. At this site, the current visitor distribution most closely approximates to 50% of people in 10% of the area, so, if management could concentrate visitors in only 1% of the area, increased aggregation is the favoured management option. Whilst management at St Abbs Head would result in benefits unlikely to be biologically meaningful, this is not necessarily the case with many combinations of visitor pressure and distance where management could increase nesting success by up to 10%.

Management guidelines are likely to vary between species (Nisbet 2000), so managers seeking to decide how to manage visitor distributions for other species would be advised to follow the process I have described here to develop species-specific guidelines. In synopsis, this process involves: (A) developing an equation relating important physical parameters to nesting success, as described by Beale & Monaghan (2004), (B) using these equations to predict the results of a range of management scenarios, and (C) assessing the assumptions upon which the guidelines are based. If the equation of nesting success accurately predicts nesting success in other colonies and the assumptions used to generate the guidelines are met, general species-specific management guidelines can be generated. If the predictions are not accurate between colonies, only guidelines for the management of the original site can be developed. I hope that the process described here will be taken up by conservationists seeking a scientific basis on which to establish management guidelines.

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FIGURE HEADINGS

Figure 1.

Optimal management scenarios for Guillemots. To use, first select appropriate grid by locating current visitor distribution (approximate minimum proportion of colony where 50% of visitors are found) down the vertical plane, then the expected visitor distribution under the new management scenario along the horizontal plane. Read grid using current average people minutes per hour and average distance between people and nests. Within shaded area, nesting success is higher when most visitors are in a smaller proportion of the reserve, in white area management should aim to spread visitors as evenly as possible. Note greater sensitivity of management options to anticipated distribution than current distribution. If current management is more clumped than anticipated scenario, the current and anticipated scenarios can be reversed.

Figure 2.

Management guidelines for Guillemots when total closure of a proportion of the reserve is anticipated under new management. Proportion of reserve open to visitors is (a) 0.3, (b) 0.1, (c) 0.05, (d) 0.01, current distribution is assumed to be even. Note similarity to equivalent line of Figure 1.

Figure 3.

Predicted and actual nesting success (\pm 95% confidence limits) for Guillemots nesting in two Orkney colonies in 2003. Note that predictions accurately mirror direction of change at both sites.

FIGURE 1

Anticipated clumping

0.3

0.1

0.05

0.01

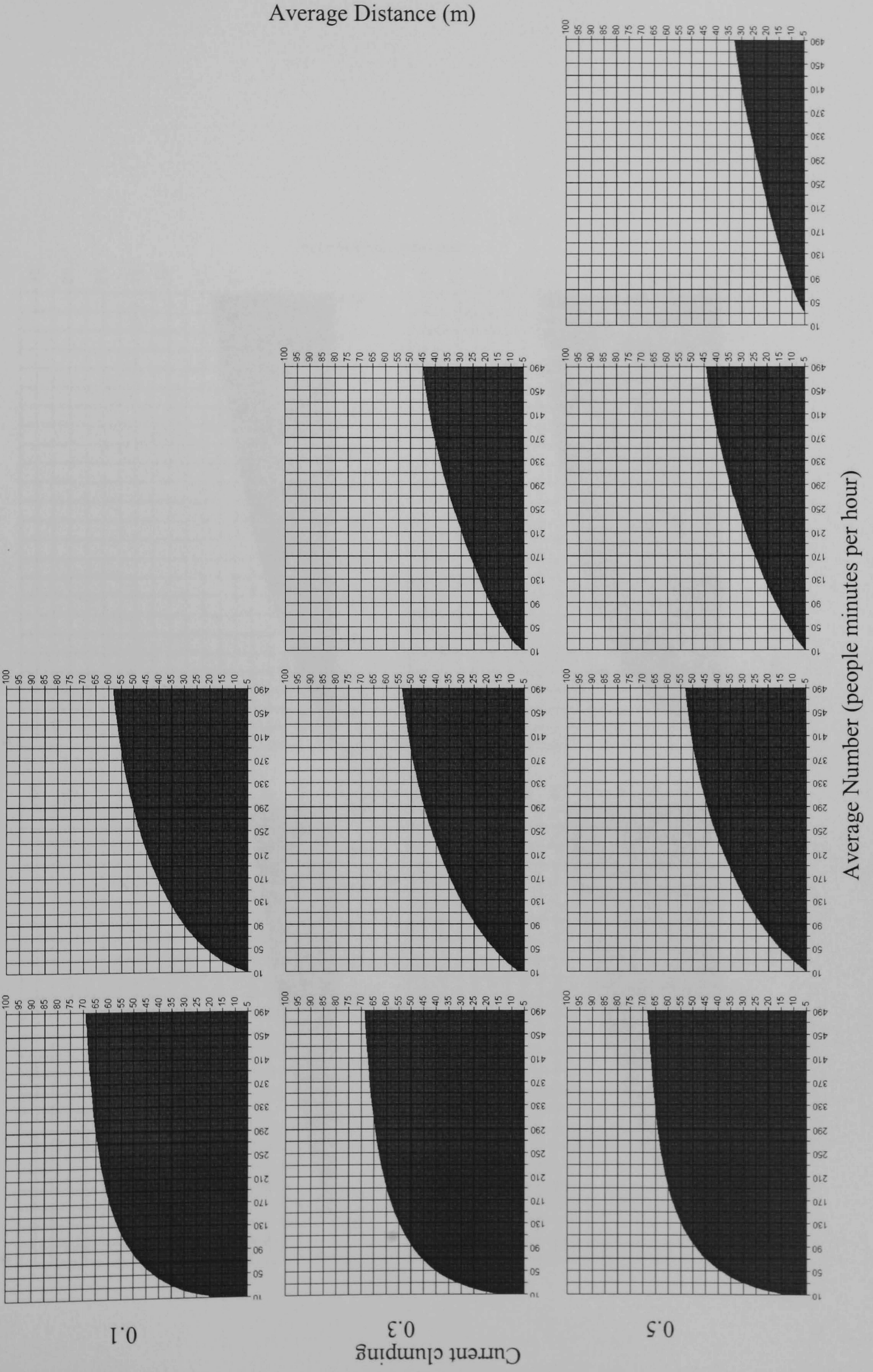


FIGURE 2

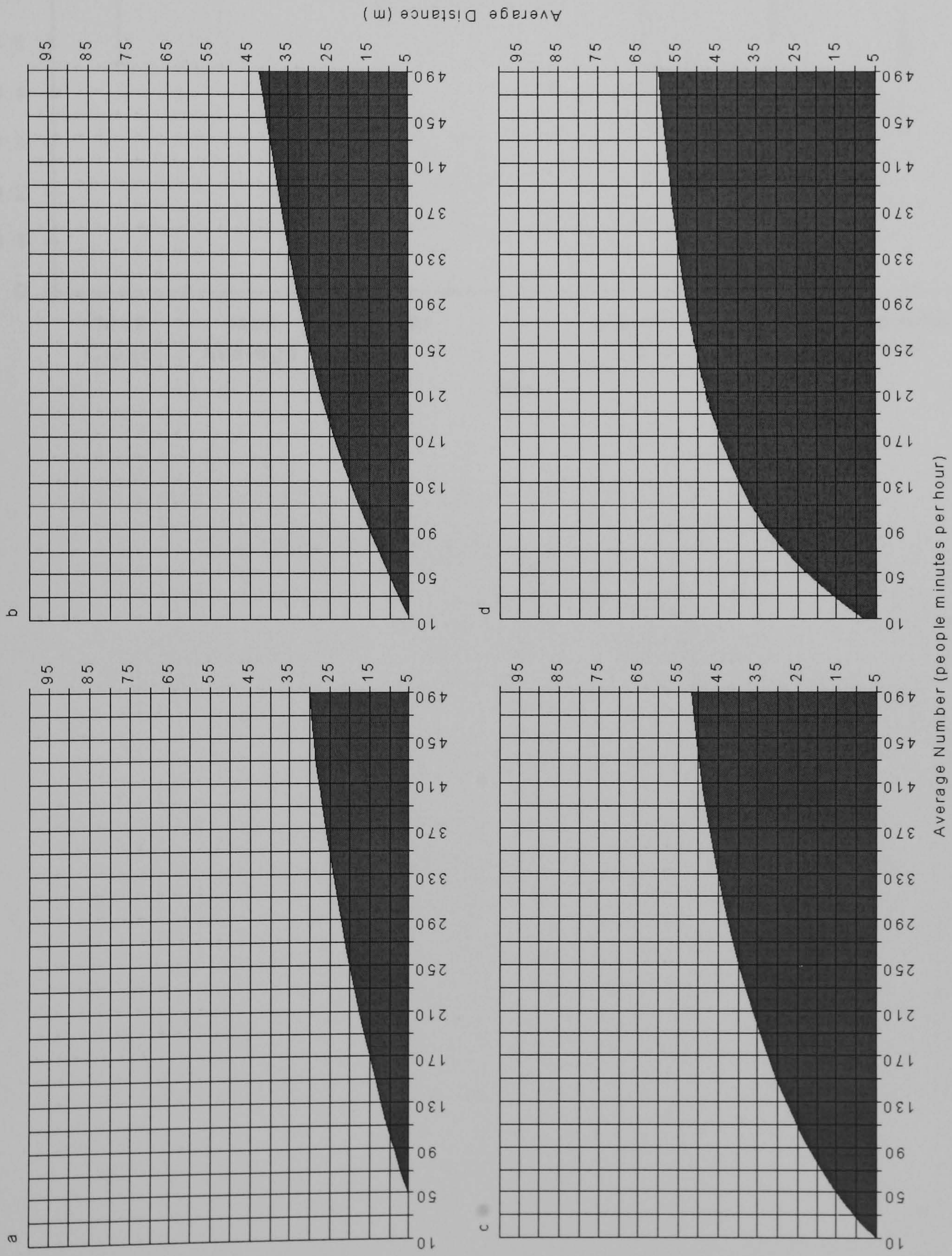
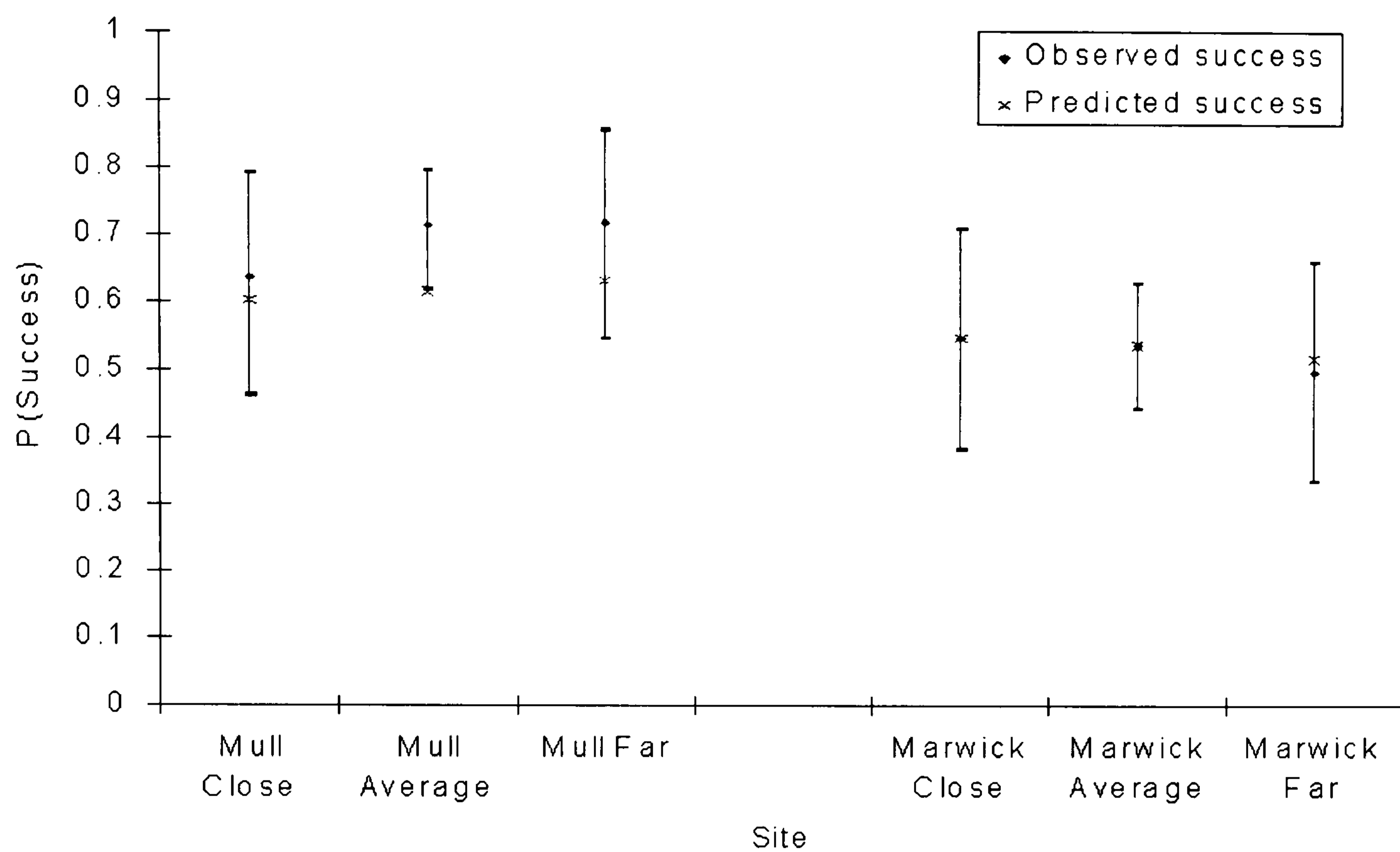


FIGURE 3.



CHAPTER 5

**Managing human disturbance by capping visitor numbers:
do nest failure rates correlate with visitor numbers?**

This chapter has been submitted for publication by:
COLIN M. BEALE & PAT MONAGHAN

ABSTRACT:

Most attempts to manage disturbance by visitors to nature reserves concentrate on limiting visitor access in some way, which is often unpopular with both visitors and managers. In a few nature reserves, the daily numbers of visitors are limited, an action that need not necessarily reduce the total number of visitors. As a test of the assumptions that underlie this management practice, we examined the relationship between daily visitor numbers and daily failure rates of nests in two species of seabirds. Daily failure rates for Black-legged Kittiwakes (*Rissa tridactyla*) were weakly correlated with daily visitor numbers. This was not the case for Common Murres (*Uria aalge*), where failure rate declined seasonally but was not significantly correlated with visitor numbers. We conclude that in fact, for some species, capping daily visitor numbers may result in lower overall breeding success.

