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PhD thesis

The dynamics of gull-puffin interactions: implications for management

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Abstract

This study investigated the impact of kleptoparasitism and predation by large gulls (*Larus* spp.) on the recruitment rate, foraging economics and reproductive performance of Atlantic puffins *Fratercula arctica* breeding on the Isle of May, Firth of Forth, southeast Scotland. The implications of the findings for nature reserve management strategies are discussed.

During the period from 1972 to 1989 the population of herring *L. argentatus* and lesser black-backed gulls *L. fuscus* nesting on the island was reduced as part of a gull control programme. Since 1989, gull management has involved maintaining gull-free areas by repeated removal of nests. Analysis of data collected over a 23 year period showed that the recruitment rate of puffins to the colony was significantly higher in the areas of the island where gull nest density was low. This suggests that, by reducing the density and spatial distribution of nesting gulls, the control programme successfully increased the attractiveness of the colony as a potential breeding site for puffins.

Maintaining gull-free areas was also effective in reducing the frequency with which puffins were attacked by gulls. Kleptoparasitism risk during the morning and evening peaks of puffin feeding activity was 37% in gull-occupied habitat compared to only 5% in gull-free areas. These results indicate that gulls predominantly attacked puffins that bred in close proximity to them and did not move outwith the main gull breeding areas to attack puffins elsewhere on the island. The presence of gulls also significantly reduced the actual rate at which adult puffins attempted to deliver food to their chicks.

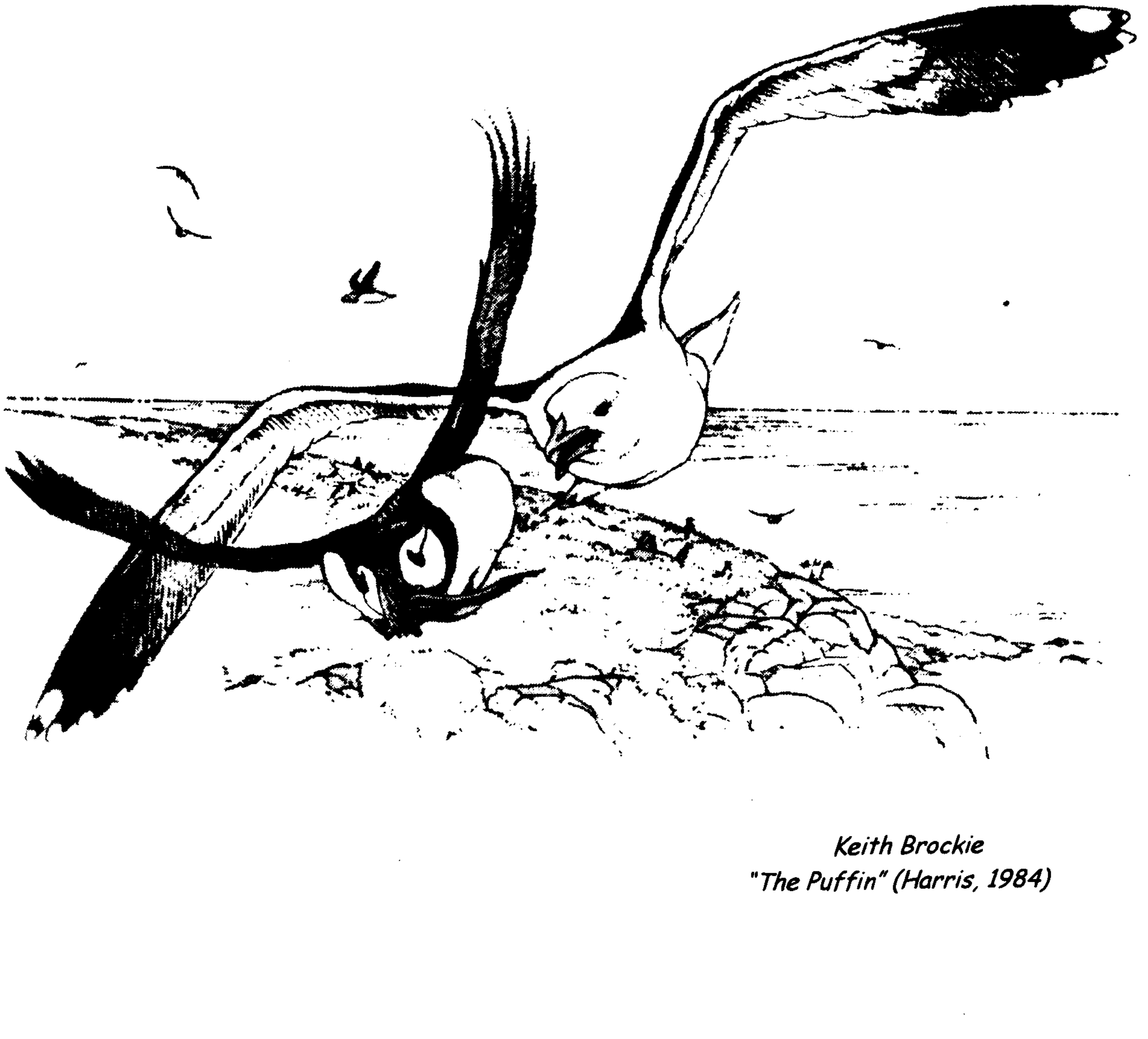
The lower provisioning rate coupled with the higher kleptoparasitism risk resulted in puffins breeding in gull-occupied habitat delivering 44% fewer food loads to their chicks in the morning and 25% fewer in the evening compared to puffins breeding in gull-free areas. However, despite this difference, there was no evidence of a significant reduction in the growth of puffin chicks or their survival to fledging.

