Impact of visitor disturbance on Atlantic puffins and Arctic terns breeding on the Isle of May

Final report to Scottish Natural Heritage

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Contents

Executive summary

- Encouraging human access to wildlife areas is a key element of generating public support for nature conservation, and has educational and economic benefits. However, human presence also causes disturbance which has a range of negative effects on wildlife. To resolve this conflict successfully, conservation practitioners need to devise appropriate visitor access strategies. This requires quantifying the impact of different visitor regimes on the population of interest.
- The effects of disturbance from recreational activities on key demographic rates, such as breeding success, are usually mediated via behavioural or physiological changes. To establish whether these changes at the individual level translate into detectable changes at the population level, we need to quantify the link between the disturbance effect and behaviour/physiology; the effect of changes in behaviour/physiology on the particular demographic rate, and the consequences of change in the demographic rate for population size.
- The aim of this study was to quantify the impact of visitor disturbance on breeding success of two seabird species, Atlantic puffin (*Fratercula arctica*) and Arctic tern (*Sterna paradisaea*) on the Isle of May NNR. To achieve this we developed a model estimating the disturbance effect on breeding success, mediated via changes in chick provisioning rates and chick body mass. The model compared peak chick mass and survival probability (as a measure of breeding success) in the absence of visitors with those in the presence of visitors under different scenarios of varying visitor numbers, and visit durations and timings.
- Five main disturbance scenarios were explored: a baseline (no visitors present); current visitor numbers and duration of visit; current visitor numbers, doubled duration of visit; doubled visitor numbers, current duration of visit and doubled visitor numbers and duration of visit. Within each scenario the timing of the boat visit was varied over the course of the day (between 9a.m. and 8p.m). In puffins there were also 8 different disturbance levels based on the distance from paths and the intensity of path usage by visitors.
- With the exception of birds nesting in the vicinity of visitor hotspots (within 10m of locations where people spend substantial amount of time), puffin provisioning rates and breeding success were little affected by the current or increased visitor disturbance levels. However, in the vicinity of the visitor hotspots, breeding success of puffins was reduced by 10 to 28% (percentage points) under the different disturbance scenarios. Effects on population-level breeding success were relatively small (1.7% decline was recorded under the highest disturbance scenario), due to a very small proportion of the population being heavily disturbed.
- Arctic terns were highly susceptible to human disturbance. In the presence of visitors parents reduced their provisioning rate by nearly 50% compared to times when visitors were absent. Under the current visitor regime, this reduction was associated with *ca*. 10% decrease in breeding success in disturbed birds. Further increasing visitor pressure resulted in substantial reduction in breeding success, by up to 79% under the highest disturbance scenario (doubled visitor numbers and duration of visit). The current visitor levels were associated with a 5% reduction in population-level breeding success. Further

increasing visitor pressure would have a more substantial impact, with a decline of 32% recorded under the highest disturbance scenario.

- In conclusion, increasing both the number of visitors and duration of stay on the island compared to the current situation had a strong negative impact on breeding success of the tern population and of a small fraction of the puffin population that breeds in the vicinity of visitor hotspots. Such a visitor regime is therefore undesirable. Of the remaining scenarios, increasing visitor numbers had a lower impact on breeding success than increasing the duration of stay on the island. Within the visitor timings we explored, the highest disturbance effect in both species was observed in late afternoon/evening, when visitor presence coincided with the evening peak in chick provisioning activity. However, if visitor hours were altered to cover the larger morning peak of activity, the impact of disturbance on breeding success would be stronger. If visitor access to the Isle of May is increased in the future, increasing visitor numbers but restricting visitor hours between 9 a.m. and 5 p.m. (outside the peak times of chick provisioning), and maintaining duration of visits at the current level (3 hours) could help reduce the impact of disturbance on both species.

1. Introduction

1.1. Background

Human access to wildlife areas is being increasingly encouraged as it enhances the public appreciation and support for nature conservation (Bogner, 1998; Gill, 2007), and can generate economic benefits (Gray et al., 2003). However, human disturbance has a number of negative effects on wildlife, such as preventing successful breeding (Boellstorff et al., 1988; Giese 1996) or restricting access to preferred feeding areas (Gander & Ingold 1997; Velando & Munilla, 2011). To resolve this conflict successfully and achieve sustainable management of protected sites, conservation practitioners need to devise appropriate visitor access strategies. A crucial step towards achieving this goal is to quantify the impact of different visitor regimes on the population in question.

Reduction in adult survival and breeding success are often seen as the key criteria when assessing whether a population is being adversely affected by human disturbance (Nisbet, 2000). However, recreational activities are relatively rarely a direct cause of adult mortality or breeding failure. Rather, their effects are typically indirect, mediated via behavioural or physiological changes such as reduced feeding rates or increased stress levels and energy expenditure (e.g. Regel and Pütz, 1997; Fowler, 1999; McClung et al., 2004). Such changes, however, should not be ignored as they can reduce individual fitness and eventually have population-level consequences.

To establish whether behavioural and physiological changes in individual birds translate into detectable changes in population size we need to quantify: 1) the link between the disturbance effect and behaviour and/or physiology; 2) the effect of changes in behaviour/physiology on demographic rates (breeding success; survival), and 3) the consequences of these changes in demographic rates for population size. Links between disturbance effects and behaviour or physiology can be addressed with empirical studies and bioenergetic modelling (Williams et al., 2006), while population modelling is a well-established approach for estimating changes in population size from changes in demographic rates (e.g. Caswell, 2001). However, translating changes in behaviour and physiology into changes in demographic rates (such as breeding success) is challenging due to the difficulty in collecting empirical data.

Managing visitor access to seabird colonies is important because large numbers of people visit the birds at their nesting grounds when they are particularly vulnerable to disturbance (Harris & Wanless, 1995; Nisbet, 2000). When approached, they often take flight, leaving the nest contents exposed to predation or the elements (Carney & Sydeman, 1999), or are prevented from provisioning their chicks. Repeated disturbance is likely to increase energetic costs due to frequent flights (when the birds are flushed), heightened vigilance or reduced prey delivery to the young. The magnitude and relative importance of disturbance effects can differ among species in relation to their breeding ecology. Furthermore, the level of disturbance depends on the number of visitors, their spatial distribution and distance to the nesting birds (Beale & Monaghan, 2004; Beale, 2007). However, the effects of human disturbance on seabird behaviour and physiology, and the knock on effect on breeding success, are relatively poorly understood. As a result, the population-level impact of disturbance is largely unknown, despite the relevance to informing appropriate visitor management strategies.

1.2. Project aim

The aim of this project is to quantify the impact of visitor disturbance on two protected seabird species with different breeding ecology, Atlantic puffin *Fratercula arctica* (burrow nester) and Arctic tern *Sterna paradisaea* (ground nester) breeding on the Isle of May NNR. To achieve this aim we developed a mathematical model estimating the effects of visitor disturbance on breeding success, mediated via changes in chick provisioning rates and chick body mass. We used a combination of empirical data from CEH's long-term study on the Isle of May and published literature to parameterise the model. The model compared peak chick mass and survival probability (as our measure of breeding success) in the absence of visitors with those in the presence of visitors under different scenarios of varying visitor numbers and visit durations and timings. This approach will allow SNH to assess potential impacts on seabird breeding success of these different options.

2. Methods

2.1. Modelling framework

The effects of visitor disturbance on breeding success were estimated in the following way:

1) <u>Visitors disturb adults breeding in proximity to footpaths, resulting in a reduction in the number of feeds delivered to chicks during the period when the visitors are on the island</u>. Estimates of the average reduction in provisioning rate during visitor hours compared to visitor-free hours were obtained from feeding watches carried out on the Isle of May (for details see section 2.3 below). In puffins, there were 8 different disturbance levels based on the distance from paths and the intensity of path usage by visitors, whereas in terns there was no spatial variation in disturbance strength as the disturbed birds were concentrated in a small area surrounding the boat landing (details are provided in section 2.3).
Several disturbance scenarios were explored: a baseline (no visitors present throughout the day), and 4 scenarios where visitor numbers and visit durations varied. Within each scenario, the timing of boat visits was varied over the course of the day (scenarios are described in detail in section 2.2 below).

2) <u>Reduced feeding rates result in reduced chick growth rate (body mass gain per day) and body mass</u>.
Each calculation of body mass was obtained by simulation, using randomly selected values from specified distributions of the input variables (see section 2.3 for details). The mass of each chick on a given day depended on its mass in the previous day and the mass gain on the day (which is a function of the number of feeds and mass gain per feed; equation 1). Food load size was assumed to be constant.
Thus, chick mass at undisturbed nests on day *t* was calculated as:

$$Mass(t) = Mass(t-1) + Feeds(t)\frac{Mass\,gain(t)}{Feeds(t)} \qquad (1)$$

This equation was then modified to allow reduction of feeding rate as a function of the strength of disturbance. This is expressed as a proportional drop in the number of feeds delivered per nest per day compared to an undisturbed situation:

$$Mass(t) = Mass(t-1) + \left(1 - Disturbance\ strength\right) Feeds(t) \frac{Mass\ gain(t)}{Feeds(t)} \tag{2}$$

The mass and growth parameters were the same as in the baseline model. Food load size was assumed to be constant and unchanged compared to an undisturbed situation.

The models estimated the daily growth (body mass gain) of chicks between hatching and reaching peak mass. Peak mass, rather than fledging mass, was used as in both species chicks typically lose weight during the last days of the growth period before fledging (Chapdelaine et al., 1985; Hatch, 2002; Lowther et al., 2002, Harris & Wanless, 2011), as a result of adults reducing feeding rates.

3) <u>Reduced chick body mass increases the likelihood of chick mortality due to starvation or poor body condition</u>.
The effects of peak body mass on chick survival probability were estimated whereby chicks were assumed to die if their body mass fell below a threshold value. Based on expert opinion, the threshold was set at the bottom 5% of the mass distribution. The 5% threshold value was determined from empirical data on peak body mass in puffins (CEH long-term data) and Arctic terns (Chapdelaine et al., 1985; Klaasen, 1994) as the mean mass - 1.67SD.