Although first-hand experience of wildlife spectacles is one of the best ways to inspire public concern for conservation issues (Hendee 1972; Bogner 1999), poorly managed visitor access can increase mortality and cause population declines and decreases in breeding success (Higham 1998; Stevens & Boness 2003). The management of this conflict is a priority for conservation because ever more people spend their free time in the countryside (e.g. Gray et al. 2003).

Managers have two main options available to them: manipulate the number of visitors entering a reserve, or limit how close visitors may approach vulnerable species (Gill et al. 2001; Rodgers & Schwikert 2002; Ikuta & Blumstein 2003). Although restricting overall visitor numbers can reduce disturbance impacts (Beale & Monaghan 2004), such restrictions are unpopular with visitors and managers (Taylor & Knight 2003). Instead, managers of some reserves limit daily visitor numbers (Harris & Wanless 1995), a simple procedure that need not alter overall visitor numbers if visitors turned away on busy days return on quieter ones. Although this is simple and could be used in many nature reserves, the effectiveness of daily visitor limits is currently unknown.

This management option assumes there is a direct temporal association between large numbers of visitors and the disturbance impact. Nest failure in birds, however, need not be directly caused by large numbers of people; rather, it could be an indirect consequence of disturbance (e.g. caused by increasing the energetic requirements of incubation [Regel & Putz 1997; Beale & Monaghan 2004]) or related only to the distance to which visitors approach (Blumstein et al. 2003). To assess the effectiveness of daily visitor limits it is therefore important to assess whether there is a direct association between large numbers of visitors and disturbance impact.

To evaluate the usefulness of imposing daily visitor limits, we measured the relationship between daily variation in visitor numbers and nest failure in Black-legged Kittiwakes (*Rissa tridactyla*) and Common Murres (*Uria aalge*) at St. Abbs Head, southeastern Scotland. Both species suffer reduced nesting success due to human disturbance, but we do not know whether failures occur on days with high

visitor disturbance or accumulate gradually through a cumulative and indirect process (Beale & Monaghan 2004). St. Abbs Head has one of the largest mainland seabird colonies in Britain and receives up to 50,000 human visitors per year (National Trust for Scotland, unpublished data), thus, it provides an ideal location to study the effects of human disturbance. We believe this to be the first study assessing the usefulness of daily visitor limits as a conservation tool.

METHODS

We collected data at St. Abbs Head in 2002. From the mainland, we took photographs of the entire seabird colony before the laying period. (Ninety-eight percent of the approximately 30,000 Black-legged Kittiwake and approximately 30 000 Common Murre pairs were visible (National Trust for Scotland, unpublished data)). We laid an acetate marked with a grid of points over the photographs to select target nests. Wherever a point fell on a nest, we selected it for study. In this manner, we selected 106 Black-legged Kittiwake nests and 241 Common Murre nests. From egg laying to fledging, we checked each nest daily from a nearby cliff top and recorded the nest contents whenever possible. Checks were carried out during the morning, before the majority of visitors arrived at the reserve. If a nest active at the previous check had failed by the following morning, we defined the failure date as the previous day. For Black-legged Kittiwakes, we considered a nest successful if it fledged at least one chick and a failure if no chicks fledged. For Common Murres that failed early in the season and then laid a new egg, we selected one of these attempts at random to avoid pseudoreplication. With this protocol, we determined laying and failure or fledging dates for each nest.

We counted visitors with an automatic electronic counter as they started around the reserve. A proportion of people who returned on the same path were counted twice, so we estimated the actual number by dividing the counted total by one plus the proportion of people returning on the same path (based on survey results from the National Trust for Scotland). Most (90%) of visitors were present between 1000 and 1800 hours. Peak visitor numbers were recorded on sunny, calm days. Visitors

used the same viewpoints each day, irrespective of the total number of visitors (Beale & Monaghan 2004).

Data analysis was carried out in Rv1.8.0 and follows Crawley (2002). Our observations provided the number of active nests present and the number that failed on each day. As many nests present on one day were also present the following day (meaning such observations are not truly independent) we first fitted a mixed effects model with binomial errors predicting the proportion of nests that failed each day and we incorporated temporal autocorrelation of 1 day. Assessing temporal autocorrelation does not remove the non-independence of the initial observations, but does allow us to account for the statistical importance of any such dependency. This model contained the parameters date, log visitor numbers, and their interaction as fixed terms and a temporal autocorrelation of 1 day. We first assessed the presence of temporal autocorrelation by fitting an identical model without the autocorrelation. Where temporal autocorrelation was not significant, we can assume that the non-independence of the observations does not undermine the statistical test (Crawley 2002). In such cases, we therefore used the standard hazard analysis technique of a generalized linear model with binomial errors to predict the proportion of nests that fail on any 1 day and tested significance with a standard backward-stepping algorithm.

Having built such a model, it can be used to explore whether imposing a visitor restriction would be useful. If daily visitor caps are imposed and people are turned away, visitors may not visit at all, reducing the total visitor numbers, or they may return on a less busy day. To determine whether visitor restrictions may be useful, one must distinguish between the effects of reducing peak daily visitor number (our focus here) and reducing total visitor numbers during the season, which is known to be beneficial (Beale & Monaghan 2004). To do this, we first used our model to predict the number of failures at current visitor levels. We estimated the number of failures each day $[F(t)]$ by reference to the identified relationship $[f(N)]$ between daily visitor numbers $[N(t)]$, failure rate $[P(f)]$, the number of nests laid $[L(t)]$ and fledged $[G(t)]$ as below.

$$\text{Day 0 : } F(t_0) = [L(t_0) - G(t_0)] \times f(N(t_0))$$

$$\text{Day 1 : } F(t_1) = \left[\sum_{j=0}^{t_1} L(j) - \sum_{j=0}^{t_1} G(j) - F(t_0) \right] \times f(N(t_1))$$

$$\text{Day 2 : } F(t_2) = \left[\sum_{j=0}^{t_2} L(j) - \sum_{j=0}^{t_2} G(j) - \sum_{j=0}^{t_2-1} F(j) \right] \times f(N(t_2))$$

...

$$\text{Day N : } F(t_N) = \left[\sum_{j=0}^N L(j) - \sum_{j=0}^N G(j) - \sum_{j=0}^{N-1} F(j) \right] \times f(N(t_N))$$

Total failures can then be calculated simply by the sum of the failures on each day of the season. To assess the impact of capping daily visitor number we compared this total with a simulated data set, where visitor numbers were capped at 250 people per day, 25% above the average level (200 people). We assumed that each person turned away on days with over 250 visitors returned on the following days until the same number of people had visited (i.e. if actual visitor numbers over three days were 442, 120 and 62, we estimated failures for days with 250, 250 and 124 people). Using the same approach, we also simulated the effects of closing the reserve for one day each week, adding the number of visitors from the closed day to the following open one.

RESULTS

Common Murre eggs were laid between 7 and 18 May, with eggs in over 90% of observed nest sites initiated on the first 5 days of this period. Laying in the Black-legged Kittiwake nests was initiated between 22 and 31 May, with over 90% started within the first 2 days of this period.

There was no significant temporal autocorrelation in daily visitor numbers (i.e., visitor numbers on one day did not correlate with visitors on the following day; $F_{1,71} = 0.91, p = 0.34$), so we treated each daily estimate of visitor numbers as independent. The number of visitors was not significantly correlated with date, so there was no evidence of seasonal change in visitor numbers ($F_{1,72} = 2.18, p =$

0.14). There were, however, more visitors on weekends and bank holidays than on weekdays (Mann-Whitney U test: $Z = -2.44$, $n = 73$, $p = 0.015$). As there was no significant temporal autocorrelation in the models (Black-legged Kittiwakes: Log Ratio Test (LRT) = 0.002, $df = 1$, $p = 0.96$; Common Murres: LRT = 0.005, $df = 1$, $p = 0.94$), further models were based on generalized linear models (see methods).

Daily visitor number (N) was the only variable significantly associated with daily failure rates ($P(f)$) in the Black-legged Kittiwake ($F_{1,71} = 5.03$, $p = 0.025$; Equation 1). There was no significant seasonal change in Black-legged Kittiwake failure rate ($F_{1,70} = 3.44$, $p = 0.064$).

$$P(f) = \frac{1}{1 + \frac{1}{e^{0.504[\log(N)] - 6.887}}}$$

This relationship shows that failure rates increase slightly on days with higher visitor numbers, and the logarithmic nature suggests that increases in visitor numbers from a small initial number has a greater impact on failure rates than increases from higher initial visitor numbers. From this equation, we estimated that capping visitor number at a maximum of 250 per day would result in 0.5 more failures per 100 nests. By contrast, closing the reserve to visitors for one day per week and adding those visitors to the total number visitor the following day resulted in a small (1.5%) decrease in the number of failures.

Common Murre failures were not significantly associated with visitor numbers ($F_{1,74} = 1.780$, $p = 0.182$) but were significantly related to date, with failures most likely early in the season ($F_{1,75} = 10.63$, $p = 0.001$).

DISCUSSION

In the Black-legged Kittiwake, the probability of nest failure appeared to be linked to visitor numbers. We can exclude some other factors that could confound this relationship. It is possible, for example, that failure rates may change through the

season due to birds of different quality nesting at different times (Falk & Møller 1997). However, we found that most Black-legged Kittiwake nests were initiated over very concentrated periods, making this unlikely. Furthermore, earlier direct measurement of the effect of laying date indicated that differences were minimal (Beale & Monaghan 2004). It was also possible that seasonal changes in failure rate may be obscured by concurrent increases in visitor numbers, but because we found no significant seasonal trend in visitor numbers we consider this unlikely. If visitors to St. Abbs Head had approached nests closer on days when there were many visitors, distance may have confounded this effect. However, the distance between visitors and birds did not change in this way because distance is limited by geography, with visitors generally approaching as close to the cliff edge as possible regardless of number. Finally, it is possible that this correlation was caused by a correlation between weather and visitor numbers observed at St. Abbs. We observed the most visitors on warm, sunny days. However, it seems unlikely that birds are more likely to abandon breeding attempts during good weather than in harsher conditions, but without directly manipulating visitor numbers we cannot rule out this possibility. Other variables unmeasured in this study may also correlate with weather and could confound the relationship between visitors and failure rates. It is possible, for example, that the number of nest predators present is higher on days with good weather, or parent birds may be more likely to take advantage of good weather conditions to leave their chicks (although this is poorly supported (Cadiou & Monnat 1996)). In order to eliminate such confounding factors, an experimental approach to visitor numbers would clearly be an advantage in future studies.

Common Murres were more likely to fail early in the season than later. Although nest losses are generally assumed not to vary with time, an early peak probably reflected higher vulnerability of eggs and small chicks (Heisey & Nordheim 1995; Dinsmore *et al.* 2002; He 2003). We expect that those Common Murre eggs laid on steep ledges would roll off soon after being laid, rather than surviving to later in the season (Harris *et al.* 1997). This does not mean that birds that breed early are most likely to fail (which would be unusual), but simply that birds that fail are most likely to do so early in their nesting attempt.

The relationship between Black-legged Kittiwake daily failure rates and visitor numbers, although statistically significant, was nonetheless weak and suggested that daily visitor limits would actually result in more failures in this species. Instead, we estimated small benefits to closing the reserve for one day each week. Because our results are based on a single season, it is possible that the effect is influenced by the season itself: Black-legged Kittiwake breeding success in 2002 was around 20% below the 10 year average (National Trust for Scotland, unpublished). It would therefore be interesting to examine the pattern in more years before quantitative estimates may be considered reliable. As species are likely to vary in sensitivity (Blumstein et al. 2003), the conservation benefit of daily visitor limits may vary greatly in other species. Indeed, even this small benefit was not found in Common Murres.

In summary, contrary to current assumptions we found that imposing a daily visitor limit that does not reduce overall visitor numbers would result in a small decrease in the nesting success of the black-legged kittiwake at St. Abbs Head. In fact, we predicted small benefits to result from management that increased visitor numbers on busy days and reduced numbers on quieter ones. However, no such relationship was found for common murres. Clearly, if capping daily visitor numbers results in a decline in total visitor numbers there will be a conservation benefit (Beale & Monaghan 2004), although at a cost in terms of public education and appreciation of wildlife. However, we expect that the relationship between daily failure rates and visitor numbers will differ between species and sites. For species or sites where the relationship between failure rates and visitor numbers is an accelerating function (e.g. where low visitor numbers have few effects but large groups cause abandonment) daily visitor limits may be useful. Moreover, for some particularly rare species, even these small benefits may be important. We conclude, therefore, that although our study found very little benefit, the management of visitor access by visitor free days could be a useful additional conservation tool where human disturbance is a problem.

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CHAPTER 6

Effect of human proximity on behavior and heart-rate in the Black-legged Kittiwake *Rissa tridactyla*

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ABSTRACT

1. Breeding failure in birds is often linked to human disturbance. However, in species that show little apparent behavioral response to human presence, the causal mechanisms underlying this link are unclear. Disturbed birds may experience raised heart-rates as a consequence of stress, which may also carry an energetic cost that could lead to increased desertions and hence breeding failures.
2. We experimentally tested the effect of human proximity on behavior and heart-rate of breeding Black-legged Kittiwakes *Rissa tridactyla*. This species showed little behavioral response to human proximity but heart-rate was raised by up to 15%. We found no evidence of habituation either within or between experimental trials but there was considerable individual variation in response to human presence at both distances tested.
3. We estimate that the raised heart-rate indicates an increase in the daily metabolic requirement of disturbed birds by at least 5-6%. This may result in disturbed birds reaching a critical body condition that triggers nest desertion prior to their chicks having fledged.

