

Human disturbance: people as predation-free predators?

COLIN M. BEALE and PAT MONAGHAN

Division of Environmental and Evolutionary Biology, Institute for Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK

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 minimizing 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, kittiwake *Rissa tridactyla* and guillemot *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.

Key-words: breeding success, guillemot *Uria aalge*, kittiwake *Rissa tridactyla*, predation risk, visitor access, visitor management

Journal of Applied Ecology (2004) **41**, 335–343

Introduction

Conservationists have long been concerned about the effects of human disturbance on wildlife (Carney & Sydean 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 (Carney & Sydean 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

Correspondence: C. Beale, Division of Environmental and Evolutionary Biology, Institute for Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK (e-mail 0102627b@student.gla.ac.uk).

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 minimize 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 realized.

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 humans 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; Sandvik & Barrett 2001).

Methods

Data were collected from 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 maximize 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 that 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

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 20 cm (guillemots) or 2 m (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

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 SD, 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 a 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 the relative perceived predation risk, if humans are perceived as predators.

STATISTICAL ANALYSIS

Statistical analysis follows procedures and recommendations from Crawley (1993, 2002). Programs 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 first 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's 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

Table 2. Minimum adequate model predicting nesting success in kittiwakes. B = parameter estimate

Parameter	Nesting success		
	B	SE	P
Mean deviance	0.89		
Date (D)	0.000	0.000	0.063
Sides (S)	-82.100	37.600	0.029*
Mainland (M)	826.700	428.200	0.054
Site height (SH)	4.220	1.830	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	-14.500	7.100	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**

* $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$.

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 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, while halving the visitor levels resulted 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

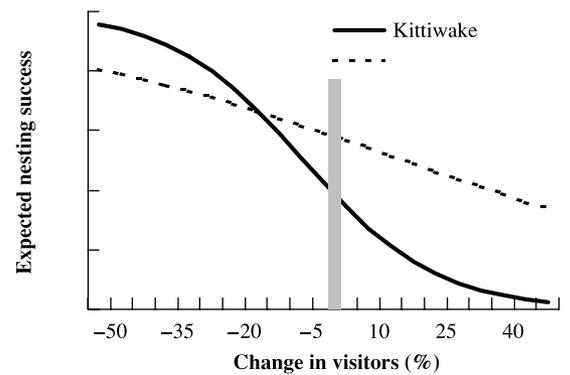


Fig. 1. The overall relationships identified between human disturbance and nesting success in kittiwakes and guillemots at St Abbs Head National Nature Reserve, Scotland. Shaded bar represents current visitor numbers.

Table 3. Minimum adequate models predicting nesting success in guillemots. B = parameter estimate

Parameter	Nesting success		
	B	SE	P
Mean deviance	0.86		
Date (D)	0.0003	0.000	0.004**
Walls (W)	1.005	0.347	0.004**
Mainland (M)	341.00	11.900	0.004**
Neighbours (N)	-17.400	7.170	0.016*
Gradient (G)	-18.700	9.060	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	18.400	7.840	0.019*
FW × SH × G	-0.013	0.004	0.002**
D × N × G	-0.493	0.210	0.019*

* $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$.

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 was 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, while 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 the average distance 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 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. a 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, although 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 (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 standardized disturbance regime and measuring the distance at which a bird shows a behavioural response (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. In 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 reassessed in the light of changing visitor numbers, or that visitor numbers should be strictly capped if effects are to be minimized.

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 minimize 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.

Acknowledgements

We thank the National Trust for Scotland for access to St Abbs Head National Nature Reserve and particularly to Kevin Rideout for help with the logistics of working at this site. Scottish Natural Heritage approved research proposals for working within the National Nature Reserve. Thanks are also due to Victoria Beale and numerous members of the public for assistance with fieldwork, and to Chris Knight, Lukas Keller and Adrian Bowman for assistance with statistical analysis. Colin Beale was supported by a scholarship from the University of Glasgow for the duration of this project.