4) <u>Only a proportion of the puffin and tern population breed sufficiently close to footpaths to be disturbed by visitors</u>.
The impact of disturbance on breeding success at the population level was therefore estimated by calculating the population breeding success where an estimated proportion of the birds are disturbed (a weighted mean of the disturbed and undisturbed components of the population). The overall average breeding success of the population including *i* disturbance strength categories and the corresponding proportions of the population falling in them, $\overline{B}$, was calculated as a weighted mean:

$$\overline{B} = \sum_{i=1}^{k} P_i \frac{Bs_i}{Bs_u} Bs_u \tag{3}$$

where P_i is the proportion of the population in disturbance category *i*, Bs_i is the breeding success in category *i* and Bs_u is the breeding success of the undisturbed population.

All simulations were run in R, version 2.14.1 (R development core team, 2012).

2.2. Model scenarios

2.2.1. Atlantic puffin

A baseline model was used to estimate the daily growth (body mass gain) of chicks between hatching and reaching peak mass in an undisturbed situation. The model was run for 10 000 chicks. The model output was a distribution of chick masses on any given day of growth between hatching and reaching peak mass. We present the distribution of peak masses as this is most informative of chick survival probability.

The visitor disturbance effect was then incorporated into the baseline model as a proportional drop in the number of feeds delivered per nest per day compared to an undisturbed situation. Several disturbance scenarios were explored, as agreed with SNH (Table 1). The baseline Scenario (S1) estimated the disturbance effect based on the current visitor numbers and duration of stay on the island, only varying the timing of the boat visit in 3-hour blocks between 9a.m. and 8p.m. The remaining three scenarios (S2-S4) were formulated as S1 but visitor numbers or duration of visit, or both were doubled (Table 1). The additional versions of scenario S1 and S3 (S1a and S3a) were included in the analysis to account for the Seabird Centre RIB bringing visitors (for example, photographers) who stay in certain locations on the island for considerable time. For scenarios S1a and S3a the hour of continuous disturbance was added immediately before or after the time of the May Princess visit, and the timing of Seabird Centre RIB visit was constrained between 9am and 8pm (as agreed with SNH). Thus, within each scenario, the number of visitors and duration of visit were fixed, whereas the timing of visit varied during the day. Mixed scenarios, with varying number of people and/or duration of visit during the same day, were not explored. Potential variation in the timing of boat visits in relation to tides was not incorporated in the models.

Table 1. Details of the visitor disturbance scenarios explored.

Scenario	Scenario description	Visiting hours	Duration of stay	Number of visitors	Boats
S1	Current visitor numbers and duration of boat stay	9am – 8pm	3 hrs	118	May Princess + 1-2 RIBs
S1a	As S1 plus additional hour of continuous disturbance	9am – 8pm; 9am – 8pm	3hrs; + 1hr	118; + 12	As S1; + Seabird Centre RIB
S2	Current visitor numbers, doubled duration of boat stay	9am – 8pm	6 hrs	118	May Princess + 1-2 RIBs
S3	Doubled visitor numbers, current duration of boat stay*	9am – 8pm	3 hrs	218	2 x May Princess + 1-2 RIBs
S3a	As S3 plus additional hour of continuous disturbance*	9am – 8pm; 9am – 8pm	3hrs; + 1hr	218; + 12	As S3; + Seabird Centre RIB
S4	Doubled visitor numbers, and duration of boat stay*	9am – 8pm	6 hrs	218	2 x May Princess + 1-2 RIBs

* NB: Only the May Princess visitor numbers doubled, RIB numbers unchanged

As the disturbance effect in many of the scenarios was negligible, particularly for the medium and low path usage categories and 10-25m distance band from paths, only the outputs for the worst case version of each scenario (in terms of timing of boat visits) per path usage category are presented in the report.

2.2.2. Arctic tern

The baseline model and main disturbance scenarios (S1-S4) were formulated as in puffins (section 2.2.1 above). Scenarios S1a and S3a are not relevant to this species because, to minimise disturbance, visitors are actively discouraged from spending prolonged periods of time in the vicinity of the tern colony. These two scenarios were therefore omitted from the analyses.

2.3. Model parameterisation

2.3.1. Atlantic puffin

Data on hourly feeding rates when visitors are on the island and in an undisturbed situation are available from a previous study on the Isle of May (Finney, 2002). A total of 26 2-hour watches (13 when there were visitors and 13 when visitors were absent) were carried out during the chick rearing period in 2001. A study plot (*ca*. 20 x 40m) was set up at a footpath that was, and still is, heavily used by visitors and passed through the main puffin colony. The plot was split into two sections, 0-10m and 10-25m from the path (Finney, 2002). The number of burrows with chicks within the study plot was established prior to the start of observations. Colony attendance (number of birds present in the colony at the beginning of each watch and subsequently at 5-min intervals), the time of arrival and departure of all people to the study area and duration of disturbance (measured as time birds were in the air above the colony), and total number of puffins going down burrows with fish were recorded during each watch.

Finney (2002) recorded that, when 100 visitors were present on the island, the average amount of time per hour that people were present in the study area was 16min. She also found that the average number of hourly feeds at burrows within 10 m from the path changed from an average of 0.60/burrow when the visitors were absent to 0.47/burrow when visitors were present. At burrows within 10-25m from the path the drop in average number of hourly feeds was 17% smaller, to 0.5/burrow. As intensity of footpath use on the Isle of May varies, we explored three additional path usage categories (very high, medium and low). The ‘very high’ usage category represents hotspots on the island where visitors spend considerable time, whereas the ‘medium and ‘low’ usage categories were used to describe paths that are more rarely used and where visitors generally pass through without stopping. For ease of comparison with Finney’s data, the additional categories were also based on 100 visitors. The amount of time people are present in the vicinity of a burrow for each category was estimated from expert opinion (SNH) as 40 min/hr, 8 min/hr and 2 min/hr for very high, medium and low usage categories, respectively. Visitor numbers were subsequently slightly modified to equal 118, to account for the visitors brought to the island by RIBs (which vary between 1 and 2 boats, each of 12 people, so we took the mean of 12 and 24 i.e. 18) and duration of visitor presence for each path usage category was adjusted accordingly (Table 2a). Under the doubled visitor numbers scenarios the duration of visitor presence was increased by 100% for low and medium path usage categories and by 50% for the high usage category (as agreed with SNH). For the very high usage category a 50% increase resulted in continuous disturbance over the whole period the boat was on, which was unrealistic given visitor activity/movements between leaving the boat and reaching the puffin colony. For this category we, therefore, set the duration of visitor presence to 45mins per hour in the first and last hour of stay on the island, and continuous duration in the remaining hour(s) (Table 2b).

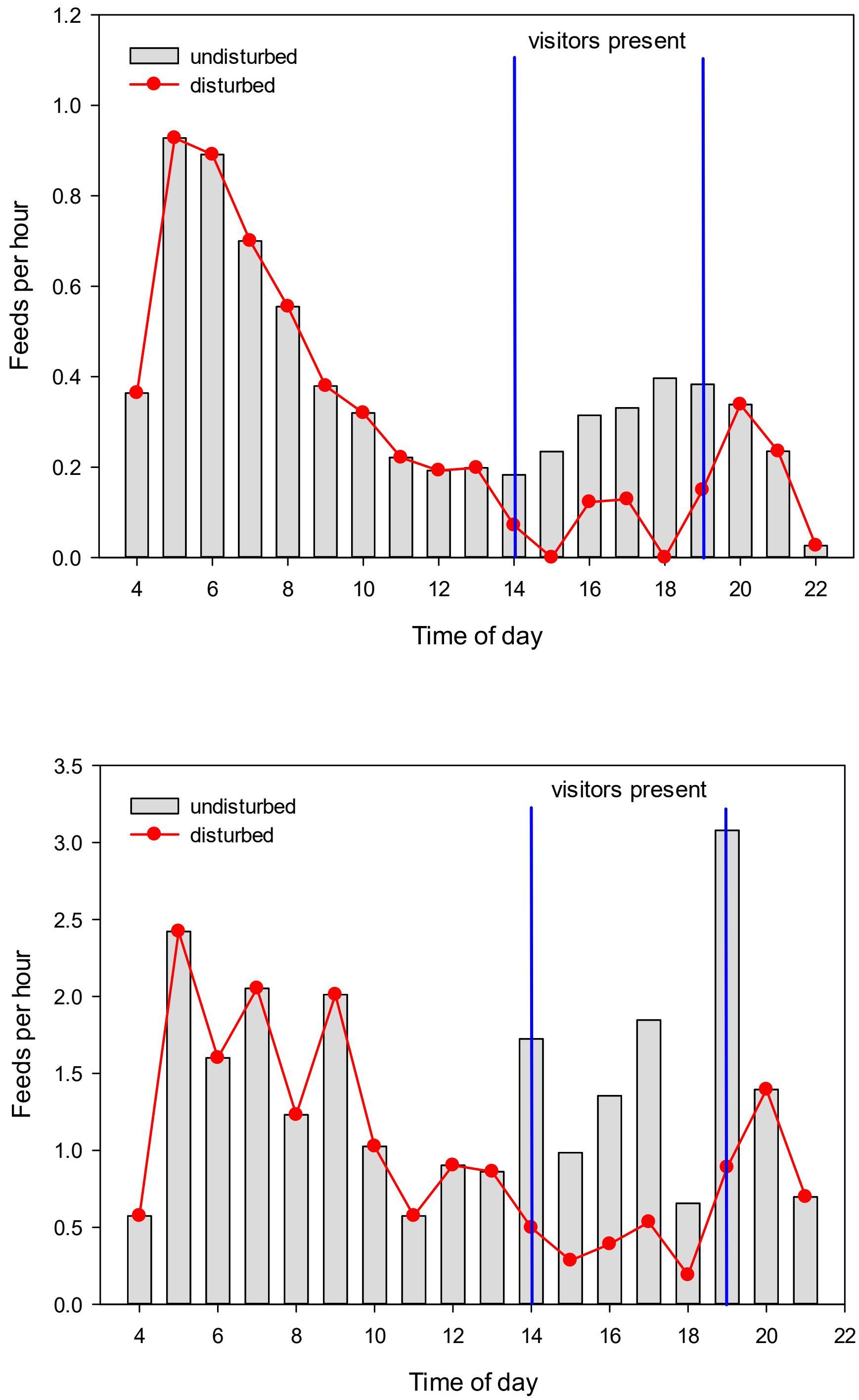
Table 2. Average duration of visitor presence and average number of feeds per hour during boat visits in nests within 0-10m and 10-25m from paths under a) current and b) doubled visitor numbers scenarios.