Many studies report behavioral changes in breeding birds associated with human presence. While some such changes, for example the temporary or permanent desertion of breeding colonies, have clear negative effects on breeding performance (Anderson 1988; Bolduc and Guillemette 2003), others have less obvious negative consequences (Gander and Ingold 1997; Fortin and Andruskiew 2003). In a number of species, no or very few behavioral changes in response to human presence are found, but nonetheless population declines still occur (Nimon et al. 1995; Wilson and Culik 1995; Fowler 1999; Beale and Monaghan 2004). Consequently, there is a need to identify the causal mechanisms that link human disturbance to breeding failure in the absence of behavioral changes. It may be that costly physiological rather than behavioral responses may underlie this link. It has been reported that penguins showing no outward behavioral response to humans exhibit stress responses including raised heart-rates (Nimon et al. 1995; Wilson and Culik 1995; Fowler 1999). Whilst these stress-related responses may in themselves have negative effects on breeding success and survival (Silverin 1986; Sapolsky 1987), heart-rates elevated during the stress responses can be associated with an increase in metabolic costs (Hubert and Hüppop 1993) that may deplete the bird's reserves forcing eventual abandonment (Coulson and Johnson 1993; Cadiou and Monnat 1996). Such a metabolic cost has been previously identified but has yet to be tied to declines in nesting success in species apparently showing few other responses to human disturbance (Regel and Putz, 1997; Weimerskirch et al. 2002).

Black-legged Kittiwakes *Rissa tridactyla* show little behavioral response to human presence, yet birds nesting closer to visitor viewpoints suffer reduced nesting success compared with those nesting further away (Beale and Monaghan 2004). The relationship between raised heart-rates as a consequence of the stress responses and energy expenditure is known in this species (Hubert and Hüppop 1993), making it ideal for assessing whether physiological stress responses may raise failure rates. Here we examine the relationships between human presence, behavior, heart-rate and nesting success at this colony in response to human disturbance. An experimental approach was used in order to examine whether Black-legged Kittiwakes subjected to human presence show physiological changes sufficient to explain observed differences in nesting success. At St Abbs Head,

human disturbance reduced overall nesting success by around 10%, but did not result in certain failure of the most disturbed birds, but only increased its probability (Beale and Monaghan 2004). It is therefore likely that the mechanism that causes these failures is not shown by the entire population but by only around 10% of birds. Consequently, we do not focus here on the average responses to disturbance, but the responses of the extreme individuals: if increases are sufficient to explain failure of these individuals, the mechanism could clearly increase the overall failure rate.

METHODS

Behavioral observations. -

Data were collected in the seabird colony of St. Abbs Head NNR, south-east Scotland, during the 2003 breeding season. St. Abbs Head holds one of the largest mainland seabird colonies in Britain and receives up to 50 000 visitors per year (unpublished National Trust for Scotland statistics). A section of cliff was selected with nesting Black-legged Kittiwakes easily visible from two viewpoints. A nearby viewpoint (at 40m) likely to cause disturbance and another much further away (at 150m, far enough away to expect no disturbance effects) were selected from which behavioral responses to human presence could be recorded with the aid of a telescope. To ensure that the angle between the observer and the nests was identical at both distances, sites were chosen such that the more distant viewpoint was directly behind the nearer one. Fieldwork took place throughout the breeding season, from 1st May to 31st July. On most days between these dates, two to six half-hour periods were spent observing a sample of 12 Black-legged Kittiwake nests. The observer sat quietly and watched the birds in a manner similar to the majority of visitors to the site. Black-legged Kittiwake behavior was recorded by scan sampling every two minutes, and the behavior of the incubating birds was recorded as either awake (with eyes open) or asleep (with eyes shut). This gave 16 scans in each half-hour sampling period. We chose to record birds as either awake or asleep as this difference is a relatively objective measure visible (with a telescope) from both distances and incorporates a measure of alertness (Fernández-Juricic et al. 2001). The incidence of chick neglect (when no adults were present at

the nest) and the occasions when two birds were present was also recorded. On each day, an equal number of sample periods were measured from both of the viewpoints, but the order of viewpoints used was randomized. This was achieved by deciding the number of sample periods to be undertaken on that day and randomly selecting the order of the viewpoints used until at least half the sample periods had been assigned to one of the viewpoints, when the remaining sample periods were set to the opposite viewpoint. The effects of repeated measures at the same nest were controlled in the statistical analysis (see below). Observations were only made in the absence of rain, to both simulate normal visitor activity (visitors generally avoid rain) and because there was little variability in bird behavior during rain, with all birds remaining stationary on their nests.

Heart-rate measurements. -

The heart-rate of birds incubating at seven nests within the colony was measured using hardware based on Nimon et al. (1996) that measures infra-red reflectance, thereby detecting pulses of blood flowing below the skin of the incubating bird. This method compares favorably with other methods for measuring heart-rate and is widespread in medical research (Mendelson 1992; Takatani et al. 1992; Elchalal et al. 1995; Bohnhorst et al. 2000). The telemetry device was housed in a model egg attached to 100m of cable and was deployed in the nest of target birds. When a model egg was installed, one real egg belonging to the incubating bird was fostered into a neighboring nest throughout the duration of monitoring, but was returned to the focal nest before hatching. The cable was laid out to ensure that the end furthest from the egg was at the top of the cliff and easily accessible for downloading data. Model eggs were fixed to the nest material with stiff wire attached to one side of the egg, which ensured that eggs were neither removed from the nest nor rolled over, thus ensuring good contact was made with the incubating bird. The number of pulses recorded every six seconds was recorded by a datalogger with 52h of memory, which was regularly downloaded (from the cliff-top) to a laptop without needing to approach the nest.

In order to measure the effect of human visitors on the heart-rate of Black-legged Kittiwakes, experimental approaches were made to viewpoints approximately 20m and 70m from each nest. The closer of these two observation is nearer to the nest than when behavioral changes were measured, but was still not close enough to cause obvious behavioral changes in the incubating birds. An experimental trial consisted of a visitor appearing within view of the nest, walking towards the nest until the appropriate distance (either 20m or 70m) was reached, watching for five minutes (close proximity) and then leaving. The exact time (to the nearest second) of each trial was recorded, starting the recording period from the moment the incubating bird could be aware of the observer. Once the designated viewpoint was reached, the time was again recorded, and for five minutes the visitor stood and observed the nest through binoculars. At the end of the five-minute period, the visitor left the viewpoint. These times, and the five-minute period before the visitor was in sight, were identified in the continuous heart-rate records. Heart-rate data were coded to identify the visitor's activity during each six-second heart-rate observation period as either pre-trial (for the five minutes before the visitor was in sight) or close proximity (for the five minutes the visitor was observing the nest). Only one trial was made at each nest each day but trials were carried out on most days when eggs were installed in nests, with at least five trials for each nest at each distance.

As parents change incubation duties or stand over the eggs to turn them, the contact between bird and the telemetry device is temporarily interrupted. This results in values of zero on cloudy days or 350 (due to hardware constraints) if direct sunlight shines on the monitor. Thus occasional extreme values will be recorded. Data were therefore filtered for heart-rate values outside the known range of Black-legged Kittiwake heart-rates (estimated from implanted heart-rate monitors: Hubert and Hüppop 1993) i.e. below 110 or over 310 beats per minute (bpm). This resulted in data from 130 trials from 7 Black-legged Kittiwake nests.

Statistical analysis. -

All analyses were carried out in R v 1.8.0, and follow Crawley (2002). Means are given with standard errors. To analyze the data on the proportion time spent asleep or awake, generalized linear mixed models (GLMM) with a binomial error were built to predict the proportion of time each bird was awake and asleep in each sample period. The saturated model included the random factors Nest (a factor identifying the individual nest) and Observation (a factor identifying the observation), with Observation nested within the variable Nest. Fixed factors were Distance, Stage (identifying whether the birds were incubating eggs or attending chicks) and their interaction. Chick neglect and the proportion of time both parents spent attending the nest were low and consequently GLMMs did not converge. Therefore, for both near and far treatments, we computed the average proportion of time two birds were present at each nest and the average proportion of time when neither bird was present. These average values were compared for each nest under both treatments using Wilcoxon's signed ranks tests.

A similar approach was used to predict heart-rate. Our model included the random factors Trial (a unique factor assigned to each experimental Trial) nested within Nest (identifying the individual nest); with Activity (either the five minutes pre-trial or the five minutes of close proximity) and Distance (a factor indicating whether the approach was made to 20 or 70m) as fixed factors. A maximal model of heart-rate involving Activity, Distance and Nest, all the interactions between these, and the two nested random factors, was built. This was reduced to a minimal adequate model using a standard backward stepping algorithm. Heart-rate during the period of Close Proximity was also analyzed, to assess whether variation was randomly spread throughout the five minutes or represented short-term habituation (an initial peak, followed by a gradual decline). To do this, heart-rate within the five minutes of Close Proximity was further modeled by dividing the period into its constituent minutes and building a similar GLMM on this subset of the data, replacing Activity with the covariate Minute (identifying the minute within the five minute period). As the identity of individual birds on the nest was not recorded, analyses focus on differences between nests, not individual birds. All analyses used

mixed models, so treatment effects are assessed within the sample periods. As individual birds did not change during our sampling periods, individuals were compared with themselves (not their partners), therefore the only effect of using nest identity rather than individual identity was to increase the variation between sampling period (when incubation changes may have occurred).

Evidence of seasonal effects and habituation was assessed by building additional GLMMs predicting heart-rate with different model structure. Each Approach was numbered sequentially for each bird and defined as a covariate. A model with the random effects structure of Distance nested within Nest, and including the fixed effects of Approach as a covariate, the factor Activity and their interaction, was built. Significance was again assessed by step-backwards selection from the maximal model.

RESULTS

Behavioral observations. -

The amount of time that birds spent awake during a behavioral sampling period was related to both human proximity and the stage of the breeding period ($LRT = 10.7$, $df = 1$, $P = 0.001$). Having the observer located at 40m rather than 150m resulted in most birds showing a small (9%) increase in the proportion of time spent awake from 72.4% to 81.4%. Birds were also more likely to be awake when attending chicks than when incubating eggs. There was no evidence for there being any difference associated with observer distance in the proportion of time both birds were present at the nest or of the incidence of chick neglect (Wilcoxon's rank signed tests: Two birds present: $Z = -0.866$, $n = 12$, $P = 0.386$; Chick neglect: $Z = -0.535$, $n = 10$, $P = 0.593$; Table 1)

Heart-rate measurements. -

Typical heart rate traces during a trial are illustrated in Fig 1. The minimum adequate model predicting heart-rate in incubating Black-legged Kittiwakes during

an experimental approach of an observer required the three way interaction between distance, visitor activity and nest identity ($LRT = 499$, $df = 18$, $P < 0.001$), ensuring all parameters were maintained within the model. Birds from different nests differed greatly in their response to human presence at 20m: the birds at the two nests showing the greatest response showed average heart-rates up to 14% higher than resting rates, while birds at other nests did not appear to respond (Fig. 2). There was also considerable variation between the birds at different nests in their response to researcher presence at 70m. This variation was such that there was no overall difference between resting heart-rate and heart-rate with researchers present at 70m (difference = -4.6 ± 8.5 bpm), but birds at some nests still exhibited heart-rates up to 15% higher than resting rates.

The analysis of heart-rate change during the five minutes of close human proximity showed significant individual variation ($LRT = 44$, $df = 6$, $P < 0.001$), but does not suggest that the heart-rate elevation waned during the period of close human proximity. Birds at some nests showed a small increase in heart-rate (e.g. increase of 4.04 ± 1.54 bpm each minute in nest 2) others showed a small decrease (e.g. decrease of 7.15 ± 2.16 bpm each minute in nest 4) and most showed no significant change over the five-minute period.

The minimum adequate model predicting heart-rate in relation to seasonal effects or between-Trial habituation required the inclusion of the two-way interaction between Nest and Trial as a covariate ($LRT = 104$, $df = 3$, $P < 0.0001$). The model predicts that Pre-Approach (basal) heart-rate declines during the course of the season (by approximately 1.56 ± 0.1 bpm per day), but that there was a very slight seasonal increase in the heart rate response to humans (by 0.38 ± 0.1 bpm per day).

DISCUSSION

We found a small but statistically significant change in the proportion of time spent awake associated with the movement of an observer from a distant viewpoint to a nearer one. We found no larger scale behavioral changes in patterns of parental

nest attendance. Such low responsiveness to human proximity in this species has been reported before (Sandvik and Barrett 2001), and is not surprising in itself. It is certainly clear that simply spending slightly more time awake when people are nearby does not directly cause the loss of clutches and chicks associated with human disturbance. At distances of 40m, therefore, visitors have very little impact on the behavior of nesting Black-legged Kittiwakes. This impact is likely to increase as distance is reduced, but while inserting heart-rate monitors into nests we noticed that incubating Black-legged Kittiwakes only showed major behavioral changes when approached to within 1m, closer than the public can approach at St Abbs Head. Whilst we recognize that the small recorded change in behavior may indirectly affect Black-legged Kittiwake nesting success, we consider it unlikely that behavioral responses are the direct cause of the 10% decline in nesting success recorded at this colony. Instead we suggest that the raised heart-rate we found to be associated with human presence indicates a more likely cause of the declines in nesting success that have been reported.

The typical vertebrate stress response is a likely outcome when a potential predator approaches a Black-legged Kittiwake sitting on a nest (Kitaysky et al. 1999). This stress response has a number of effects, including an increase in heart-rate, which primes the animal's muscles with ready oxygen in case rapid escape is necessary (Seigal 1980). As humans are likely to be perceived as a potential predator by Black-legged Kittiwakes, the raised heart-rate we observed when a human was near the nest is unsurprising (Wilson and Culik 1995; Beale and Monaghan 2004). The considerable between-nest variation in the stress response triggered by human presence was also observed in Magellanic penguins (Fowler 1999), and may perhaps indicate the existence of different 'personality' types (Dingemanse et al. 2003). As expected, there was a lower response to human presence at 70m than at 20m, but birds at some nests still showed strong responses at the greater distance. As heart-rate is considered a good index of stress (Wilson and Culik 1995; Romero 2004) it is possible that the observed declines in breeding success are influenced by negative effects of high levels of circulating stress hormone (Silverin 1986).