References

- Abrams, P.A. (1993) Why predation rate should not be proportional to predator density. *Ecology*, **74**, 716–733.
- Birkhead, T.R. & Nettleship, D.N. (1987) Ecological relationships between common murres, *Uria aalge*, and thick-billed murres, *Uria lomvia*, at the Gannet Islands, Labrador. II. Breeding success and site characteristics. *Canadian Journal of Zoology—Revue Canadienne de Zoologie*, **65**, 1630–1637.
- Blumstein, D.T., Anthony, L.L., Harcourt, R. & Ross, G. (2003) Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation*, **110**, 97–100.
- Bolduc, F. & Guillemette, M. (2003) Human disturbance and nesting success of common eiders: interaction between visitors and gulls. *Biological Conservation*, **110**, 77–83.
- Boulinier, T. & Danchin, E. (1996) Population trends in kittiwake *Rissa tridactyla* colonies in relation to tick infestation. *Ibis*, **138**, 326–334.
- Cadiou, B. & Monnat, J.Y. (1996) Parental attendance and squatting in the kittiwake *Rissa tridactyla* during the rearing period. *Bird Study*, **43**, 164–171.
- Carney, K.M. & Sydeman, W.J. (1999) A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds*, **22**, 68–79.
- Coulson, J.C. & Johnson, M.P. (1993) The attendance and absence of adult kittiwakes *Rissa tridactyla* from the nest-site during the chick stage. *Ibis*, **135**, 372–378.
- Coulson, J.C. & Porter, J.M. (1985) Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth-rates and parental quality. *Ibis*, **127**, 450–466.
- Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publishing, Oxford, UK.
- Crawley, M.J. (2002) *Statistical Computing. An Introduction to Data Analysis Using S-Plus*. Wiley, New York, NY.
- Falk, K. & Møller, S. (1997) Breeding ecology of the fulmar *Fulmarus glacialis* and the kittiwake *Rissa tridactyla* in high-arctic northeastern Greenland, 1993. *Ibis*, **139**, 270–281.
- Feare, C.J. (1976) The breeding biology of the sooty tern *Sterna fuscata* L. in the Seychelles, and the effect of the experimental removal of its eggs. *Journal of Zoology, London*, **179**, 317–360.
- Fowler, G.S. (1999) Behavioural and hormonal responses of magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitations. *Biological Conservation*, **90**, 143–149.
- Frid, A. & Dill, L.M. (2002) Human caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 11 [online <http://www.consecol.org/vol6/iss1/art11>].
- Fyhn, M., Gabrielsen, G.W., Nordoy, E.S., Moe, B., Langseth, I. & Bech, C. (2001) Individual variation in field metabolic rate of kittiwakes (*Rissa tridactyla*) during the chick-rearing period. *Physiological and Biochemical Zoology*, **74**, 343–355.
- Gander, H. & Ingold, P. (1997) Reactions of male chamos *Rupicapra r. rupicapra* to hikers, joggers and mountainbikers. *Biological Conservation*, **79**, 107–109.
- Giese, M. (1996) Effects of human activity on Adélie penguin *Pygoscelis adeliae* breeding success. *Biological Conservation*, **75**, 157–164.
- Giese, M. (1998) Guidelines for people approaching breeding groups of Adélie penguins (*Pygoscelis adeliae*). *Polar Record*, **34**, 287–292.
- Gill, J.A., Norris, K. & Sutherland, W.J. (2001) Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**, 265–268.
- Golet, G.H. & Irons, D.B. (1999) Raising young reduces body condition and fat stores in black-legged kittiwakes. *Oecologia*, **120**, 530–538.
- Golet, G.H., Irons, D.B. & Costa, D.P. (2000) Energy costs of chick rearing in black-legged kittiwakes (*Rissa tridactyla*). *Canadian Journal of Zoology—Revue Canadienne de Zoologie*, **78**, 982–991.
- Götmark, F. (1992) The effects of investigator disturbance on nesting birds. *Current Ornithology*, **9**, 63–104.
- Harris, M.P. & Wanless, S. (1995) *Impacts of Visitors on Breeding Seabirds on the Isle of May National Nature Reserve*. Report to Scottish Natural Heritage. Institute of Terrestrial Ecology (NERC), Banchory.