Path usage category	Time visitors present/hr (min)	Feeds/hr 0-10m	Feeds/hr 10-25m
a) Current visitor numbers			
Very high	47	0.22	0.31
High	19	0.45	0.48
Medium	9	0.52	0.54
Low	2	0.58	0.59
b) Doubled visitor numbers (May Princess only; RIB numbers unchanged)			
Very high	45/60/45*	0.23/0/0.23	0.33/0.15/0.33
High	26	0.39	0.44
Medium	17	0.46	0.50
Low	4	0.57	0.58

* The values represent duration of visitor presence in the first, middle and last hour of stay on the island. 15 min at the start and end of the visit were removed to account for visitor movement between the boat and the puffin colony. Hourly feeds were calculated accordingly.

Puffins show a diurnal pattern of feeding their single chick with a pronounced peak early in the morning, low feeding rate in the middle of the day and a smaller peak in the evening (Harris & Wanless, 2011); therefore the number of feeds delivered per hour is not equal over all daylight hours. To explicitly take into account the timing of visitor disturbance, the proportion of daily feeds delivered in each daylight hour was obtained from CEH data from 2005 to 2013 (to match temporally the data for the growth parameters; see below). For undisturbed nests, the hourly number of feeds was calculated as the proportion of the daily number of feeds delivered in this hour. For disturbed nests, the hourly number of feeds was reduced according to the estimated % drop in feeding rates resulting from disturbance (Fig. 1a).

a)



b)

Fig. 1. Diurnal pattern of feeding in undisturbed and disturbed nests of a) puffins and b) Arctic terns. Disturbance effect is based on the highest disturbance scenario, S4 (for details of scenarios see section 2.2.1).

The remaining input parameters were obtained from the CEH long-term study on the Isle of May or from the published literature (Table 3a). On the Isle of May, there has been a long-term decline in peak chick mass and increase in the length of growth period resulting in a decrease in growth rate (Harris & Wanless, 2011), so we used CEH data since 2005 to obtain values representative of the current situation. The input parameters were drawn randomly and independently from appropriate distributions (Table 3a).

Table 3. Model input parameters for each species.

Parameter	Distribution	Mean	SD	Source
a) Atlantic puffin				
Hatching mass (g)	normal	42	3.7	Birkhead & Nettleship, 1984
Growth period to peak (d)	normal	38	5	CEH data (since 2005)
Feeds per day	Poisson	7.2	-	CEH data (since 2005)
Growth rate to peak (g/day)	normal	6.7	1.5	CEH data (since 2005)
b) Arctic tern				
Hatching mass (g)	normal	13	1.3	Østnes et al., 1997
Growth period to peak (d)	normal	19	1.6	Pearson, 1968; Klaasen, 1994
Feeds per day	Poisson	206	-	CEH data (2013)
Growth rate to peak (g/day)	normal	5.4	0.7	Østnes et al., 1997

2.3.2. Arctic tern

To determine the impact of disturbance on feeding rates, 2-hour watches (12 when there were visitors and 12 when visitors were absent) were carried out at the colony at Kirkhaven, the harbour where all visitors land, during chick-rearing in 2013. The watches covered the hours between 9 a.m. and 6.30 p.m., and were paired on each observation day. A study plot was selected and the total number of chicks within the plot was estimated from observations. Colony attendance (number of birds present in the colony at the beginning of each watch), arrival and departure time of boats and visitor numbers, number of people passing through the study area and duration of disturbance (time birds were in the air above the colony), total number of feeds delivered at study nests in 5-min intervals and predation events were recorded.

Parents were assumed to raise one chick, as the younger chick in the brood often dies within the first few days of life (Lemmetyinen, 1972; Hatch, 2002), a pattern that is also observed on the Isle of May (SNH, pers. obs). From the raw data the average amount of time per hour that visitors were present, and the average number of feeds per nest per hour in the disturbed and undisturbed situation were calculated. To estimate these parameters for the doubled visitor numbers scenarios, we increased the duration of visitor presence and correspondingly decreased the number of feeds by 50% (as for the heavy path usage categories in puffins).

Arctic terns show a diurnal pattern of provisioning chicks similar to that of puffins, with higher number of feeds delivered to the nest in the morning and in the late afternoon/evening (Fig. 1b; Pearson, 1968). The proportion of daily feeds delivered in each daylight hour was obtained from the literature (Pearson, 1968). Number of feeds per hour for disturbed and undisturbed nests was then calculated using the same method as in puffins. Although tidal pattern of feeding has been observed in closely related species (Dunn, 1972; Becker et al., 1993), it was not evident in Arctic terns (Dunn, 1972) and was therefore not incorporated in the models.

The remaining input parameters were obtained from the published literature (Table 3b). Where data for a given parameter were available from several studies, we used the estimate from the study with the largest sample sizes and/or most complete information (e.g. variation also reported), and of UK (or European) populations where possible.

2.4. Population level effects of disturbance

2.4.1. Atlantic puffin

The proportion of the Isle of May puffin population exposed to different disturbance levels (8 in total: within 0-10m and 10-25m of very high, high, medium and low usage paths) was calculated using the following steps:

1) All public paths were drawn in ArcMap (ESRI) using satellite imagery of the island, and sections of the paths were assigned to 4 categories (very high, high, medium and low; described in section 2.3.1) based on the extent of their use by visitors (Fig. 2). Then 0-10m and 10-25m distance bands around the paths of each category were created and their area extracted using FME (Safe Software; Fig. 2).
2) As the density of puffin burrows on the island varies spatially, we used fine-scale information on the distribution of nests available from the puffin count carried out in 2013. The island was split into sectors and the number of burrows within each sector was counted (Harris et al., 2013). The outlines of all count sectors were drawn in ArcMap and their area extracted using FME (Fig. 2).
3) For all path usage categories, the area of the two types of distance bands lying within each count sector was extracted, and the proportion of the count sector area they represent was calculated. In cases where paths of different categories intersect and the distance bands overlap, we used the stronger disturbance category.
4) The total number of puffin burrows per count sector (available from the 2013 count), and the proportion of each count sector area covered by the two types of buffer zones under the different path usage categories (derived in step 3 above) were used to estimate the number of nests falling into each disturbance category. For this, the distribution of puffin burrows within count sectors was assumed to be uniform. As nest density in the immediate vicinity of paths is lower in some parts of the island, possibly due to visitor disturbance in earlier times, this assumption represents a worst-case scenario.

The effect of visitor disturbance on population breeding success was calculated using our estimates of reduction in chick survival in disturbed nests and the proportion of the population they represent (see Methods, equation 3).

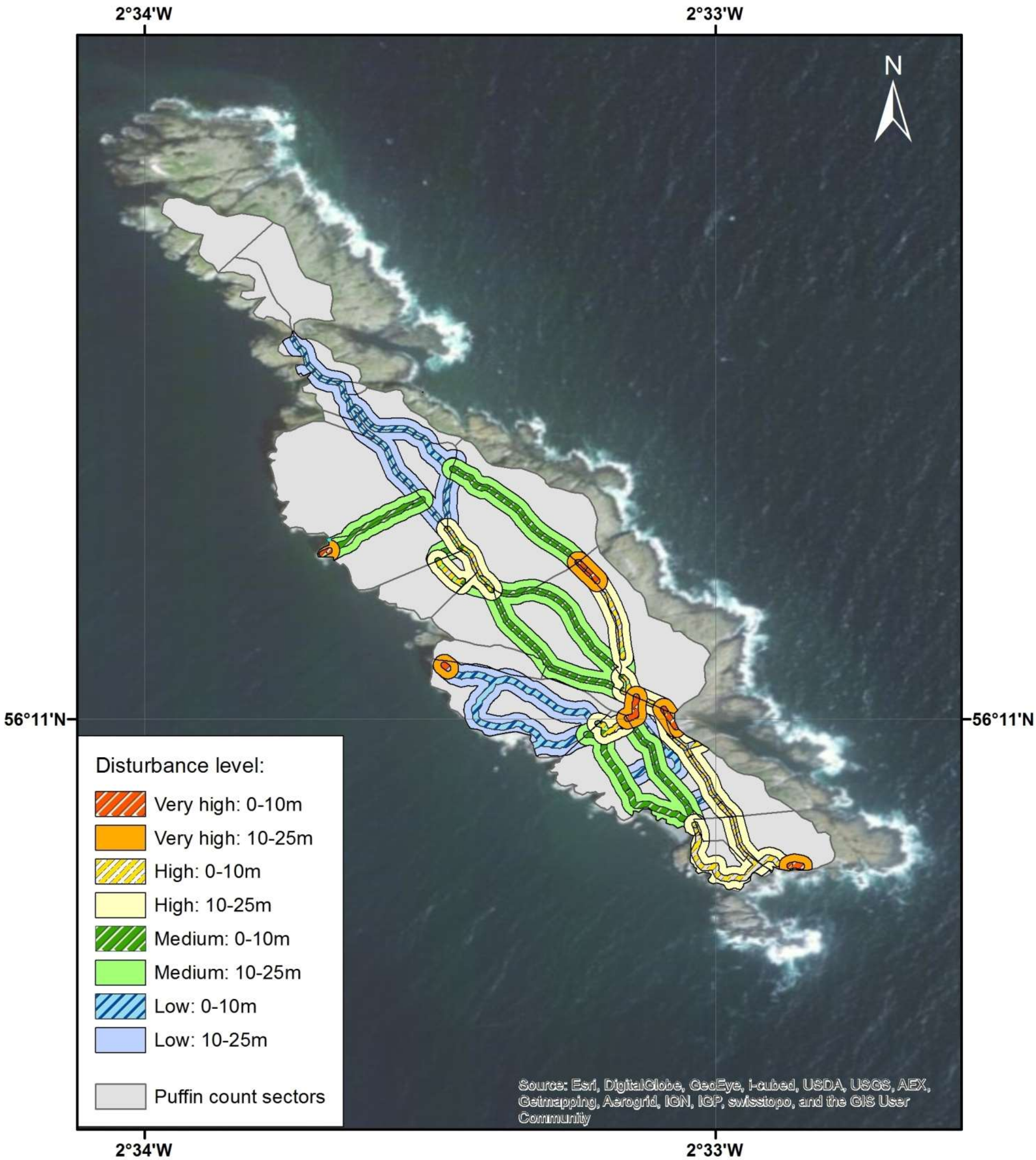


Fig. 2. Distance bands (0-10m and 10-25m) from paths for the 4 visitor usage categories (very high, high, medium, low) overlaid on puffin count sectors.