However, an elevated heart-rate also indicates a direct increase in the energy budgets of incubating birds. It is known that heart-rate is a good index of energy expenditure and changes in heart-rate have been widely used to measure such energetic consequences (Butler 1993). Most studies attempting to calibrate changes in heart-rate and associated changes in energy expenditure refer to exercise-related increases in heart-rate (e.g. Bevan et al. 2002; Froget et al. 2002; Ward et al. 2002; Weimerskirch et al. 2002), and should not be used to estimate energetic consequences of the stress response (Romero 2004). For Black-legged Kittiwakes, however, the energy expenditure associated with stress related increases in heart-rate has been measured, and is only slightly smaller than the exercise induced relationship (Hubert and Hüppop 1993). This relationship allows us to estimate the increase in energy expenditure associated with a 14% increase in heart-rate when people were present at 20m as around 25-30% higher than the usual incubation rate. For some birds, this effect is similar at 70m. As there was no consistent change between nests in heart-rate over the five minute period of close proximity, such costs are likely to be experienced by some birds as long as visitors are present. It is possible, however, that if visitors are present for longer than five minutes the effect may reduce in the longer term. These increases are smaller than those reported for hand-reared Black-legged Kittiwakes subject to visual and auditory stimuli in the laboratory (Hubert and Hüppop 1993), but direct comparisons are difficult as the experimental stimuli and previous experience of the birds were different from ours.

While our heart-rate increases were measured from different distances (20m and 70m) to the close behavioral observations (40m), susceptible birds showed significant heart-rate changes even at 70m. As the lack of any substantive behavioral response at 40m suggests that behavioral effects do not explain declines in nesting success, if the changes in heart-rate of susceptible birds at both distances (14% increases) can explain the declines, it is clear that the difference in distances between methods was not important. It is important to note again that this estimate is not intended to be an average cost paid by all birds subjected to disturbance events, but an estimate for those birds that show strong heart-rate responses. Whilst all birds may be exposed to human disturbance, only those showing the strongest heart-rate response will fail in their nesting attempts. This suggests that disturbance

results only in a change in the proportion of birds failing, with little obvious reason to explain why some birds fail and others succeed in apparently identical areas, just as at St Abbs Head. The average response, therefore, may be only small, but as some birds appear to be highly stressed by human presence, the overall nesting success may still decrease. The variation in individual response to changes in distance also suggests that reliance on fixed set-back distances to protect wildlife from human disturbance is inappropriate, as this approach assumes that response distances are fixed for each species (Blumstein et al. 2003).

As visitors are only present at St Abbs between 0600 & 2200 BST (National Trust for Scotland, unpublished), we decrease the 25-30% additional cost by $1/3^{\text{rd}}$ to estimate the overall increase in incubation costs. Thomson et al. (1998) report that, during incubation, daily energetic expenditure for Black-legged Kittiwakes is 915 ± 134 kJ day⁻¹, with around 30% (285 kJ day⁻¹) of this spent whilst on the nest. An increase of 17-20% in the cost of incubation would result in a new total energy expenditure of 963 - 972 kJ day⁻¹, around 5 - 6% higher than in the absence of humans. Although this increase may seem small as a cost incurred daily, the cumulative impact is likely to be highly significant. In addition, we consider that this estimate is likely to be an underestimate of the overall costs, for a variety of reasons. Firstly, at St. Abbs Head, tourists approach Black-legged Kittiwake nests closer (to 3m) and in larger numbers than we simulated. We found no evidence that birds nesting in heavily visited areas of St Abbs Head had habituated to human disturbance (Beale and Monaghan 2004), so nests of strongly responding birds may be closer to viewpoints than we approached. Heart-rate for birds at such close proximity is conceivably even higher (increases of 75% were reported by Hubert and Hüppop (1993)). We have also found that larger visitor groups have a greater impact than do single observers (Beale and Monaghan 2004), further increasing the overall costs experienced by birds at St Abbs. Moreover, we used estimates from two of only seven nests to identify the extreme increases in heart rate associated with human presence and our estimate of the true extremes of individual variation is therefore unlikely to be complete. If two of seven nests (29%) show heart-rate increases of 14%, the responses shown by the most extreme 10% of the population

(all that is necessary to cause the 10% increase in failure rates) are likely to be significantly higher.

During the breeding season, Black-legged Kittiwakes decline in body condition as they use up previously stored reserves (Golet and Irons 1999). Any increased energetic cost must lead to faster declines, which can lead to greater responsiveness to stress (Kitaysky et al. 1999) setting up a positive feed-back mechanism. Further evidence for this may be found in the slight seasonal increases in responsiveness we found here. Declining body reserves lead, in turn, to an increased likelihood of nest desertion when the birds run out of resources (Coulson and Johnson 1993; Cadiou and Monnat 1996). The very few Black-legged Kittiwake eggs and small chicks left unattended at St Abbs were predated by waiting corvids within a few seconds of the parent leaving. As the likelihood of desertion will be increased by a bird experiencing increased metabolic costs as a consequence of human disturbance, we have demonstrated a mechanism linking human disturbance, bird behavior and heart-rate to declines in nesting success in a species showing only subtle behavioral responses to humans. If other species showing few behavioral changes associated with human disturbance also show this response, it is possible that the number of species where disturbance effects are important has been underestimated.

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Table 1.

Proportion of time two birds were present at the nest, and the proportion of time chicks were left unattended in each nest, as observed from near and far viewpoints.

Wilcoxon's signed rank test: Two birds present: $Z = -0.866$, $n = 12$, $P = 0.386$;

Chick neglect: $Z = -0.535$, $n = 10$, $P = 0.593$.

Nest	Two Birds		Chick Neglect	
	Near	Far	Near	Far
1	0.00673	0.00769	0	0
2	0.0481	0.0173	0	0
3	0.0202	0.00288	0	0
4	0.0154	0.0308	0	0
5	0.0462	0.0212	0	0
6	0.00865	0.0269	0	0
7	0.0698	0.0625	0	0
8	0	0	NA	NA
9	0.0317	0.0115	0.0994	0.0256
10	0.00721	0.0168	NA	NA
11	0.00769	0.0173	0.125	0.0875
12	0.00192	0.00192	0.159	0.216

FIGURE LEGENDS

FIGURE 1.

Typical traces of Black-legged Kittiwake heart-rate during experimental trials. Shaded bars identify the visitor's activity: pre-approach is the five minutes before the visitor was in sight of the nest, advancing is the period between the visitor appearing within sight of the nest and arriving at the viewpoint, close proximity is the five minutes of observation at either 20m or 70m and post-approach is the period following the observation period. Data from both the pre-approach and close proximity periods were used in the analysis. Low values (below 11 bpm) and the periods of instability in both traces whilst the visitor advanced towards the nest result from movement error, the thicker line is the average over 30 seconds.

FIGURE 2.

Average increase in mean heart-rate of Black-legged Kittiwakes at seven nests associated with human presence at 20m. The variation in response both within and between nests is clear. Errors are standard errors, and the number of Trials used to create the means is listed. Note that these graphs show only general patterns of response and cannot be directly compared with the statistical analysis described.

FIGURE 1.

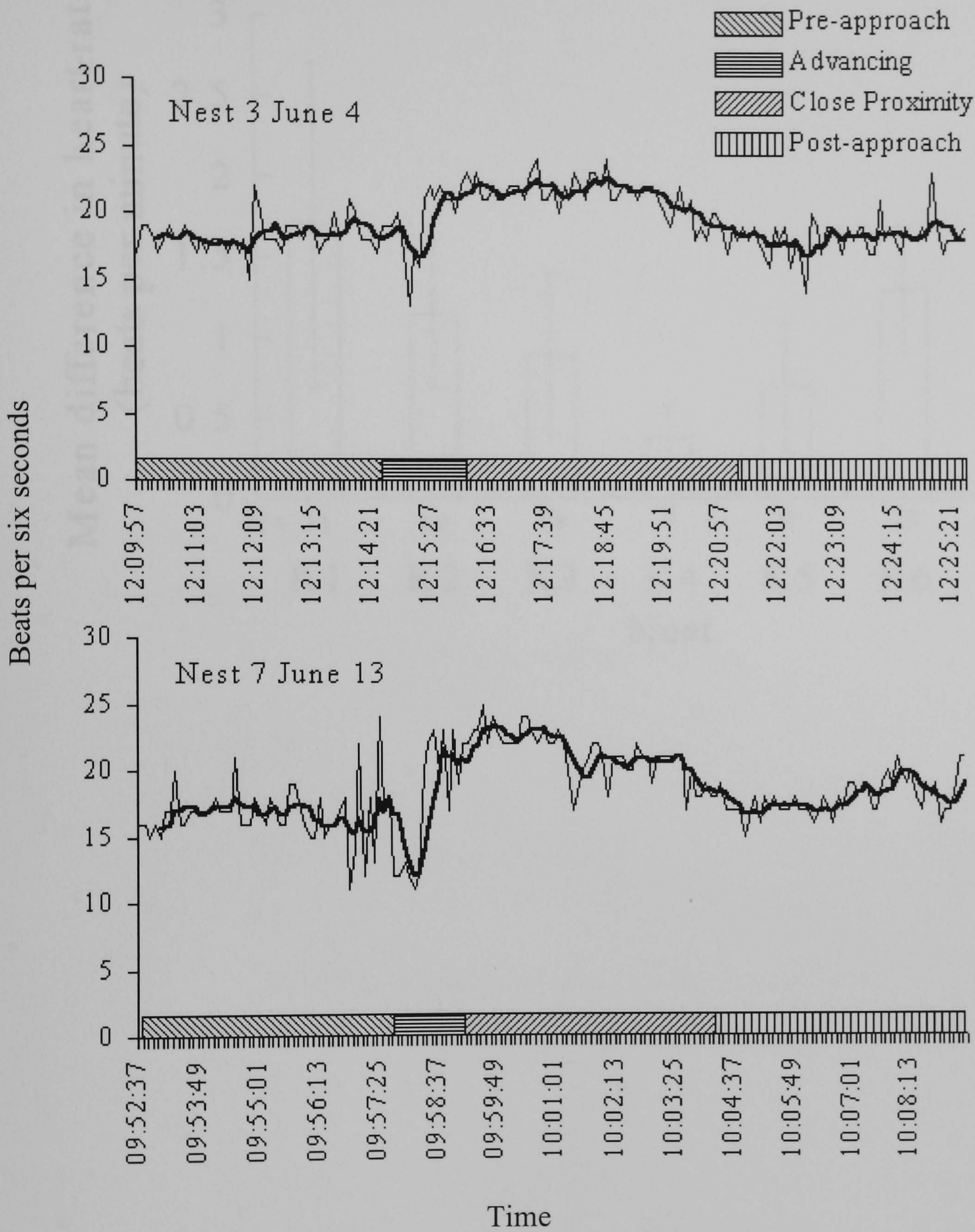
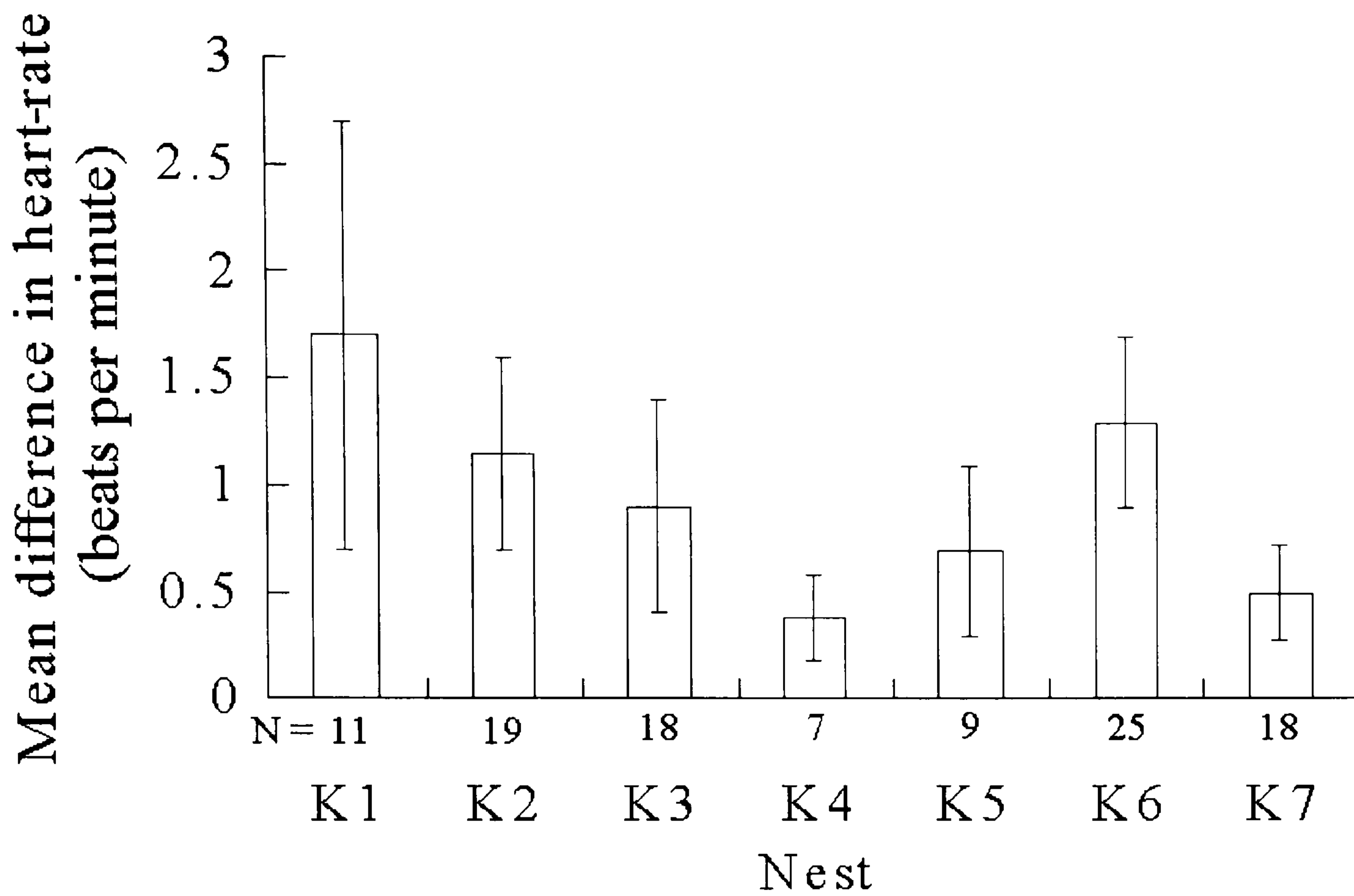


FIGURE 2.



CHAPTER 7

Effects of human disturbance on the pattern of parental nest attendance in Kittiwakes *Rissa tridactyla*: chick predation versus parental foraging time.