- Harris, M.P., Wanless, S., Barton, T.R. & Elston, D.A. (1997) Nest site characteristics, duration of use and breeding success in the guillemot *Uria aalge*. *Ibis*, **139**, 468–476.
- Hatchwell, B.J. (1991) An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*). *Journal of Animal Ecology*, **60**, 721–736.
- Higham, J.E.S. (1998) Tourists and albatrosses: the dynamics of tourism at the Northern Royal Albatross Colony, Taiaroa Head, New Zealand. *Tourism Management*, **19**, 521–531.
- Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R. & Treweek, J. (1997) Bird disturbance: improving the quality and utility of disturbance research. *Journal of Applied Ecology*, **34**, 275–288.
- Lafferty, K.D. (2001) Disturbance to wintering western snowy plovers. *Biological Conservation*, **101**, 315–325.
- Lord, A., Waas, J.R., Innes, J. & Whittingham, M.J. (2001) Effects of human approaches to nests of northern New Zealand dotterels. *Biological Conservation*, **98**, 233–240.
- Maccarone, A.D. (1992) Predation by common ravens on cliff-nesting black-legged kittiwakes on Baccalieu Island, Newfoundland. *Colonial Waterbirds*, **15**, 253–256.
- Madsen, J. & Fox, A.D. (1995) Impacts of hunting on waterbirds: a review. *Wildlife Biology*, **1**, 193–207.
- Massaro, M., Chardine, J.W. & Jones, I.L. (2001) Relationships between black-legged kittiwake nest site characteristics and susceptibility to predation by large gulls. *Condor*, **103**, 793–801.
- Murphy, E.C. & Schauer, J.H. (1994) Numbers, breeding chronology, and breeding success of common murres at Bluff, Alaska, in 1975–1991. *Canadian Journal of Zoology—Revue Canadienne de Zoologie*, **72**, 2105–2118.
- Murphy, E.C. & Schauer, J.H. (1996) Synchrony in egg-laying and reproductive success of neighboring common murres, *Uria aalge*. *Behavioral Ecology and Sociobiology*, **39**, 245–258.
- Nimon, A.J., Schroter, R.C. & Stonehouse, B. (1995) Heart rate of disturbed penguins. *Nature*, **374**, 415.
- Nisbet, I.C. (2000) Disturbance, habituation and management of waterbird colonies. *Waterbirds*, **23**, 312–332.
- Olsthoorn, J.M.C. & Nelson, J.B. (1990) The availability of breeding sites for some British seabirds. *Bird Study*, **37**, 145–164.
- Parrish, J.K. (1995) Influence of group size and habitat type on reproductive success in common murres (*Uria aalge*). *Auk*, **112**, 390–401.
- Regehr, H.M., Rodway, M.S. & Montevecchi, W.A. (1998) Antipredator benefits of nest-site selection in black-legged kittiwakes. *Canadian Journal of Zoology—Revue Canadienne de Zoologie*, **76**, 910–915.
- Rodgers, J.A. & Smith, H.T. (1995) Set-back distances to protect nesting bird colonies from human disturbance in Florida. *Conservation Biology*, **9**, 89–99.
- Sandvik, H. & Barrett, R.T. (2001) Effect of investigator disturbance on the breeding success of the black-legged kittiwake. *Journal of Field Ornithology*, **72**, 30–42.
- Silverin, B. (1986) Corticosterone binding proteins and behavioural effects of high plasma levels of corticosterone during the breeding period in the pied flycatcher. *General and Comparative Endocrinology*, **64**, 67–74.
- Sutherland, W.J. & Crockford, N.J. (1993) Factors affecting the feeding distribution of red-breasted geese *Branta ruficollis* wintering in Romania. *Biological Conservation*, **63**, 61–65.

- Thomson, D.L., Furness, R.W. & Monaghan, P. (1998) Field metabolic rates of kittiwakes *Rissa tridactyla* during incubation and chick rearing. *Ardea*, **86**, 169–175.
- Wanless, S. & Harris, M.P. (1988) The importance of relative laying date on breeding success of the guillemot *Uria aalge*. *Ornis Scandinavica*, **19**, 205–211.
- Wauters, L.A., Somers, L. & Dhondt, A.A. (1997) Settlement behaviour and population dynamics of reintroduced red squirrels *Sciurus vulgaris* in a park in Antwerp, Belgium. *Biological Conservation*, **82**, 101–107.
- Wilson, R.P. & Culik, B. (1995) Penguins disturbed by tourists. *Nature*, **376**, 30–302.

Received 27 August 2003; final copy received 18 December 2003