2.4.2. Arctic tern

The proportion of the tern population disturbed by visitors was estimated using data from tern counts carried out by SNH during the 2013 breeding season. Arctic terns nested in 3 areas on the island: Beacon, Chapel and Kirkhaven. 248 nests (59%) were recorded in the first two areas which are largely disturbance-free and 171 nests (41%) in Kirkhaven which were subjected to visitor disturbance.

3. Results

3.1. Atlantic puffin

3.1.1. Feeding rates under different disturbance scenarios

Under the current visitor numbers, the average hourly feeding rate in nests within 10m of the paths was reduced by 64%, 26%, 13% and 3% for the very high, high, medium and low path usage categories, respectively, compared to times when visitors were absent. For nests within 10-25m of the paths the corresponding values were 48%, 19%, 10% and 2%. Under the doubled visitor numbers scenarios, the corresponding values for nests within 10m of the paths were 74%, 35%, 23% and 5%, and for nests within 10-25m of the paths were 55%, 26%, 17% and 4%.

The decrease in feeds per day under each scenario is shown in Tables A1-4 (Appendix). The largest disturbance effect (19% drop, from 7.2 to 5.8 feeds per day on average) was recorded under scenario S4 (doubled visitor numbers and duration of stay), at nests within 10m of the path and where path usage is very high, during the visitor hours between 2 and 8pm which partially overlap with the evening peak in feeding activity.

Under the current visitor numbers and duration of stay (scenario S1), the largest disturbance effect (10% drop, from 7.2 to 6.5 feeds per day) was also recorded at nests within 10m of heavily used paths, during visitor hours between 5 and 8pm which coincide with the evening peak in feeding activity.

The disturbance effect for the medium and low path usage categories, even at nests within 10m of the path and under the scenario of doubled visitor numbers and duration of stay was very small (maximum recorded drop in feeds per day was 6%, from 7.2 to 6.8).

3.1.2. Effects of reduced feeding rate on chick body mass and survival probability

Mean peak mass (±SD) of puffin chicks obtained from CEH's long-term data from the Isle of May was 288 ± 32.7g. Based on this, the threshold mass (bottom 5% of mass distribution) below which chicks were unlikely to survive was estimated as 230g. For all scenarios and path usage categories, the disturbance effect on chick mass was strongest at nests within 10m of the paths and during the (late) afternoon hours when visitor presence overlapped with the afternoon/evening peak of puffin feeding activity (Table 4b). The same diurnal pattern was observed in nests further away (within 10-25m) from the paths but the disturbance effect was overall smaller (Table 4c).

Table 4. Mean peak mass and percentage of puffin chicks below the threshold peak mass (230g) in undisturbed nests (baseline) and under the worst case version of each disturbance scenario for each path usage category. Percentage drop in number of feeds/day is also shown.

Scenario	% drop in feeds/day	Peak mass (g) ± SD	Percentage below threshold
a) Baseline	0	286.1 ± 42.4	6.5
b) 0-10m from path			
b1) Very high path use			
S1, 5-8pm	9.8	262.4 ± 37.4	15.1
S1a, 4-8pm	14.6	251.0 ± 35.3	23.3
S2, 2-8pm	16.3	246.8 ± 34.8	27.3
S3, 5-8pm	11.6	258.2 ± 37.7	17.4
S3a, 4-8pm	16.0	247.3 ± 34.9	26.6
S4, 2-8pm	19.0	240.2 ± 33.1	34.3
b2) High path use			
S1, 5-8pm	4.0	276.9 ± 40.3	8.5
S2, 2-8pm	6.6	270.3 ± 39.7	11.1
S3, 5-8pm	5.3	272.9 ± 40.3	10.2
S4, 2-8pm	8.9	264.9 ± 38.5	13.7
b3) Medium path use			
S1, 5-8pm	2.0	281.0 ± 41.3	7.4
S2, 2-8pm	3.3	278.2 ± 40.6	8.2
S3, 5-8pm	3.6	277.1 ± 40.3	8.6
S4, 2-8pm	5.9	272.0 ± 39.3	10.6
b4) Low path use			
S1, 5-8pm	0.5	285.3 ± 41.1	6.6
S2, 2-8pm	0.8	284.6 ± 41.4	6.9
S3, 5-8pm	0.8	284.6 ± 41.7	6.8
S4, 2-8pm	1.4	282.5 ± 41.3	7.3
c) 10-25m from path			
c1) Very high path use			
S1, 5-8pm	7.4	268.0 ± 38.7	11.6
S1a, 4-8pm	10.9	259.4 ± 37.5	16.8
S2, 2-8pm	12.2	256.8 ± 37.2	18.3
S3, 5-8pm	8.7	265.1 ± 38.3	13.3
S3a, 4-8pm	12.0	256.7 ± 36.9	19.3
S4, 2-8pm	14.3	251.9 ± 36.4	21.9
c2) High path use			
S1, 5-8pm	3.0	279.3 ± 40.7	8.0
S2, 2-8pm	4.9	273.8 ± 39.7	10.0
S3, 5-8pm	4.0	276.4 ± 40.9	9.2
S4, 2-8pm	6.6	270.1 ± 39.8	11.2

c3) Medium path use			
S1, 5-8pm	1.5	283.1 ± 40.9	7.0
S2, 2-8pm	2.4	280.9 ± 41.9	7.6
S3, 5-8pm	2.7	280.4 ± 40.3	7.9
S4, 2-8pm	4.4	275.2 ± 39.6	9.5
c4) Low path use			
S1, 5-8pm	0.4	285.5 ± 41.7	6.6
S2, 2-8pm	0.6	285.3 ± 40.9	6.7
S3, 5-8pm	0.6	284.6 ± 41.6	6.6
S4, 2-8pm	1.0	283.7 ± 42.9	7.2

Mean peak mass decreased with severity of disturbance and under the scenario where disturbance was highest (S4) it approached the threshold mass of 230g (Table 4-b1). Under S4 there was a 28% unit increase in the number of chicks below the threshold mass compared to the baseline scenario (Table 4-b1; Fig. 3). This was reflected in the shift of peak mass distribution towards smaller values compared to the baseline scenario (Fig. 3).

The effects of disturbance on peak chick mass and chick survival probability were weaker in nests surrounding paths in the high (Table 4-b2; Fig. 4) and medium usage categories (Table 4-b3; Fig. 5), and negligible in nests surrounding paths in the low usage category (Table 4-b4; Fig. 6).

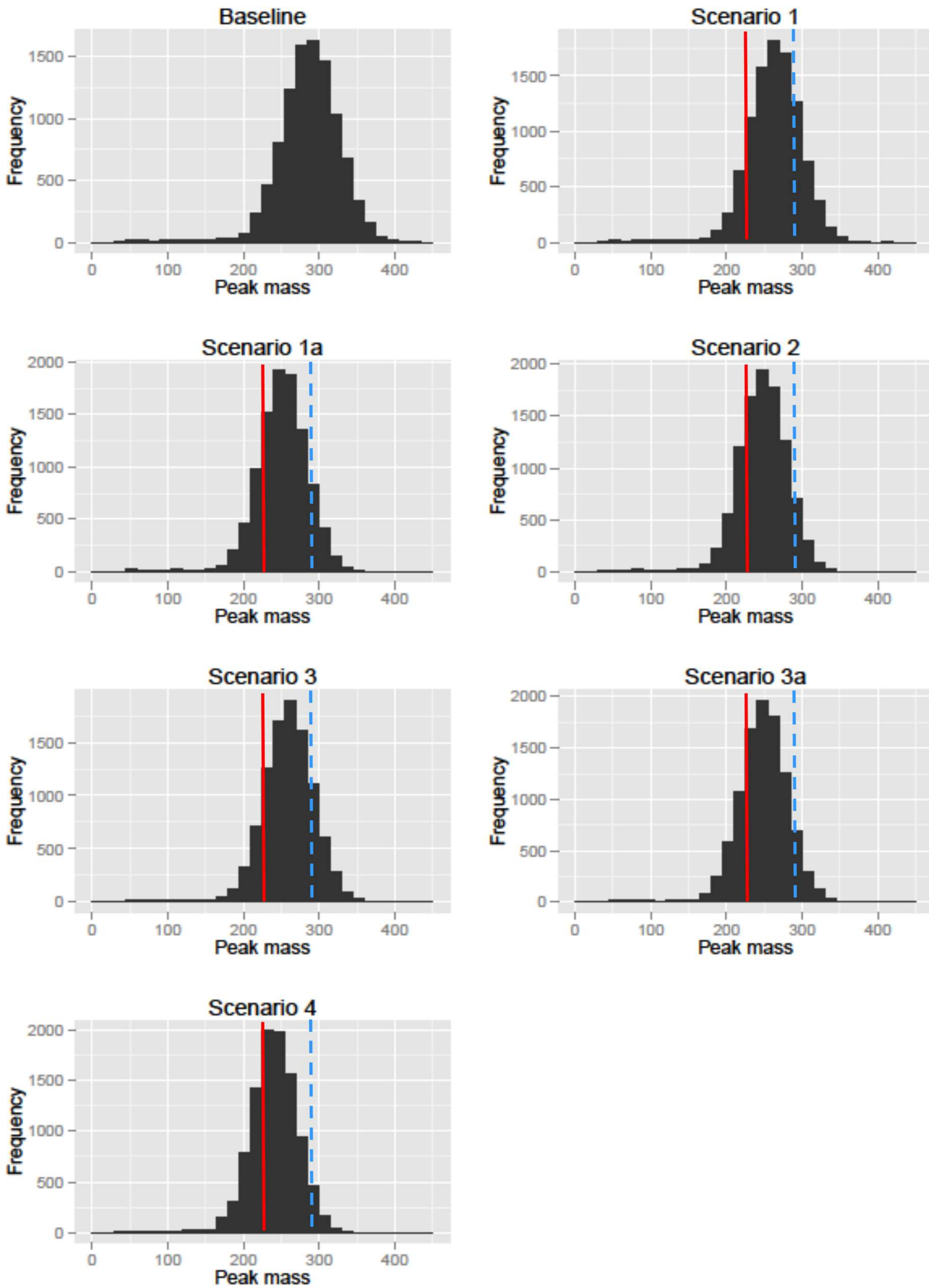


Fig. 3. Peak puffin chick mass distribution in undisturbed nests (baseline) and in very high path usage nests under the worst case version of each disturbance scenario (see Table 4b). The vertical red line shows the threshold mass below which chicks were assumed to have died; the dashed blue line shows the average baseline peak mass.