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ABSTRACT

Declines in avian breeding success due to human disturbance have been widely reported. However, in many cases it is hard to determine how this effect is mediated, since the birds involved may show no immediate behavioural response to human presence. A possible mechanism linking human disturbance and nesting failure in such species is via elevated metabolic costs in disturbed individuals. If this occurs, the incidence of parental absence from the nest, and hence of chick neglect, will progressively increase in birds exposed to high levels of human disturbance, since parental condition will deteriorate faster, necessitating more time to be spent foraging. We investigate the relationship between chick neglect and levels of human disturbance in the Kittiwake *Rissa tridactyla*. In this species, declines in nesting success occur with human disturbance, despite the birds showing little immediate behavioural response. We show that patterns of parental attendance are consistent with human disturbance affecting parental energy budgets.

Consequently, instead of management protocols based on the distance at which birds show a behavioural response to human presence the active management of visitor numbers to reduce sustained exposure levels may be more effective in mitigating disturbance effects.

The management of human access to wildlife areas has been of concern to conservationists for a long time (Hunt 1972; Anderson 1988). It is clear that the effects of unmanaged visitor access on breeding birds and mammals can be devastating, with total failure of breeding colonies and substantial population declines occurring in many cases (Anderson 1988; Stevens & Boness 2003). Other changes less directly associated with population declines have also been reported, including behavioural responses such as animals being scared away from favoured feeding areas, which is assumed to have some later fitness cost (Pfister *et al.* 1992; Gill *et al.* 2001; Mann *et al.* 2002). While it is clearly important to measure and manage the impact of human disturbance on vulnerable species, the use of simple behavioural-responsiveness indexes has been challenged on both theoretical and empirical grounds (Gill *et al.* 2001; Beale & Monaghan, in press). In addition, there is increasing evidence that local population size may be negatively affected by human disturbance even in the absence of any immediate behavioural responses in the affected animals (Nimon *et al.* 1995; Wilson & Culik 1995; Beale & Monaghan 2004). In such cases, there is clearly a need for a more profound understanding of the mechanisms that lead to breeding failure if we are to adequately protect animals from the negative effects of visitor access.

A typical example is the Kittiwake *Rissa tridactyla*, in which declines in breeding success apparently linked to heavy visitor pressure have been reported (Beale & Monaghan 2004). Although Kittiwakes appear to ignore visitors only 3m away from their nests, we found a 9% decline in the breeding success of birds attributable to human disturbance. This increase in nest failure may be mediated by increases in heart-rate in response to humans as observed in other species (Nimon *et al.* 1995; Wilson & Culik 1995). Such heart rate elevation will result in increased metabolic requirements at a time of already high demand (Thomson *et al.* 1998; Golet & Irons 1999; Golet *et al.* 2000; Fyhn *et al.* 2001). This in turn means that disturbed individuals decline in condition faster, eventually changing their nest attendance behaviour in favour of time spent foraging rather than brood guarding and hence increasing the likelihood of brood desertion (Coulson & Johnson 1993;

Cadiou & Monnat 1996; Jones *et al.* 2002). Thus, disturbed birds may show increased failure rates despite their lack of immediate behavioural response to human presence. There is also evidence that condition-mediated changes in parental nest attendance occurs in Kittiwakes. Kittiwakes in poor condition are known to increase the incidence of chick neglect (i.e. both parents leaving unfledged chicks unattended in the nest), presumably in order to spend more time foraging (Wanless & Harris 1992; Cadiou & Monnat 1996; Gill *et al.* 2002). Chick neglect is also known to increase in probability as chicks get older and better able to thermoregulate and defend themselves from potential predators, again probably linked to changes in parental condition and in the costs and benefits of being absent from the nest (Cadiou & Monnat 1996; Gill *et al.* 2002).

However, theoretical modelling suggests that the response of seabirds such as Kittiwakes to increased predation risk should be to remain on the nest with their chicks, though the lack of supporting data suggests that this effect is perhaps smaller than that of body condition (Jones *et al.* 2002). As it appears that humans are perceived as predators by disturbed birds (Frid & Dill 2002; Beale & Monaghan 2004) two processes may be at work: if parental condition is poor, chick neglect will increase; when predation risk is high, chick neglect will decrease. These two processes are not exclusive, but the time scale over which they operate is different. The effect resulting from a decline in parental body condition is cumulative, and thus a delayed rather than an immediate response, and therefore forms an underlying pattern most evident later in the season. The effect produced by changes in perceived predation risk is likely to be an immediate response to predator presence, and thus will fluctuate on a daily basis with changes in visitor numbers. Therefore, if human disturbance accelerates the decline in parental condition during breeding, birds most exposed to human disturbance will show more chick neglect overall. To examine the effects of human disturbance on perceived predation risk, we also measured the daily variation in chick neglect in relation to visitor numbers.

We predicted that Kittiwakes nesting in heavily disturbed areas would show higher levels of chick neglect than conspecifics in less disturbed areas. This difference between heavily disturbed and less disturbed birds is likely to be

strongest when parents have older chicks, as the energetic cost accumulates throughout the season. Within this overall pattern, however, we predicted that responses to perceived predation risk would result in direct effects on the daily patterns of neglect, with lower chick neglect on busier visitor days (Jones *et al.* 2002; Beale & Monaghan 2004).

METHODS

Data were collected in the seabird colony of St. Abbs Head National Nature Reserve (NNR), south-east Scotland, during the 2002 breeding season. St. Abbs holds one of the largest mainland seabird colonies in Britain and receives up to 50 000 visitors per year (National Trust for Scotland, unpublished). Around 30 000 pairs of Kittiwakes nest at St. Abbs and we have shown that there is a decline in nesting success associated with the most heavily visited areas of the reserve, although behavioural responses are minimal (Beale & Monaghan 2004). During the nest building period, photographs of the whole colony were taken from the mainland. Target nests were selected throughout the colony using a grid of points marked on an acetate which was laid over the photographs: wherever a point fell on a nest this was selected for study. A total of 106 Kittiwake nests were selected in this manner, representing independent data points (at least 4m apart). Each nest was observed daily throughout the chick rearing period from a nearby cliff top (between 4 and 100m away), and the nest contents were recorded whenever possible to determine nest success. Each day (between the hours of 0900 and 1700) we recorded once the number of parent birds attending each nest. While such a measure provides only a coarse (but unbiased) index of the level of chick neglect (Coulson & Johnson 1993), when collected daily from a large sample of nests it should be sufficient to allow comparisons of parental attendance patterns.

Visitor numbers and distribution were studied on the nature reserve as described fully by Beale & Monaghan (2004). To summarise, the numbers of people visiting St. Abbs Head each day were estimated from an automatic counter located near the start of their route around the reserve. There was no temporal auto-correlation in daily visitor numbers (i.e. visitor numbers on one day did not correlate

with visitors on the following day; $F_{1,71} = 0.912$, $P = 0.343$) so for data analysis of temporal variation in chick neglect we assumed each daily estimate of visitor numbers to be an independent estimate, thereby providing a measure of perceived predation risk on each day. We then identified 19 viewpoints where people stopped to observe the breeding colony and on 14 warm sunny days (average number of visitors \pm S.D. = 370 ± 61.5) we recorded the number of people present at each viewpoint once per day. Each day between 10:00 and 15:00 we counted the people present at the instant the researcher appeared within sight of each viewpoint. This allowed us to generate a parameter measuring the average people minutes per hour for each viewpoint on busy days, similar to other measurements common in disturbance research (e.g. Lafferty 2001). Using a 1:5000 OS map, we measured the distance between each focal nest and the two nearest viewpoints with direct line of sight. For each nest we then divided the average people minutes per hour at the two nearest viewpoints by the distances to these same viewpoints, and averaged the two values (as most nests were visible from two viewpoints). This parameter (which we call “exposure”) is similar in magnitude when large numbers of people are at a distant site and when small numbers are present nearby and we use it as a measure of human disturbance specific to each nest site. We have shown that compared to a suite of physical parameters commonly measured, this parameter shows the single strongest association with nesting success (Beale & Monaghan 2004). We predicted that sites with high exposure would have the highest overall incidence of chick neglect, a difference that would increase as parents progress through the season, due to the likely indirect effects of human disturbance on energy expenditure. We also predicted that within this overall pattern, chick neglect would be lowest on days with high visitor number, due to the likely direct effects of human disturbance on perceived predation risk.

DATA ANALYSIS

Data analysis was carried out in Rv1.8.0 and follows Crawley (2002). We used general linear mixed models (GLMM) to predict the daily incidence of chick neglect for each of the 81 monitored Kittiwake nests that hatched chicks. As both daily people numbers and exposure showed a left-skewed frequency distribution we

used a log transformation to normalise their distribution. We included a factor indicating the nest outcome (success/failure) to assess whether patterns differed between these two groups due to inherent differences in parental quality. We built a maximal model with binomial errors involving nest identity as a random factor, with chick age, nest outcome, log daily people numbers, log exposure and all their interactions as fixed factors. We assessed significance of the parameters by a standard backward stepping elimination procedure.

RESULTS

Chick neglect was recorded in 46 of the 81 nests that hatched chicks on a total of 39 days out of the 55 days when chicks were present in the colony. Of those nests that did show chick neglect, the incidence ranged from nests with chicks recorded neglected on only one day to nests where the chicks were unattended on up to 17 days before fledging. Our model fitted the data well, with normally distributed errors and a residual error of 0.79. The minimum adequate model predicting daily chick neglect involved the four-way interaction between chick age, nest outcome, log daily people numbers, log exposure ($LRT = 67.02$, $df = 1$, $P < 0.0001$). Overall, the incidence of chick neglect increased as chicks got older, and was highest in nests that failed, with more complex patterns involving aspects of human disturbance (Fig. 1).

Significant relationships between chick neglect and human disturbance are as follows. For nests that fledged chicks, early in the season there was more neglect on days with high visitor numbers, but no real difference between nests in areas of high exposure to visitors and those in less exposed regions (Fig. 1a). Close to fledging (at around 35 days of age), we found greater differences between nests in areas with high exposure to visitors and those in less exposed areas. In high exposure areas, overall neglect was higher (the expected energy expenditure effect), was greatest on days with low visitor numbers and declined as the number of visitors increased (the expected predation risk effect); whilst nests with low exposure to visitors showed little change in neglect in relation to daily visitor pressure (Fig. 1b).

Turning to those nests that did not successfully fledge chicks, young chicks (5 days old) were unlikely to be neglected, particularly among nests with high exposure on days with low visitor numbers (Fig. 1c). For those nests that failed, but succeeded in raising chicks to 20 days (all chicks older than 25 days subsequently fledged) of age, patterns of chick neglect were similar to patterns in nests that succeeded. Nests with low exposure to humans showed little change in the frequency of chick neglect in relation to change in daily visitor numbers; nests with higher exposure showed more overall neglect (the expected energy expenditure effect) but low chick neglect on days with many visitors and more neglect on days with low visitor numbers (Fig. 1d), the expected predation risk effect.

DISCUSSION

As expected, the overall patterns of our data show a general increase in the likelihood of chick neglect as chicks get older. This pattern is strongly supported by other studies of chick neglect in this species (Wanless & Harris 1992; Coulson & Johnson 1993; Cadiou & Monnat 1996; Gill *et al.* 2002). Unsurprisingly, we also found that nests that failed had higher incidences of chick neglect, particularly early in the season (indeed, each of the eight nests that showed chick neglect before the chicks were ten days old subsequently failed). Despite this quantitative difference, we found little qualitative difference in the patterns of chick neglect between nests that failed and those that succeeded. Consequently, the rest of our discussion focuses on general patterns found among all nests. Whilst chick age and nest success had the greatest effects on the incidence of chick neglect; we also found significant associations between chick neglect and both the temporal and spatial pattern of human disturbance.

We believe that the changes in the relationships that we observe over time reflect the changing priorities of the parent birds. The first priority of an adult bird should always be maximising its lifetime fitness (Trivers 1972; Jonsson & Tuomi 1994). For long-lived birds this has two main components: maximising reproductive output whilst ensuring its own survival to the next breeding season

(Trivers 1972; Montgomerie & Weatherhead 1988; Jonsson & Tuomi 1994). Raising chicks is known to reduce the probability of adult Kittiwakes returning to breed the following year, interpreted as a consequence of the increased energetic demands placed on them by raising chicks (Golet *et al.* 1998). It seems likely, therefore, that neglecting chicks will allow parents to minimise the total energetic costs of chick rearing, and therefore that chick neglect is adaptive (Cadiou & Monnat 1996). However, if parent birds neglect their chicks this may expose them to greater predation risk, suggesting a balance must be reached between maximising the parents' and chicks' likelihood of survival (Cadiou & Monnat 1996). The way this balance is achieved is expected to vary as the season progresses. To raise young chicks to fledging requires significant further parental investment, whilst older chicks require little more to ensure fledging (Pavel & Bures 2001; Jonsson & Tuomi 1994; Rytönen *et al.* 1995). Consequently, early in the season adults should hedge more towards their own survival, and later towards their chick's survival. However, at the same time the costs associated with neglect decrease as chicks grow older, but adult condition declines (Cadiou & Monnat 1996; Golet & Irons 1999; Gill *et al.* 2002). We believe the changing balance between these conflicting factors explains much of the changing patterns in neglect that occurs as chicks grow older.

Our data show that chick neglect is initially low and varies little between nests of high or low exposure to humans. However, as the chicks grow older neglect rapidly increases in nests in the areas most exposed to humans, relative to those in quieter areas. Therefore, as predicted, we found that birds nesting in areas of the nature reserve where exposure to visitors was greatest showed the highest levels of chick neglect with older chicks. It seems likely, therefore, that birds in heavily visited areas experience an increased energetic cost of reproduction, which appears to increase the likelihood of chick neglect. This, we believe, further supports our proposed mechanism linking human disturbance and breeding failure via a metabolic cost associated with maintaining elevated heart-rates. As the distribution of visitors around the reserve was manipulated in 2002 (Beale & Monaghan 2004) we do not think there are significant confounding variables (such

as intrinsically higher quality birds preferentially nesting in sites with low human disturbance) that lead us to doubt this result.

We also found that within the general pattern outlined above, chick neglect was lowest on days when there were most people around. Closer inspection reveals that this effect was only apparent in nests with high exposure to visitors, such that nests with low visitor exposure showed few changes in chick neglect associated with daily variation in visitor numbers. We interpret this result as providing evidence that birds show behavioural flexibility in their response to perceived predation risk: as the risk increases they are less likely to abandon their chicks (Jones *et al.* 2002). Although it is possible that the correlation between daily visitor numbers and weather conditions could confound this pattern (birds may be more likely to neglect when thermal conditions are favourable, for example), it is hard for weather conditions alone to explain why birds nesting in areas with lower exposure to humans do not show the same pattern. It is perhaps interesting to note that this pattern is completely the opposite effect to what may be expected from many studies of the effects of human disturbance. Many studies report that human presence is related to temporary or even permanent nest abandonment (e.g. Anderson 1988; Bolduc & Guillemette 2003). If the declines in chick neglect associated with high visitor numbers were observed in isolation, therefore, it would be quite possible to conclude that human disturbance is not even a slight concern for Kittiwake conservation.

These findings have a number of practical implications. Firstly, it is interesting that two superficially alternative measures of human disturbance (i.e. daily variation visitor numbers, and overall exposure of nests to visitor pressure) result in apparently opposite behavioural responses. It is clear, therefore, that as others have also suggested, the interpretation of behavioural indices of human disturbance is fraught with problems (Gill *et al.* 2001; Beale & Monaghan, in press). As parent birds that neglect older chicks are able to spend more time foraging, this behaviour may buffer birds from the energetic cost associated with human presence (Wanless & Harris 1992; Cadiou & Monnat 1996). We conclude, therefore, that if conservationists can allow birds needing to forage for themselves

to neglect older chicks, the effect of human disturbance can be reduced. This could perhaps be achieved by placing a cap on the daily visitor numbers, as we have shown that neglect of older chicks is lowest on busy visitor days. The changing priorities of adult birds as the chicks grow older may also have management implications. For example, it suggests that disturbance impacts may be greatest in years when adult condition is initially poor, perhaps due to lower than normal food availability. In the ideal situation in reserves where annual food availability is known we therefore recommend that management guidelines consider this.

The restriction of daily visitor numbers has been used in a few nature reserves (e.g. Harris & Wanless 1995), but it is hard to find evidence for the efficacy of such measures in the literature. For example, Carney and Sydeman (1999) review human disturbance effects and visitor management protocols, but mention no studies of the likely effects of capping visitor numbers. We suggest, therefore, that the effectiveness of daily visitor limits be more widely studied. Although limits may reduce the overall numbers of people experiencing a wildlife spectacle, overcrowding of nature reserves may not only harm wildlife, but also decrease visitor enjoyment of the experience (Higham 1998).

In addition, this study provides evidence that birds nesting in areas of high exposure to visitors suffer increased energetic costs, supporting the proposed mechanism linking human disturbance and failure via energetic costs (Beale & Monaghan 2004). As the negative effects of human disturbance are related to how exposed a nest is to humans (a parameter involving both visitor numbers and distance) our findings suggest that reserve managers consider visitor numbers as well as distance between visitors and wildlife. We therefore recommend that where a disturbance problem is apparent conservationists move away from management based on distance alone and, if possible, towards active management of visitor numbers.

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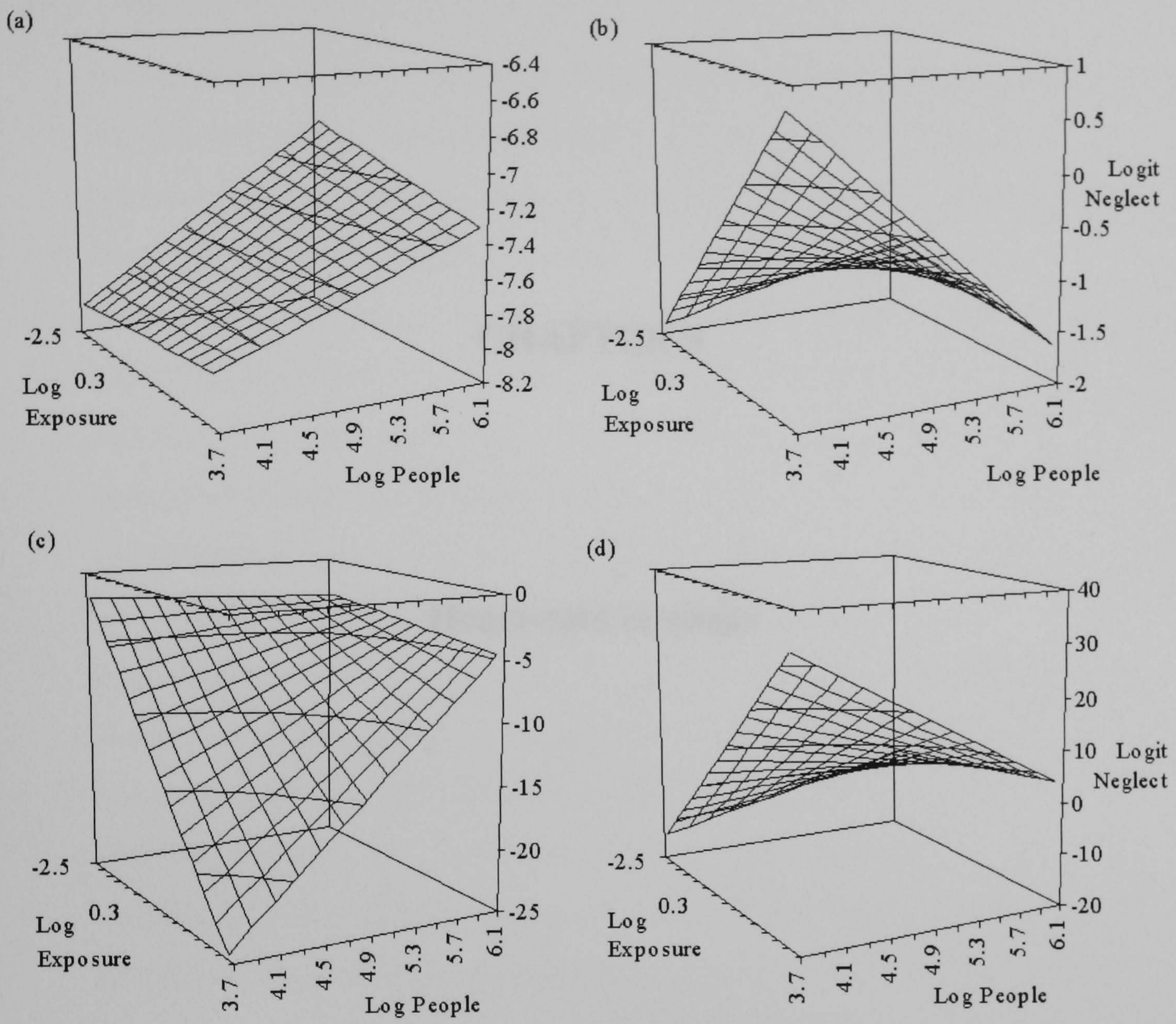
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FIGURE HEADING

Figure 1. Three-dimensional interaction plots of chick neglect in Kittiwakes in relation to spatial and temporal measures of human disturbance, as revealed by GLMM. Note that chick neglect is plotted on a logit scale, which linearises the sigmoidal shape of the binomial distribution, and that the scale varies between plots. Figs (a) and (b) show patterns in nests that succeeded, with neglect of young chicks (a) and older chicks (b) plotted separately. Figs (c) and (d) show the same patterns for nests that subsequently failed. Note particularly the similarity between (b) and (d).

FIGURE 1.



CHAPTER 8

Heart-rate in shags

ABSTRACT

Human disturbance can lead to breeding failure in seabirds, a process that may be mediated by increases in heart-rate in association with human presence. Such increases in heart-rate in response to human presence can show considerable individual variation. If susceptible birds can be identified through correlated attributes without having to measure individual heart-rate, it may be possible to reduce the impact of disturbance on these individuals. I measured heart-rate increases associated with human presence in the shag *Phalacrocorax aristotelis* and attempted to identify correlates of such responses. Such correlates may also be useful in identification of behavioural syndromes, or personalities. None of the measured variables (age, behaviour, distance to observer, number of observers or previous experience of people) correlated significantly with average heart-rate increases in shags attending 15 nests. The variation in response rendered analysis insufficiently powerful to eliminate the possibility of relationships between these parameters and heart-rate responses, but does suggest that any such relationship is only weak. I conclude that the data are not yet sufficient to allow alternative individual parameters to be measured in place of heart-rate increases.

With increasing numbers of people seeking to get close to wildlife, there is a growing concern about possible disturbance effects (Fairbanks & Tullous 2002; McCoy 2003; Fernández-Juricic *et al.* 2004). Widespread reports of declines in breeding success associated with human disturbance are clearly of great conservation concern (Anderson 1988; Bolduc and Guillemette 2003; Beale & Monaghan 2004). Other studies report that animals in disturbed areas show indications that they may be suffering from both chronic and acute stress (Wilson & Culik 1995; Fowler 1999; Millspaugh *et al.* 2001). Whilst clearly an animal welfare issue, there is also concern that stress responses may indirectly lead to breeding failure, and hence be a conservation concern too (Chapter 6, Dunlap & Schall 1995). In several studies where stress responses to human disturbance have been measured, significant individual variation in response has been reported (Fowler 1999; Kitaysky *et al.* 1999; Romero 2004). If it were possible to identify the individuals showing the strongest stress responses, it may be possible for managers to avoid providing visitor access to these individuals, enhancing animal welfare and potentially improving the conservation status of the population.

Two sets of parameters may cause the variation in response to humans that has been reported in the literature: extrinsic factors relating to the disturbance event and intrinsic factors such as the genetic make up, condition and experience of the bird (Table 1). Of the extrinsic factors, it is clear that a single human a great distance from an animal may be expected to elicit a smaller stress response than a number of people close to the individual (Frid & Dill 2002; Beale & Monaghan 2004). Intrinsic factors include an animal's previous experience of humans, both in terms of frequency (through habituation to a familiar stimulus) and intensity of the experience (birds that have recent negative experience of humans may be expected to show greater responses than those with more mild experiences). Variation may also change systematically with age, especially where older birds can be expected to have longer experience of humans. Finally, a number of recent studies have highlighted the importance of individual 'personalities' in birds (Dingemanse *et al.* 2003), which often refer to correlations between apparently unrelated behavioural traits grouped into behavioural syndromes (Sih *et al.* 2004). For example, an individual that shows a strongly aggressive response to a predator may also show a

strong tendency to disperse greater distances and an increased propensity to inappropriately attack potential mates, than other, less aggressive individuals. In this context, Fowler (1999) reported that Magellanic penguins showed a correlation between a population's average behavioural responses and the average stress response to humans, which suggests that individuals may show similar correlations. It seems plausible, therefore, that the strength of an individual's behavioural response to humans may correlate with the strength of the stress response. Here I attempt to assess the likely contribution of these alternative and complementary factors in determining the heart-rate response (part of the typical vertebrate stress response) of shags *Phalacrocorax aristotelis* to human presence.

METHODS

Shag heart-rates were measured using egg-based telemetry on the Isle of May, Scotland, during May 2004. The heart-rate monitors are described elsewhere (Chapter 6) but, in brief, they measure infra-red reflectance, thereby detecting pulses of blood flowing through the feet of the incubating bird. This telemetry device was housed in a model egg, attached to 100m of cable and was deployed in the nest of target birds. The number of pulses recorded every six seconds was recorded by a datalogger with 52h of memory, which was regularly downloaded without needing to approach the nest. I placed devices in 15 nests with the modal complement of three eggs for 6 days in each nest. When a device was installed I manipulated the number of eggs (including the telemetry device) to a clutch of either 2, 3 or 4 to manipulate the experience of the incubating birds. Surplus eggs were temporarily fostered into nearby nests, being returned to their original nest when the monitors were removed after six days. As I approached the nest to fit the device, I classified the behavioural response of the incubating bird to one of three categories: Defensive (birds did not leave the nest and actively attacked the observer); Mild (birds left the immediate nest site, but remained close by during the fitting and did not attack the observer), or Flighty (birds flew off and away from the nest as the observer approached and did not return until after the observer left). Many shags breeding on the Isle of May are colour ringed and of known age –

whenever a ring on a bird at a target nest was sighted I recorded the ring number and noted the age of the bird.

Once monitors were fitted in the target nests, the birds were left for at least 18 hrs to recover. On subsequent days, I made experimental approaches with either one or two observers to both 70m and 15m from the nests. On each day I made two approaches to all the nests, one to 70m and one to 15m. The distance to which the first approach was made each day was chosen randomly and there was a minimum of 4 hrs between approaches, with one made during the morning and the other in the afternoon. I timed approaches to occur between around 9am and 5pm, throughout the hours when visitors are normally active. Each approach consisted of an observer appearing within view of the nest, walking towards the nest until the appropriate distance was reached, watching for five minutes and then leaving. The exact time (to the nearest second) of each approach was recorded, starting the recording period from the moment the approach began and the target nest was in sight (and therefore the incubating bird could be aware of the observer). Once the required distance was reached, the time was again recorded, and for five minutes the observer stood and observed the nest through binoculars. At the end of the five-minute period the observer left the viewpoint. These times were then identified in the downloaded heart-rate data, and these data and those of the five minutes before the experimental approach, were extracted from the file for analysis. Each approach was numbered (Approach Number) to assess the potential significance of the number of times an individual had been approached before in determining the individual's response. This enabled us to assess whether the responses of birds declined as visits were repeated.

As parents alternate incubation duties or stand over the eggs to turn them, the contact between bird and the telemetry device is lost. This results in values of zero if the monitor remains in the shade or 500 (due to hardware constraints) if direct sunlight shines on the monitor. Six-second periods where contact was made for only some portion of the time give periods intermediate between actual heart-rate and 0 or 500, and can be identified from values in subsequent periods. As shags frequently readjust their position on the eggs after turning, there are numerous

partial records, but very few higher values. I therefore filtered data for heart-rate values outside the normal range of the related South Georgian shag *P. georgianus* (Bevan *et al.* 1997), which the frequency distributions of beats per 6 sec period in this study confirmed to be towards the tail of the distribution (Fig. 1).

Consequently, values equating to heart-rates below 50 or over 400 beats per minute (bpm) were excluded.