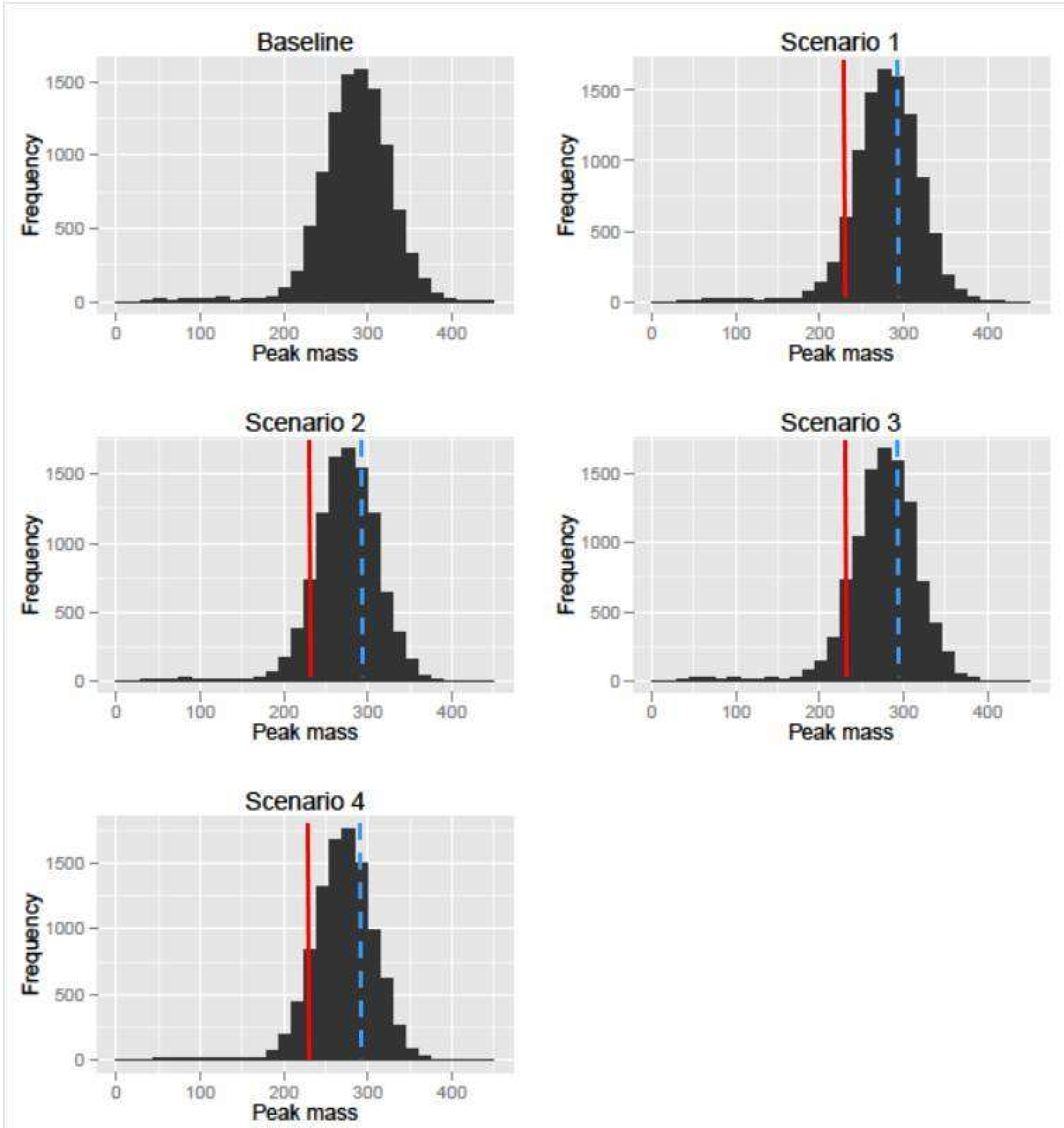


Fig. 4 . Peak puffin chick mass distribution in undisturbed nests (baseline) and in high path usage nests under the worst case version of each disturbance scenario (see Table 4c). The vertical red line shows the threshold mass below which chicks were assumed to have died; the dashed blue line shows the average baseline peak mass.

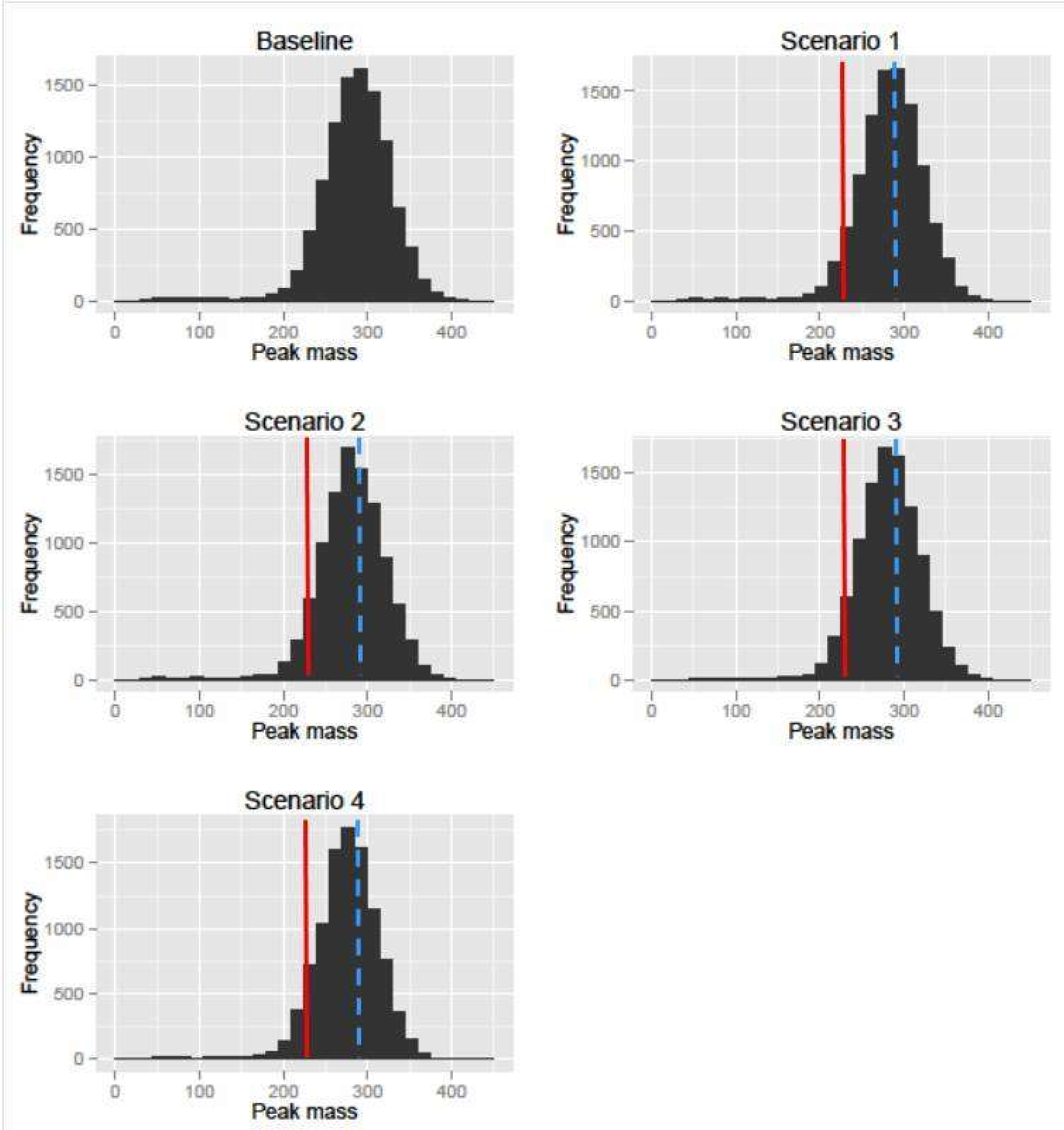


Fig. 5. Peak puffin chick mass distribution in undisturbed nests (baseline) and in medium path usage nests under the worst case version of each disturbance scenario (see Table 4d). The vertical red line shows the threshold mass below which chicks were assumed to have died; the dashed blue line shows the average baseline peak mass.