Data analysis was carried out in R v 1.8.0 and follow Crawley (2002). For each experimental approach I calculated the average heart-rate over the five minutes before the approach began (the initial rate) and the five minutes when researchers were present at the designated viewpoint (disturbed rate). I subtracted the average initial rate from the disturbed rate, to estimate the average increase in heart-rate caused by the approach. This value was divided by the average initial rate to obtain the relative increase observed for each approach. I used Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM) to assess the effects of the various treatments and measured parameters on both the initial heart-rate and the heart-rate response of the shags. As individual birds were not identified on each approach, these analyses focus of differences between nests, rather than individuals. However, the increases in heart-rate used as data points were estimated within each approach, during which time parents did not change incubation shifts, so the increases in heart-rate are truly individual increases, not differences between partners.

Analysis started by assessing the importance of the nest identity and the order of the visit on the mean response rate. I first assessed whether there was significant variation between nests by building a GLM to predict relative increase in heart-rate using Nest Identity and Approach Number. Having found significant variation in the increases in heart rate between nests ($F_{14,73} = 2.252$, $P = 0.013$), analysis of the correlates of this variation proceeded using GLMMs with Approach Number nested within Nest Identity as random factors. The likelihood of the various factors (Table 1) having significant affects on heart-rate responses were assessed by a standard step-backwards elimination process from a maximal model containing all the main effects and the interaction between distance and number of

observers. I performed this analysis twice: firstly, a complete analysis on the data from the subset of nests for which age was known of at least one parent, and secondly, using data from all nests but not including parental age. Where the age of both parents was known I used the average age, if only one parent was known I used this value, as parental age is usually correlated in the shag (Daunt *et al.* 2001).

As the clutch size manipulations could potentially manipulate the energetic costs of incubation, which may result in increases in metabolic rate, I also assessed the significance of clutch size on initial rate. To do this I built a GLMM with Approach Number (initial heart-rate declined slightly but significantly with Approach Number: $F_{1,84} = 4.748$, $P = 0.032$) nested within Nest Identity as a random factors and clutch size (either decreased to two eggs, maintained at three eggs, or increased to four eggs) as a fixed factor.

RESULTS

I found significant variation among nests in both initial heart-rate (Fig 2a; $F_{14,85} = 2.444$, $P = 0.006$) and relative heart-rate responses to close human proximity (Fig. 2b; $F_{14,85} = 2.252$, $P = 0.012$). There was no significant correlation between individual nests in the average relative heart-rate increase and the average initial heart-rate ($F_{1,13} = 0.242$, $P = 0.631$), so nests attended by birds averaging a high initial heart-rate did not necessarily show greatest increases. By contrast, GLMMs accounting for the repeated measures revealed that within an approach there was a weak, but significant, negative correlation between initial heart-rate and heart-rate increase ($LRT = 7.7$, $df = 1$, $P = 0.006$). Therefore, during approaches where initial heart-rate was high the heart-rate increase associated with human presence was lower than that nest's average. Overall, the average initial heart-rate was 96.6 (s.e. = 4.7) bpm and the average heart-rate during the period of close human proximity was 112.5 (s.e. = 5.6) bpm. Thus, there was similar variation in elevated heart-rates and initial heart-rate ($F_{1,13} = 1.42$, $P = 0.256$).

None of the factors measured was significantly associated with variation in heart-rate response, neither when all data were included, or from the subset of nests

where parental age was known (Table 2). However, for all variables, parameter estimates were wide and also did not provide evidence for accepting the null hypothesis. The effect of the clutch size manipulation was the only parameter approaching significance: the heart-rate showed a slight (but non-significant) tendency to be higher when birds were incubating a reduced clutch. I found no evidence that clutch size manipulations altered the initial heart-rate of incubating birds ($F_{1,13} = 0.002$, $P = 0.967$).

DISCUSSION

As expected, I found considerable individual variation in heart-rate responses to close human presence between shags incubating at different nests. I was not able to identify significant parameters that affect the degree to which shags responded to human presence. Far from meaning that none of these factors affect the stress response of individual shags, I interpret these results as showing that there is much unexplained variation in response, which masks any potential effects of the alternative measures. While my data set is limited, it is clear, however, that, of the factors I measured, no one variable has a very strong association with stress-response. This is perhaps surprising, but a number of factors may affect the strength of any individual signal. One important point is the fact that the measures of heart-rate were not based on individuals, but on nests. Although for some parameters we know that birds of many species generally pair with individuals more similar to themselves than chance would predict (Bridge & Nisbet 2004; Kraaijeveld *et al.* 2004), this is not necessarily general and the differences between members of a pair could add significantly to the variation I recorded. Additional sources of variation include the possibility that my estimates of initial heart-rate may not be accurate estimates of resting rate: if the bird on the nest had recently arrived from a period of exercise the estimate of initial rate would not be the resting rate and any increase due to human presence may be reduced. Evidence for this effect may be found in the small, but significant, negative relationship between relative increase and initial heart-rate.

That there is considerable individual variation in both initial heart-rate and the increases in heart-rate is of interest. Clearly, the identification of correlates of this variation are worthy of further study, both to answer the applied questions concerning disturbance and to further explore the ‘personality’ differences between individuals. Such personality differences need not correlate only with the obvious behavioural traits I have studied here. For example, future studies may seek to quantify the amount of time off-duty birds spend at the nest: as high heart-rate responses lead to increased energetic costs (Chapters 6 & 7), highly sensitive individuals may need more foraging time and consequently spend less time at the nest. There is also individual variation in whether off-duty parents remain near the nest or sit closer to the water, perhaps correlating with some sort of propensity to take risks, which may be correlated with stress-responses to humans. Future studies should also aim to increase the sample size and to use individually identifiable birds to ensure the individual incubating during any one approach can be identified accurately. This could be achieved with minimal disturbance to the birds by, for example, marking one of the members of the pair with a plumage dye visible from a distance (Nimon *et al.* 1996). As body condition is also known to affect the strength of stress response (Astheimer *et al.* 1995; Hood *et al.* 1998; Kitaysky *et al.* 1999), some measure of condition may also be considered. If this is attempted, it is important that this be done after measurement of heart-rate to ensure the birds do not learn to associate the researcher with this procedure. If studying the variation in initial heart-rate, it would be beneficial to control for the effects of body size: a feature often correlated with heart-rate in animals (Kuikka 2003). In the light of these results, therefore, it is perhaps wisest to consider the current study only a trial, highlighting some of the difficulties and considerations that future studies should address.

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Table 1. Factors potentially correlated with the heart-rate response of shags to humans and the method described here used to assess the importance of each factor.

Type	Factor	Method
Extrinsic	Distance to observer	Distance to which experimental approaches were made were alternated between 15m and 70m
	Number of observers	Experimental approaches were made by either 1 or 2 observers.
Intrinsic	Previous experience of people: frequency	Repeated approaches were made to each nest and analysis examined whether response waned with approach number.
	Previous experience: intensity	When telemetry device was installed, nests contents were manipulated to clutches of 2, 3 or 4: birds with smaller clutches may associate humans with partial nest predation.
	Age	All birds that were colour-ringed were individually identified and the average age of the pair, where known, used for analysis.
	Behavioural response	On installation of the telemetry device the behavioural response of the birds to the observer was recorded for analysis.

Table 2. Results of backward-stepping elimination of variables from GLMMs predicting relative increase in heart-rate in shags. Variables eliminated are presented in order of removal. Two analyses are presented: one using data from all nests but not incorporating Age, the other a complete analysis using data only from nests where age was known for at least one parent. In both cases, random variables were Approach Number nested within Nest Identity.

Analysis	Variable eliminated	<i>df</i>	<i>LRT</i>	<i>P</i>
Excluding Age, based on data from all nests	Behaviour	2	0.519	0.772
	Distance x Number interaction	1	0.873	0.350
	Distance	1	0.237	0.627
	Clutch	1	1.077	0.300
	Number	1	1.945	0.163
Including Age, based on a subset of nests	Distance x Number interaction	1	1.273	0.259
	Distance	1	0.109	0.741
	Number	1	0.514	0.473
	Clutch	1	3.529	0.060
	Behaviour	2	4.087	0.130
	Age	1	1.372	0.241

FIGURE LEGENDS

FIGURE 1.

Typical frequency distribution of the number of heart beats in six second periods recorded for four shags.

FIGURE 2.

(a) Mean (\pm S.E.) heart-rate (bpm) in shags. (b) Mean (\pm S.E.) relative increase in shag heart-rate associated with close human presence.

FIGURE. 1

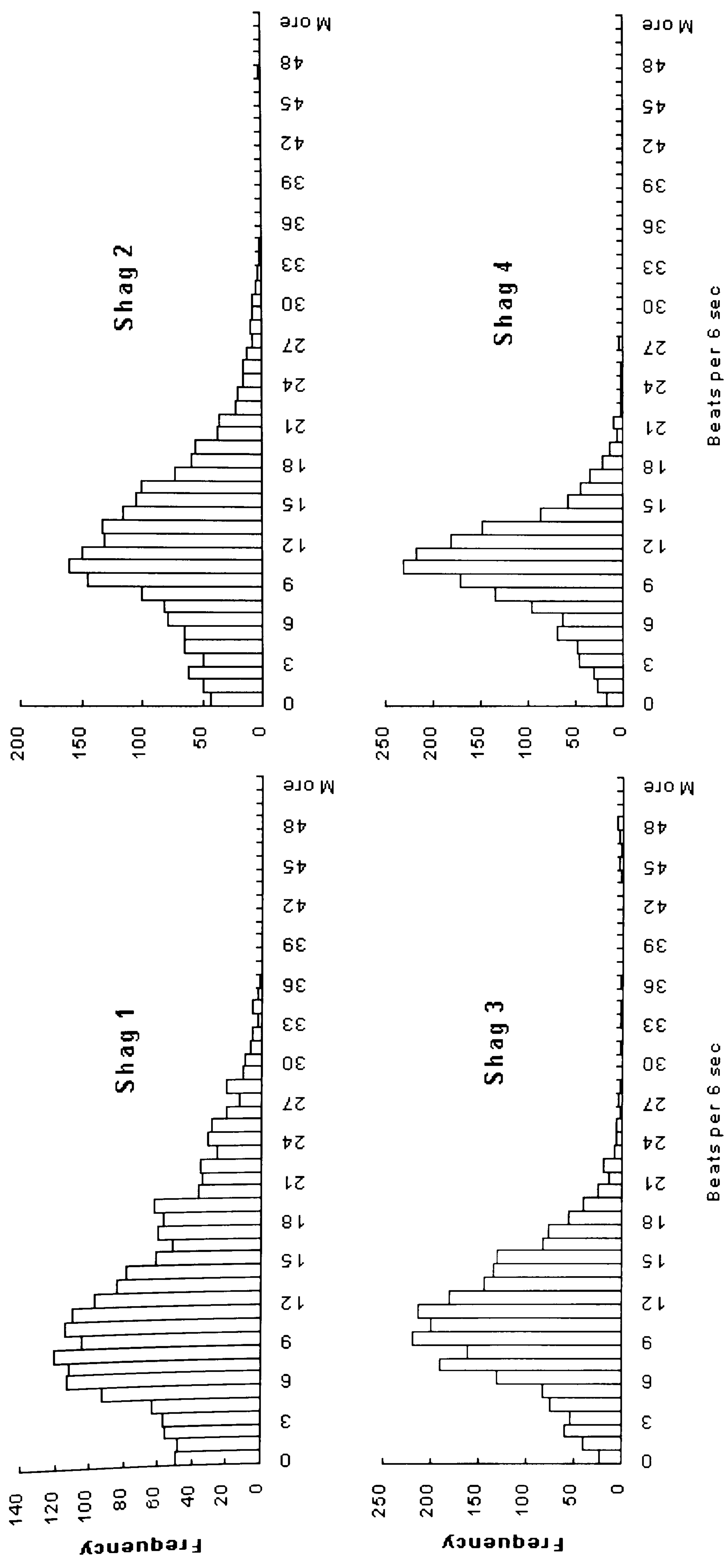
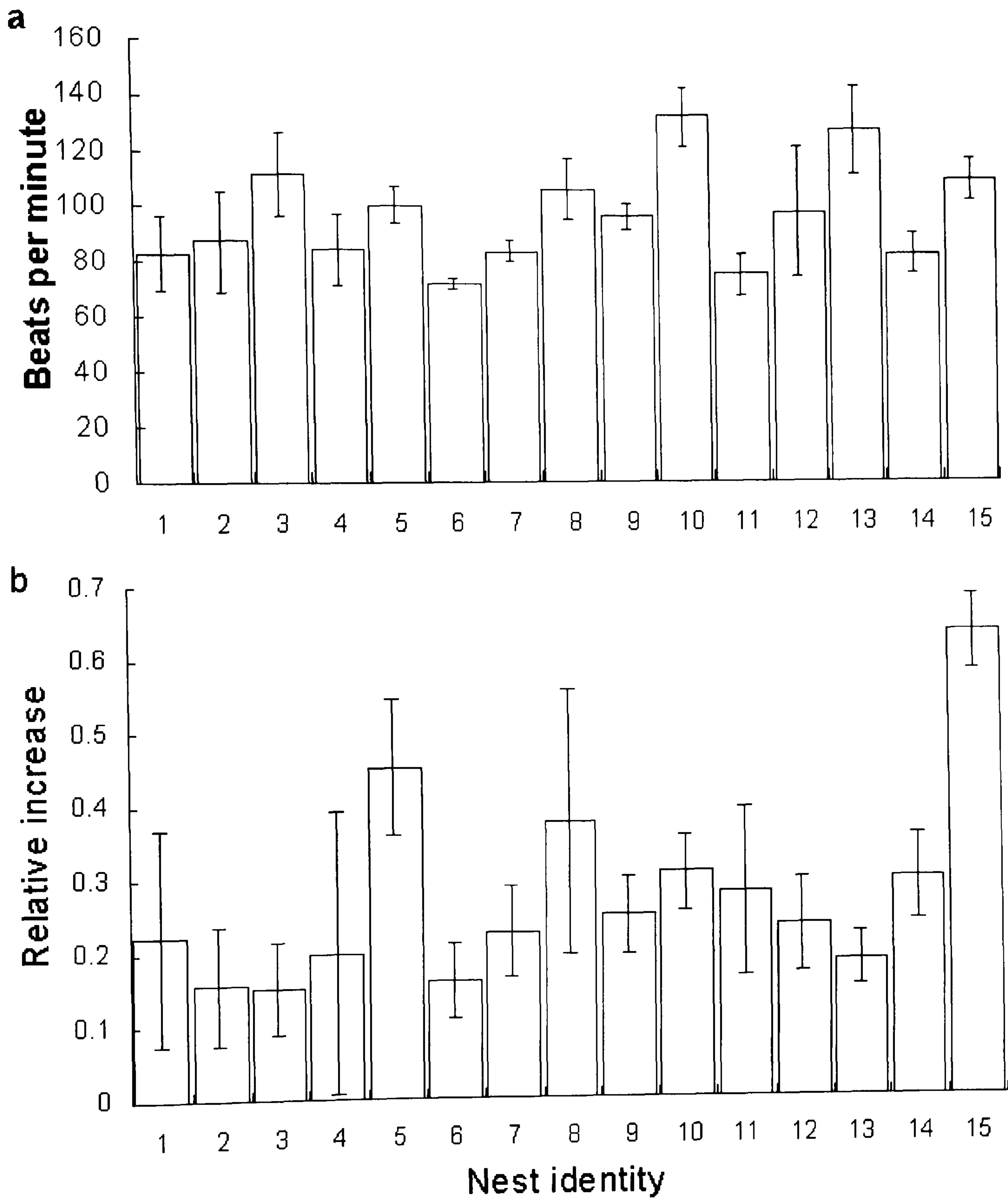


FIGURE 2



CHAPTER 9

General discussion and conclusions

A number of issues affecting our understanding of the effects of human disturbance have been addressed in this thesis. In summary, I have repeatedly shown that behavioural measures of disturbance can be misleading and potentially lead to inappropriate management (Chapters 2, 6, 7 & 8). Despite this, I showed in chapters 3, 5 and 6 that human disturbance can have impacts that could be of conservation concern. In chapters 6, 7 and 8 I showed how changes in heart-rates could underlie declines in breeding success and in chapter 3 I suggested that human disturbance may best be understood as a form of unrealised predation risk. All these findings have applications for visitor management: set-back distances are shown to be inappropriate management tools (Chapters 2, 3 & 6) and I suggest alternatives involving management of visitor numbers and distribution in chapters 3, 4 and 5. Throughout this thesis I have discussed specific conclusions in each chapter. Here, therefore, I seek not to repeat these discussions but to focus instead on drawing these results together to form a general picture of disturbance effects and to discuss these results in a wider context.

As others have reported before, I found that human disturbance can reduce breeding success in birds (Chapter 3; de la Torre *et al.* 2000; Fortin & Andruskiew 2003; Ikuta & Blumstein 2003). However, it is necessary to stress again the distinction between human disturbance effects and human impacts. It is just as important to question whether the declines in nesting success that I found reflect an impact of genuine conservation concern, as it is to question whether behavioural responses necessarily have fitness costs. I noted in Chapter 1 that breeding success is not necessarily a good surrogate of fitness thanks in part to density dependent effects (Olijnyk & Brown 1999; Frederiksen *et al.* 2001). Moreover, there is ample evidence to suggest that breeding success is far less important in determining seabird population trends than winter mortality (Weimerskirch *et al.* 1996; Russell 1999). A decrease in breeding success of 9% is, in fact, unlikely to have a major impact on the population as a whole, although there is an undeniable animal welfare issue here. It is possible, therefore, that disturbance is less of a conservation concern than an animal welfare issue, with individual birds suffering from the effects of stress and some chicks dying but effects not necessarily feeding into population declines. In general, however, to concentrate conservation efforts on

human disturbance during the breeding season but to ignore the fundamental effects of changes in adult survival would be futile.

In the specific case of the declines in breeding success I found associated with human disturbance in the kittiwake *Rissa tridactyla* and guillemot *Uria aalge*, I believe that human disturbance is probably not a major concern. Indeed, I believe it is better to allow visitor access to the wonderful sights, sounds and smells of a busy seabird colony and thereby engender an empathy with conservation concerns, than it is to attempt to restrict access and maximise the breeding success of the birds in question if the costs are, as here, acceptably small. However, it is clear that species differ greatly in their responses to disturbance, and it is therefore likely that they also differ in the impact human disturbance has upon them. In particular, for species where it is believed that a decline in nesting success is likely to be responsible for any population declines (e.g. Lapwings *Vanellus vanellus* (Peach *et al.* 1994)), then it is clearly critical that additional impacts of human disturbance are assessed and, if necessary, ameliorated. Furthermore, it is quite possible that disturbance impacts are not limited to the breeding season, though such impacts are probably less common than initial readings of the literature may suggest.

During the course of this thesis a number of management recommendations have been made, and it would be useful to bring these together to build a complete picture of the available management options. Firstly, I note that the current use of fixed set-back distances is likely to be unsound (Chapters 2, 3, 6 & 8). As these are usually fixed by reference to an approach by one or two researchers (Rodgers & Schwikert 2002; Blumstein *et al.* 2003; Fernández-Juricic *et al.* 2004), they are likely to be set well short of safe distances when groups of tourists approach. It might be possible to simply move set-back distances further away when disturbance effects are noticed at greater distances (Fernández-Juricic *et al.* 2001), and I have shown that this is likely to work for kittiwakes and guillemots (Chapter 3). However, this is not always practicable: for example, in some seabird colonies birds on the cliff face may only be visible when visitors are right on the cliff top. Furthermore, my measurement of individual variation in heart-rate response to humans (Chapters 7 & 8) suggests that as long as people are in sight, some

susceptible birds will suffer significant impact. If we want to minimise overall impact, therefore, we would be better not setting strict daily visitor caps, but providing the wildlife with visitor free periods (Chapters 5, 6 & 7). Such methods are already in place in some nature reserves (Harris & Wanless 1995, UNESCO 1974), but the efficacy of such measures had not been widely studied previously. Within these recommendations, I have also provided guidelines that allows managers of seabird colonies to decide whether to limit visitor access to some areas or by encouraging an even spread of visitors throughout the reserve (Chapter 4). I showed that as visitor numbers in a reserve increase, the best strategy of management may change, although there are welfare and ethical issues associated with such management that should be addressed. For the reserve at St Abbs Head, for example, the effect of human disturbance could be reduced without necessarily reducing the total number of visitors present each year by limiting the number of visitors each day; by allowing their access only for limited periods of the day, and by encouraging an even spread of visitors throughout the reserve.

Although this thesis concentrates entirely on the effects of disturbance on birds, it would be useful to compare the results I report for birds with the far fewer studies in other taxa (mostly mammals). If the limited data are available for other taxa are similar, whilst (as in birds) responses of individual species may differ in magnitude, overall conclusions may be similar and offer a short cut to management guidelines for these taxa. Firstly, it is worth noting that as in birds much of the research that has been published relates to behavioural responses to disturbance (Walther 1969; Gander & Ingold 1997; de la Torre *et al.* 2000; Shirley *et al.* 2001; Engelhard *et al.* 2002; Fairbanks & Tullous 2002; Johnson 2002; Mann *et al.* 2002; Williams *et al.* 2002; Zeng *et al.* 2002; Fortin & Andruskiew 2003; Frid 2003; Lusseau 2003; Petram *et al.* 2003; Stevens & Boness 2003; Altrichter & Boaglio 2004; Dyck & Baydack 2004; Nowacek *et al.* 2004). Although there has been no direct test of the idea in other taxa, the suggestion that perceived predation risk underlies disturbance effects is not specific to birds and has recently been recognised by a few researchers working with other taxa (Frid & Dill 2002; Williams *et al.* 2002). Very little has been published assessing other impacts of disturbance on animals other than birds, but the few that are published report

similar disparate effects. For example, disturbance has been shown to reduce growth rates and body condition in baboons (Altmann *et al.* 1993), though not in southern elephant seals *Mirounga leonina* (Engelhard *et al.* 2002). There is some evidence that red squirrel *Sciurus vulgaris* survival can be affected by human presence (Wauters *et al.* 1997) and a few studies also report on stress responses of other animal taxa (MacArthur *et al.* 1982; Millspaugh *et al.* 2001; Romero & Wikelski 2002). Although the data are very limited, therefore, the overall patterns reported for taxa other than birds are similar to those found in this thesis and other ornithological research. It is therefore reasonable to assume that the conclusions I reach here are of interest to managers of all animal groups.

It would also be useful to use the understanding developed to generate ‘rules of thumb’ that may help us assess the likely impact of human disturbance on a declining species of unknown susceptibility to disturbance. Are there, for example, any life-history or behavioural traits that might be correlated with likely impact of human disturbance? The first such consideration must be, as already stated, the question of whether it is known that declines in breeding success are the cause of any observed decline in population. If declines are not due to changes in breeding success, then the only impacts of conservation importance that human disturbance may have must be in the non-breeding season. In such cases, I recommend that if an impact is suspected, careful use of resource-based models be used to assess the nature of this impact (Gill *et al.* 1996). If it is not known whether the decline in population is mediated by changes in breeding success or changes in survival, then consideration of possible impacts of human disturbance during the breeding season must be considered.

An understanding of general life-history trade-offs reveals that population declines in long-lived species are most likely to be caused by changes in survival, whereas short-lived animals are more susceptible to the effects of changes in breeding success (Trivers 1972; Russell 1999; Coulson & Hudson 2002; Crook *et al.* 2003). Moreover, for the majority of species where the causes of declines are known, annual survival of adults or independent young seems to be the key variable (Weimerskirch 1996; Russell 1999; Heppell *et al.* 2000). Only in certain, probably

unusual, circumstances are declines in breeding success the cause of population change. This assertion is backed up by the observation that in birds the population effects of the deliberate destruction of nest contents as part of population control measures are often more than compensated for by density dependent mortality (Olijnyk & Brown 1999; Frederiksen *et al.* 2001). It is, therefore, perhaps most likely that significant impacts of disturbance may only be found on mortality rates during the non-breeding season, when the impact of disturbance is hardest to accurately measure. However, it is also possible that non-lethal impacts during the breeding season will carry over into an impact on winter mortality. For example, Great Skuas marked with satellite transmitters showed only minor changes to behaviour and breeding success in the summer, but subsequently suffered far higher winter mortality than control birds (J. Crane, pers. com.). Further work investigating the links between disturbance and mortality rates would be useful, although there are considerable practical problems associated with this work; not least the level of accuracy of measurement of survival rates needed to ensure good statistical power (Hatch 2003).

Whilst most population declines seem to be driven by changes in mortality rates rather than breeding success, there are further generalisations to be made about the impact of disturbance on breeding success if we know basic life-history parameters. For example, once a long-lived bird such as a kittiwake starts breeding, it can probably expect to survive around 15 breeding seasons (Oro & Furness 2002). In each season it will probably make one nesting attempt, though some birds that fail very early in the season may re-lay if there is time. Still, each nesting attempt therefore represents only around one fifteenth of the total breeding effort of the average breeding individual. By contrast, a small passerine such as the Florida grasshopper sparrow *Ammodramus savannarum floridanus* typically has an adult annual survival probability of only 50% (Perkins & Vickery 2001), though two or three nesting attempts may be made each season. Being generous in the calculation, therefore, the average number of nesting attempts per adult bird may be around four, so each attempt represents one quarter of the total breeding effort of that bird. It is instantly clear that each nesting attempt for a small lived bird is significantly more valuable than it is for a longer-lived species. It is clearly more sensible for a

long-lived animal to sacrifice a breeding attempt in favour of maximising its chances of breeding successfully the next year than it would be for a shorter-lived species, which is not particularly likely to survive to the next year. I therefore predict that changes in breeding success associated with disturbance will correlate with average lifespan, and that disturbance impacts on short-lived species are probably minimal. Unfortunately, even in the ornithological literature there are so far few studies showing the impact of human disturbance on shorter-lived species, making this prediction as yet untestable. However, preliminary unpublished results from three ongoing studies (in the woodlark *Lullula arborea*, the Dartford warbler *Sylvia undata* and the twite *Carduelis flavirostris*) apparently show the expected pattern of minimal impact. It is worth noting, therefore, that the impacts of disturbance on long-lived animals such as the kittiwakes and guillemots studied in this thesis were not considered to be of conservation concern, so smaller impacts than these are even less likely to be important. Consequently, it is possible that with only certain rare exceptions the literature over-emphasises the effects of disturbance on wildlife and suggested management practices are often overly restrictive.

In all the results, conclusions and management recommendations of this thesis, it is clear that many questions of conservation interest should be approached from an understanding of animal behaviour. Knowing how animals respond to predation risk gives us important insights into the likely fitness consequences of human disturbance and suggests possible management options that are not immediately obvious if addressed without reference to behaviour. An understanding of the significance of differing life-histories on the decisions made by individual animals can help us predict how species are likely to respond to disturbance even if there are few data available about these species. And understanding that animals are individuals that make context-dependent decisions, rather than being an abstract average or 'ideal' bird, helps us recognise that management appropriate for the average individual will not help all the population. The recognition that understanding animal behaviour is important for conservation is not new, but is only slowly being acted upon (Sutherland 1998). Research on the effects of human disturbance is slowly taking account of the need to understand behaviour (Stillman *et al.* 2000; Gill *et al.* 2001; Fernández-Juricic *et al.* 2003), though papers continue

to be published that overlook decision-making behaviour (Frid 2003; Fortin & Andreskiew 2003; Fernández-Juricic *et al.* 2004). Consequences of individual decision making behaviour are also being recognised in other areas of conservation science; for example, decisions about how and when to migrate appear to be critical to understanding how different species respond to climate change (Drent *et al.* 2003). If animal conservation is to be based upon a sound scientific basis, rather than a superficial overview of the obvious, it is vital that these behavioural insights are more widely recognised within conservation science. Another area where such research may prove particularly fruitful involves the decisions animals make when recruiting into populations. If healthy populations are to be maintained within nature reserves, the processes driving immigration and emigration must be understood. Similarly, decisions involved in mate selection may be important in determining the viability of small populations. Such areas are largely neglected within conservation science, but an understanding of these processes may offer insights of practical importance. Ultimately, therefore, this thesis illustrates some of the mistakes that can be made in the absence of a sound understanding of decision making behaviour, and conversely some of the practical insights that can be gained from such an approach. I therefore urge more behavioural ecologists to consider applied conservation questions within their work.

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