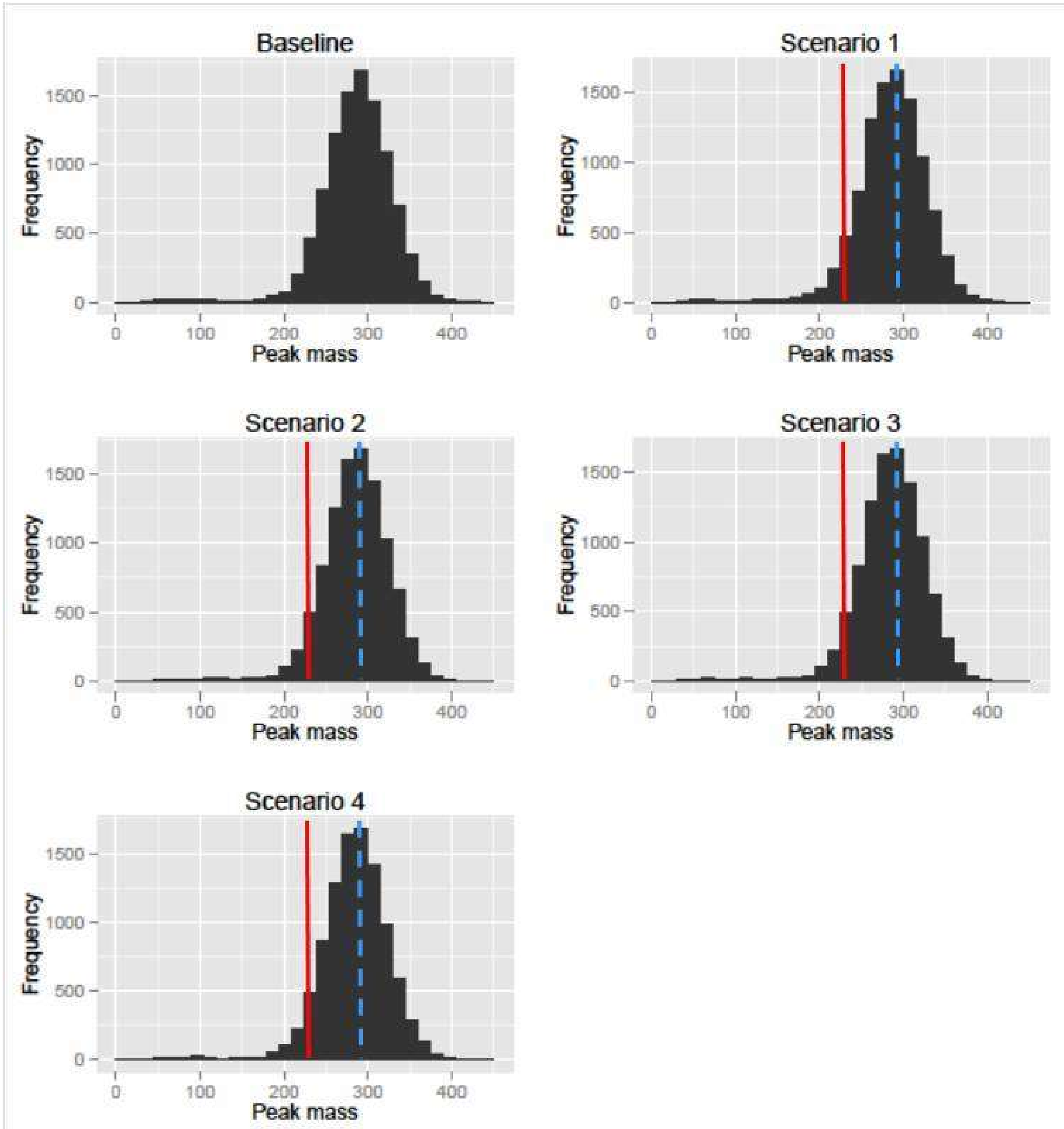


Fig. 6. Peak puffin chick mass distribution in undisturbed nests (baseline) and in low path usage nests under the worst case version of each disturbance scenario (see Table 4e). The vertical red line shows the threshold mass below which chicks were assumed to have died; the dashed blue line shows the average baseline peak mass.

3.1.3. Effects of disturbance on population level breeding success

In total 36% of the puffin nests on the island experienced some degree of disturbance (Table 5). However, the proportion of nests that fell within the high disturbance areas (within 10m from heavily used paths) was less than 4% (Table 5).

Table 5. Numbers of puffin nests within 0-10 and 10-25m of paths for each path usage category, and proportion of the Isle of May population (n=46 187) they represent.

Path usage category	N nests	Proportion of population (%)
a) 0-10m		
very high	343	0.7
high	1296	2.8
medium	1872	4.1
low	1211	2.6
b) 10-25m		
very high	1375	3.0
high	3223	7.0
medium	4381	9.5
low	2782	6.0
Total	16135	35.7

Full breakdown by puffin count sector of the number of nests within each distance band from the paths for each path usage category is provided in the Appendix (Table A5).

For ease of comparison of the different scenarios, breeding success of the undisturbed part of the population was standardised to equal 1 (equation 3 in Methods: $Bs_u = 1$). In nests within 10m of paths, breeding success at disturbed nests was 10% lower compared to undisturbed ones under the worst case version of scenario S1, 18% lower under S1a, 25% lower under S2, 12% lower under S3, 20% lower under S3a, and 28% lower under S4 (Table 4b). In nests within 10 to 25m of paths, the corresponding figures were 5%, 10%, 12%, 7%, 13% and 15% under scenarios S1, S1a, S2, S3, S3a and S4, respectively (Table 4c). However, as a very small proportion of the population was heavily disturbed by visitors, the overall impact of disturbance on population level breeding success was relatively small (0.5%, 0.7%, 1.1%, 0.8%, 1.2% and 1.7% reduction compared to undisturbed for scenarios S1, S1a, S2, S3, S3a and S4, respectively).

Average breeding success of Isle of May puffins (based on undisturbed nests) is 0.72 chicks per nest (CEH long-term data). The whole population's breeding success would be slightly reduced as a result of visitor disturbance (0.717, 0.715, 0.712, 0.714, 0.711 and 0.708 chicks per nest under scenarios S1, S1a, S2, S3, S3a and S4, respectively).

3.2. Arctic tern

3.2.1. Feeding rates in disturbed and undisturbed nests

Visitors spent on average 18 ± 9 min per hour within the Kirkhaven colony (average number of visitors was 114 ± 6), resulting in a 47% decrease in the average hourly feeding rate compared to undisturbed periods. For the doubled visitor numbers scenarios the time people were present within the area was increased by 50% to 27 min/hr, resulting in a predicted drop in the average hourly feeding rate by 71%. The decrease in feeds per day under each version of each scenario is shown in Tables A6-9 (Appendix).

As in puffins, the largest disturbance effect (27% drop from 206 to 150 feeds per day on average) was recorded under scenario S4, during the visitor hours between 2 and 8pm which included the evening peak hours of feeding activity.

The largest disturbance effect under the current visitor numbers and duration of stay (S1; 11% drop from 206 to 183 feeds per day) was recorded during visitor hours between 5 and 8pm which overlap with the evening peak in feeding activity.

3.2.2. Effects of reduced feeding rate on chick body mass and survival probability

Mean peak mass (±SD) of tern chicks obtained from the literature (Chapdelaine et al, 1985; Klaasen 1994) was 111 ± 13.1g. Based on this, the threshold mass below which chicks were unlikely to survive was estimated as 90g. For all scenarios, the disturbance effect on chick mass was strongest during the (late) afternoon hours when visitor presence overlapped with the afternoon/evening peak of feeding activity (Table 6).

Mean peak mass decreased substantially with strength of disturbance. Under scenarios S2 and S3 it approached the threshold mass of 90g and under the highest disturbance scenario (S4) it was below that (Table 6). Accordingly, under S4 there was a very large (79%) unit increase in the number of chicks below the threshold mass compared to the baseline scenario (Table 6; Fig. 7).

Table 6. Mean peak mass and percentage of arctic tern chicks below the threshold peak mass (90g) in undisturbed nests (baseline) and under the worst case version of each disturbance scenario. Percentage drop in number of feeds/day is also shown.

Scenario	% drop in feeds/day	Peak mass (g) ± SD	Percentage below threshold
Baseline	0	110 ± 9.3	1.4
S1, 5-8pm	10.6	100 ± 8.3	12.0
S2, 2-8pm	18.3	93 ± 7.7	35.6
S3, 5-8pm	15.9	95 ± 7.9	27.9
S4, 2-8pm	27.4	84 ± 7.0	80.4

As in puffins, there was a shift of peak mass distribution towards smaller values compared to the baseline scenario, however the change in terns was much larger (Fig. 7).

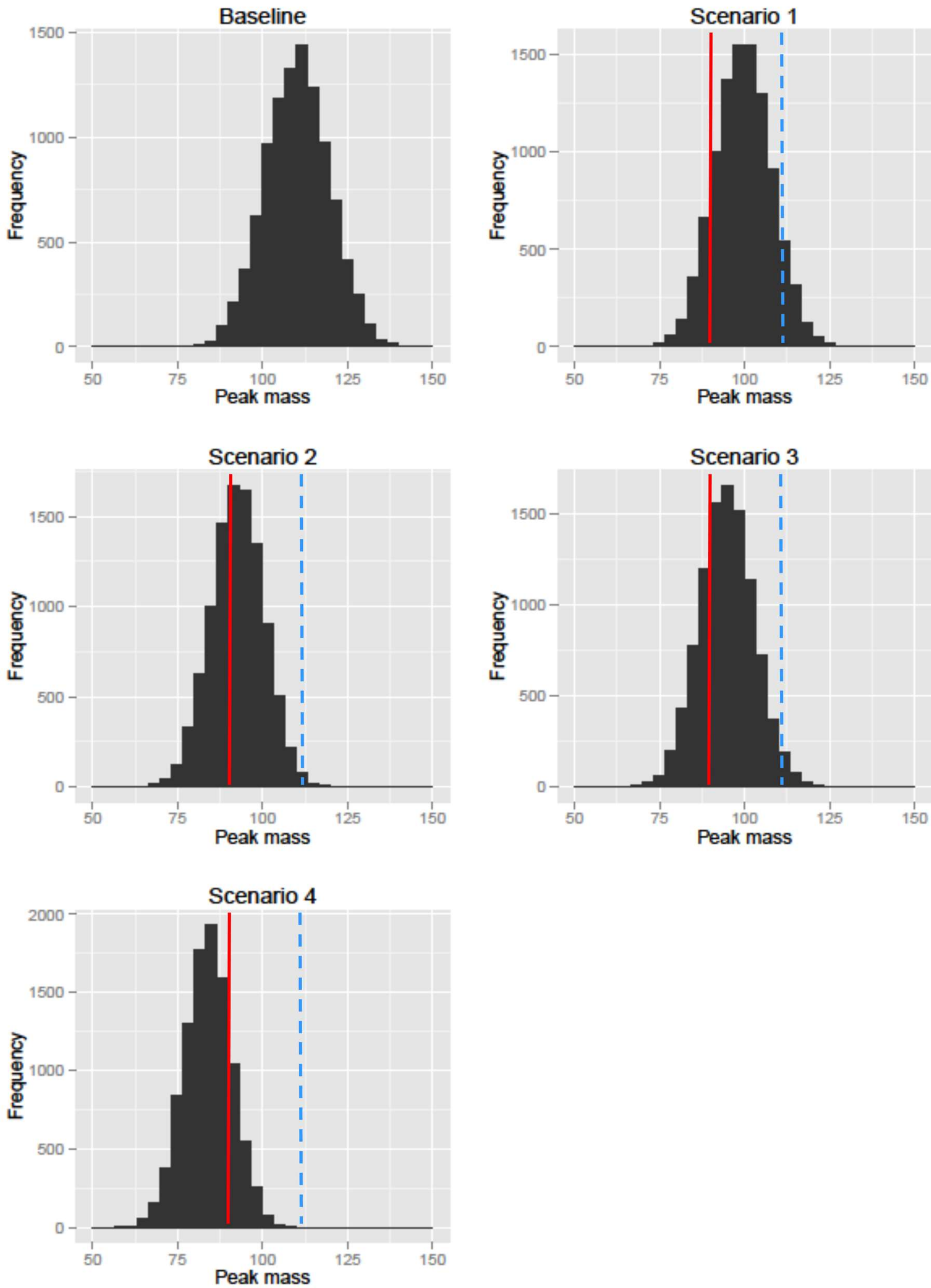


Fig. 7. Peak arctic tern chick mass distribution in undisturbed nests (baseline) and under the worst case version of each disturbance scenario (see Table 6). The vertical red line shows the threshold mass below which chicks were assumed to have died; the dashed blue line shows the average baseline peak mass.

3.2.3. *Effects of disturbance on population level breeding success*

In 2013, a substantial proportion of the Isle of May tern population (41%) nested within the area disturbed by visitors (Kirkhaven). Breeding success at disturbed nests was 11% lower compared to undisturbed ones under the worst case version (in terms of timing of boat visits) of scenario S1. The corresponding values for scenarios S2, S3 and S4 were 34%, 27% and 79%, respectively (Table 6). Based on this reduction in breeding success and the proportion of the tern population being disturbed, the overall population breeding success was 5% lower than in undisturbed situation under S1, 14% lower under S2, 11% lower under S3 and 32% lower under S4. As in puffins, for ease of comparison of the different scenarios, breeding success of the undisturbed part of the population was standardised to equal 1.

The average breeding success of Arctic terns on the Isle of May (based on 13 years of data, 1986-2010) is 0.31 chicks per nest (JNCC Seabird Monitoring Programme). As a result of visitor disturbance, the population breeding success would be reduced to 0.30, 0.27, 0.28, and 0.21 chicks per nest under scenarios S1, S2, S3 and S4, respectively.

4. Discussion

4.1. *Impact of visitor disturbance on individual- and population-level breeding success*

With the exception of birds nesting in the direct vicinity of visitor hotspots, puffin provisioning rates and breeding success were not substantially affected by the current or more severe hypothetical visitor disturbance levels. Adults returning to their burrows with fish were prevented from feeding their chick when people were present in the vicinity of the burrow (Finney, 2002). However, it is possible that puffins are partly able to compensate for the reduced provisioning rate during the boat visiting hours by increasing the number of feeds or amount of food brought to the chick at other times of the day. As the chick is fed on average 7 times a day (in undisturbed situation; Harris & Wanless, 2011), there may be room for flexibility in the timing of feeds. Furthermore, the chick can be left unattended for prolonged periods as it is generally protected from predation and the elements while in the burrow. However, such compensatory response may increase the foraging costs for the parents, which in turn can adversely affect their body condition and future performance (e.g. Harding et al., 2011). In addition, the average feeding frequency on the Isle of May is currently *ca*. 1 feed per day higher than it was in the early 2000s (Harris & Wanless, 2011), which may reduce the adults' capacity to offset the effects of visitor disturbance.

Arctic terns, in contrast, were highly susceptible to human disturbance, as suggested by studies of related species (Burger & Gochfeld, 1991; Burger et al., 1995). In the presence of visitors parents reduced their provisioning rate by nearly 50% compared to times when visitors were absent. Under the current visitor regime, this reduction was associated with *ca*. 10% decrease in breeding success. Further increasing visitor pressure (number of people, length of stay, or both) resulted in substantial reduction in predicted chick provisioning rates and breeding success. Under scenario S2 breeding success was reduced by 34%; the corresponding figures for scenarios S3 and S4 are 27% and 79%. There is an indication that the fish Arctic terns brought to their chicks in 2013 were small and of low energy value (M.Newell, pers.obs). As terns are single-prey loaders, to compensate for the poor energy value of food items, parents would need to greatly increase their provisioning rate to meet the daily energetic requirements of the chick. Furthermore, the daily chick energy needs are likely to be high because of their fast growth rate. The data from our feeding watches indeed revealed a very high provisioning rate of 206 feeds/day compared to the values reported in the literature (e.g. 25 feeds/day, Pearson, 1968; 13 feeds/day, Chapdelaine et al., 1985). However, if the daily number of foraging trips the adults make is already close to the limit of their feeding rate, disturbed birds may not be able to make up for the lost provisioning opportunities during visitor hours by increasing their effort at other times. To match the daily prey delivery of undisturbed birds, they would have to provide 1.1, 2.7, 1.6 or 4 extra feeds per hour under scenarios S1, S2, S3 and S4, respectively, during the visitor-free part of the day.

Population level breeding success in puffins was reduced by less than 1.5% under scenarios S1-S3, and by 1.7% under the highest disturbance level scenario (S4), as a very small proportion of the population was heavily disturbed. However, if visitor numbers and the time they stay on the island were doubled, breeding success of puffins within 10m of heavily used paths (*ca.* 350 nests or 0.7% of the population) would be reduced by 28%. The current visitor levels resulted in 5% reduction in the tern population's breeding success, and further increasing the number of visitors or the duration of their stay at the colony, or both, would have a substantial impact on population level breeding success in this species (14%, 11% and 32% reduction under S2, S3 and S4, respectively).

4.2. Data and modelling issues

There was some uncertainty associated with the data used to parameterise the models. For example, data on the effects of visitors on provisioning rates of puffins were obtained 13 years ago in a limited area within the colony and such short-term and spatially limited data may not be representative of the whole population. In terns, there is some indication that the number of feeds per hour was slightly overestimated due to difficulty in counting the number of chicks in the study plot, and some of the input parameters were obtained from studies of different populations. However, for both species, the peak chick mass distribution produced by the model matched very closely the equivalent distribution based on empirical data obtained from CEH's long-term study on the Isle of May (puffins) or the literature (terns). Therefore, we are confident that the model mimics the basic elements of the real process sufficiently well.

Due to lack of empirical data, the threshold below which chicks were assumed to have died (bottom 5% of mass distribution) was defined using expert opinion and is therefore inevitably associated with some uncertainty. Our model did not include variation in the quality of food delivered to chicks. In years when environmental conditions are poor, adults may be able to maintain provisioning rates similar to those in average years but the fish brought to chicks may be of lower nutritional value. In extreme cases, poor food quality can be a proximate cause of breeding failure, as shown in the Common guillemot (Wanless et al., 2005). Under adverse conditions both adults and chicks are likely to be in poor condition, and consequently the effects of human disturbance may be more severe. For example, a decrease in adult mass may result in reduced survival probability (Erikstad et al., 2009). Therefore, a precautionary approach may need to be applied, whereby visitor regime is devised so that it is sustainable even under unfavourable environmental scenarios. Such approach would be most relevant to terns which, as single-prey loaders, are particularly vulnerable to decline in the energy value of food items (Wanless et al., 2005).

Potential effects of visitor disturbance on breeding success mediated via changes in predation rates were not explored as these were outside the scope of this study. However, disturbance effects on provisioning and predation rates may be inter-related. For example, hungry chicks may be more likely to leave the burrow/nest site in search for their parents and thus be exposed to higher predation risk.

4.3. Implications for visitor management on the Isle of May

Our results support the current visitor management strategy on the Isle of May, with respect to both number of people and timing and duration of their stay on the island. The scenarios reflecting the current visitor regime did not reveal major adverse effects of disturbance on population-level breeding success in either species (reduction was less than 1% in puffins and 5% in terns). A further increase in visitor pressure within the parameters explored in this study would not result in substantial decline in population-level breeding success in puffins; however note that it may result in more damage to burrows near the paths. Further increasing visitor pressure would have a substantial negative impact on the tern population's breeding success. Increasing both the number of visitors and the duration of their stay in the colony would have the worst effect and is therefore undesirable. Our results suggest that increasing visitor numbers but maintaining the length of visits as it is currently (3 hours) would have less impact on the tern population than keeping the visitor numbers as they are currently but increasing the length of time they spend on the island. The same conclusion applies to the small but heavily disturbed group of puffin nests around visitor hotspots. The option of higher visitor numbers and restricted stay may also be the most logistically plausible due to tidal constraints on the timing and duration of boat visits.

Under the scenarios we explored, boat visiting hours substantially overlapped with the evening peak in feeding activity in both species, whereas the larger morning peak of activity remained mostly outside the visiting hours. Accordingly, the highest disturbance effect was observed in late the afternoon/evening. However, if visitor hours were altered to cover the earlier morning, the impact of disturbance would be much larger. Therefore, this should be avoided if possible. If increasing visitor access to the island is considered in the future, our results suggest that maintaining visitor hours outside the morning (5-9 a.m.) and evening (5-8 p.m.) peak of chick provisioning, and duration of stay at the current level (3 hours) can help reduce the impact of disturbance on both species relative to other management options.

The Scottish populations of these species, in particular the Arctic tern, are declining (JNCC Seabird Monitoring Programme), likely linked to changes in marine ecosystems and associated deterioration in feeding conditions. As the opportunities to revert such changes in the marine environment through management are very limited, it is becoming increasingly important to ensure that the conditions for the birds at the breeding colonies are as favourable as possible. Devising appropriate visitor strategies that minimise the negative effects of human disturbance is an integral part of this process.

5. Acknowledgements

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7. Appendix

Table A1. Number of feeds per day and percentage drop compared to undisturbed nests under Scenario 1 (current visitor numbers and duration of boat stay) in puffins.

Visitor hours	Path usage category									
	Very high(+1hr)		Very high		High		Medium		Low	
	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop
a) 0-10m										
9-12	6.42	10.8	6.61	8.2	6.96	3.3	7.08	1.6	7.17	0.4
10-13	6.53	9.3	6.73	6.5	7.01	2.6	7.11	1.3	7.18	0.3
11-14	6.63	8.0	6.81	5.4	7.04	2.2	7.12	1.1	7.18	0.3
12-15	6.60	8.3	6.83	5.1	7.05	2.1	7.13	1.0	7.18	0.3
13-16	6.49	9.8	6.81	5.5	7.04	2.2	7.12	1.1	7.18	0.3
14-17	6.40	11.1	6.73	6.5	7.01	2.6	7.11	1.3	7.18	0.3
15-18	6.24	13.3	6.64	7.8	6.97	3.2	7.09	1.6	7.17	0.4
16-19	6.15	14.6	6.54	9.2	6.93	3.7	7.07	1.8	7.17	0.5
17-20	6.49	9.8	6.49	9.8	6.91	4.0	7.06	2.0	7.16	0.5
b) 10-25m										
9-12	6.62	8.1	6.76	6.1	7.02	2.5	7.11	1.2	7.18	0.3
10-13	6.70	6.9	6.85	4.9	7.06	2.0	7.13	1.0	7.18	0.2
11-14	6.77	6.0	6.91	4.1	7.08	1.6	7.14	0.8	7.19	0.2
12-15	6.75	6.3	6.93	3.8	7.09	1.5	7.15	0.8	7.19	0.2
13-16	6.67	7.4	6.91	4.1	7.08	1.7	7.14	0.8	7.18	0.2
14-17	6.60	8.3	6.85	4.9	7.06	2.0	7.13	1.0	7.18	0.2
15-18	6.48	10.0	6.78	5.8	7.03	2.4	7.12	1.2	7.18	0.3
16-19	6.41	10.9	6.70	6.9	7.00	2.8	7.10	1.4	7.17	0.4
17-20	6.67	7.4	6.67	7.4	6.98	3.0	7.09	1.5	7.17	0.4

Table A2. Number of feeds per day and percentage drop compared to undisturbed nests under Scenario 2 (current visitor numbers but doubled duration of boat stay) in puffins.

Visitor hours	Path usage category							
	Very high		High		Medium		Low	
	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop
a) 0-10m								
9-15	6.25	13.2	6.81	5.4	7.01	2.6	7.15	0.7
10-16	6.34	12.0	6.85	4.8	7.03	2.4	7.16	0.6
11-17	6.34	11.9	6.85	4.8	7.03	2.4	7.16	0.6
12-18	6.27	12.9	6.83	5.2	7.01	2.6	7.15	0.7
13-19	6.14	14.7	6.77	5.9	6.99	2.9	7.15	0.8
14-20	6.02	16.3	6.72	6.6	6.96	3.3	7.14	0.8
b) 10-25m								
9-15	6.49	9.9	6.91	4.0	7.06	2.0	7.16	0.5
10-16	6.55	9.0	6.94	3.6	7.07	1.8	7.17	0.5
11-17	6.56	8.9	6.94	3.6	7.07	1.8	7.17	0.5
12-18	6.50	9.7	6.92	3.9	7.06	1.9	7.16	0.5
13-19	6.41	11.0	6.88	4.5	7.04	2.2	7.16	0.6
14-20	6.32	12.2	6.84	4.9	7.02	2.4	7.15	0.6

Table A3. Number of feeds per day and percentage drop compared to undisturbed nests under Scenario 3 (doubled visitor numbers but current duration of boat stay) in puffins.

Visitor hours	Path usage category									
	Very high(+1hr)		Very high		High		Medium		Low	
	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop
a) 0-10m										
9-12	6.32	12.2	6.51	9.5	6.88	4.4	6.99	2.9	7.15	0.7
10-13	6.47	10.2	6.67	7.4	6.95	3.5	7.03	2.3	7.16	0.6
11-14	6.57	8.8	6.75	6.2	6.99	2.9	7.06	2.0	7.17	0.5
12-15	6.54	9.2	6.77	5.9	7.00	2.8	7.07	1.8	7.17	0.4
13-16	6.44	10.6	6.75	6.2	6.99	3.0	7.06	2.0	7.17	0.5
14-17	6.33	12.1	6.66	7.5	6.95	3.5	7.03	2.3	7.16	0.6
15-18	6.14	14.7	6.54	9.2	6.90	4.2	7.00	2.8	7.15	0.7
16-19	6.05	16.0	6.43	10.6	6.84	5.0	6.96	3.3	7.14	0.8
17-20	6.37	11.6	6.37	11.6	6.82	5.3	6.94	3.6	7.14	0.8
b) 10-25m										
9-12	6.54	9.2	6.69	7.1	6.96	3.3	7.04	2.2	7.16	0.5
10-13	6.65	7.6	6.80	5.6	7.01	2.6	7.07	1.8	7.17	0.4
11-14	6.73	6.6	6.86	4.7	7.04	2.2	7.09	1.5	7.18	0.3
12-15	6.70	6.9	6.88	4.5	7.05	2.1	7.10	1.4	7.18	0.3
13-16	6.63	7.9	6.86	4.7	7.04	2.2	7.09	1.5	7.17	0.3
14-17	6.55	9.1	6.80	5.6	7.01	2.6	7.07	1.8	7.17	0.4
15-18	6.41	11.0	6.71	6.9	6.97	3.2	7.05	2.1	7.16	0.5
16-19	6.34	12.0	6.63	8.0	6.93	3.8	7.02	2.5	7.16	0.6
17-20	6.58	8.7	6.58	8.7	6.91	4.0	7.01	2.7	7.15	0.6

Table A4. Number of feeds per day and percentage drop compared to undisturbed nests under Scenario 4 (doubled visitor numbers and duration of boat stay) in puffins.

Visitor hours	Path usage category							
	Very high		High		Medium		Low	
	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop	feeds/day	% drop
a) 0-10m								
9-15	6.09	15.5	6.68	7.2	6.86	4.8	7.12	1.1
10-16	6.22	13.6	6.73	6.5	6.89	4.3	7.13	1.0
11-17	6.21	13.7	6.73	6.5	6.89	4.3	7.13	1.0
12-18	6.11	15.1	6.70	7.0	6.86	4.7	7.12	1.1
13-19	5.99	16.8	6.63	8.0	6.82	5.3	7.11	1.3
14-20	5.83	19.0	6.56	8.9	6.77	5.9	7.10	1.4
b) 10-25m								
9-15	6.36	11.6	6.81	5.4	6.94	3.6	7.14	0.8
10-16	6.46	10.2	6.85	4.9	6.97	3.2	7.15	0.8
11-17	6.46	10.3	6.85	4.8	6.97	3.2	7.15	0.8
12-18	6.38	11.3	6.82	5.2	6.95	3.5	7.14	0.8
13-19	6.29	12.6	6.77	6.0	6.91	4.0	7.13	0.9
14-20	6.17	14.3	6.72	6.6	6.88	4.4	7.12	1.0

Table A5. Numbers of puffin nests within 0-10 and 10-25m of paths for each puffin count sector and path usage category.

Puffin count sector	Sector area (m^2)	Number of puffin nests	Path usage category							
			Very high		High		Medium		Low	
			0-10m	10-25m	0-10m	10-25m	0-10m	10-25m	0-10m	10-25m
West Rona	16395	902	0	0	0	0	0	0	0	0
Northeast Rona	39683	166	0	0	0	0	0	0	0	0
Southeast Rona	45763	906	0	0	0	0	0	0	0	0
Tarbet flats	15588	44	0	0	0	0	0	0	6	16
Drumcarrach basin	2919	104	0	0	0	0	0	0	22	40
Drumcarrach	27704	1692	0	0	0	0	0	0	209	516
Burrian	68159	7353	13	113	0	0	533	1362	32	117
Colm - Kirkhaven	90457	6795	129	523	447	818	76	151	0	0
Ardcarran Gully - Kirkhaven	37314	813	27	29	93	196	0	0	0	32
Lady’s Bed	47315	2907	67	219	220	539	0	0	0	0
Standing Head	5430	17	0	0	0	0	0	0	4	9
Altarstanes - Horse Hole	12739	145	0	0	0	0	0	0	25	58
Horse Hole - N Plateau	4698	70	0	0	0	0	0	0	11	21
Horse Hole - Three Tarn Nick	127067	9346	0	0	0	0	217	546	177	509
Three Tarn - Sheep Well	69949	2664	31	75	35	176	210	423	40	86
Sewer Pipe - Sheep Well	37371	740	0	0	63	161	2	34	0	0
Sewer Pipe - Craigdhu	42313	584	0	0	11	52	60	103	0	0
South Plateau to Cornerstone	102517	2798	17	90	5	50	4	49	595	1196
Cornerstone to Pilgrims Haven	87244	525	1	9	16	43	82	170	13	40
South Horn	25129	560	0	0	170	269	0	3	0	0
East Braes	39525	3986	58	291	150	690	407	884	0	0
St Andrews Well	44098	108	0	0	0	1	1	8	30	45
Beacon	90076	1877	1	14	60	151	142	344	43	78
West Braes	58587	723	0	0	7	25	135	283	0	0
Crosspark	11045	97	0	0	15	46	1	1	0	0
Other fields	60012	26	1	3	2	5	3	6	4	4
Loch Sides	25837	243	0	9	0	0	0	14	0	14

Table A6. Number of feeds per day and percentage drop compared to undisturbed nests under Scenario 1 (current visitor numbers and duration of boat stay) in terns.

Visitor hours	Feeds/day	% drop
9-12	191.9	6.8
10-13	196.2	4.7
11-14	196.9	4.4
12-15	192.4	6.6
13-16	192.1	6.8
14-17	190.1	7.7
15-18	189.6	7.9
16-19	190.9	7.3
17-20	184.2	10.6

Table A7. Number of feeds per day and percentage drop compared to undisturbed nests under Scenario 2 (current visitor numbers but doubled duration of boat stay) in terns.

Visitor hours	Feeds/day	% drop
9-15	178.3	13.5
10-16	182.3	11.5
11-17	181.0	12.1
12-18	176.0	14.6
13-19	177.0	14.1
14-20	168.3	18.3

Table A8. Number of feeds per day and percentage drop compared to undisturbed nests under Scenario 3 (doubled visitor numbers but current duration of boat stay) in terns.

Visitor hours	Feeds/day	% drop
9-12	184.8	10.3
10-13	191.3	7.1
11-14	192.3	6.7
12-15	185.6	9.9
13-16	185.1	10.2
14-17	182.2	11.6
15-18	181.5	11.9
16-19	183.4	11.0
17-20	173.3	15.9

Table A9. Number of feeds per day and percentage drop compared to undisturbed nests under Scenario 4 (doubled visitor numbers and duration of boat stay) in terns.

Visitor hours	Feeds/day	% drop
9-15	164.4	20.2
10-16	170.4	17.3
11-17	168.5	18.2
12-18	161.0	21.8
13-19	162.5	21.1
14-20	149.5	27.4