Adult puffins did not compensate for the reduced rate of food delivery to chicks in the morning and evening by increasing foraging effort in the middle of the day; the frequency and energy content of food loads delivered to chicks did not differ significantly between puffins breeding in gull-occupied and gull-free areas. There was also no evidence that kleptoparasitism risk had a significant negative impact on the body condition of adult puffins. The body mass, haematocrit and mean corpuscular volume of puffins breeding in areas of high kleptoparasitism risk did not differ significantly from that of puffins breeding in areas where kleptoparasitic attacks were rare.

The results from this study are important given the changing population trends of gulls in Britain and Europe. In the past, when gull populations were expanding, the perceived threat of gulls to other breeding birds was often considered sufficient justification for the implementation of control procedures. More recently, gull populations have stabilised and have even shown large declines in some areas. This has lead to an increase in the conservation status of both herring and lesser black-backed gulls, which have now been designated as being of medium conservation concern. It is now no longer acceptable to base management decisions on the assumption that gulls invariably have deleterious effects on the breeding performance of other birds and should be removed. When formulating management programmes, it is important to quantify the actual impact of gulls on the species targeted for protection to ensure that any future control programmes implemented are both necessary and effective.

Chapter 1

General Introduction



Keith Brockie
"The Puffin" (Harris, 1984)

General Introduction

Interspecific interactions, such as competition and predation, are important factors affecting population dynamics and, in natural ecosystems, the maintenance of biodiversity. However, human-induced changes in the environment have caused major shifts in the balance and nature of interspecific interactions with often significant ecological consequences. For example, much conservation concern and public interest has focused on the potentially detrimental impact of introduced, exotic species on native wildlife through competition, predation and hybridisation (Manchester and Bullock, 2000). Well known examples include the introduction of the North American mink *Mustela vison* to Britain (Aars et al., 2001), the red fox *Vulpes vulpes* to Australia (Burbidge and McKenzie, 1989) and the zebra mussel *Dreissena polymorpha* to North America (Ricciardi et al., 1998).

A closely related problem, but one that has received much less attention, is the potentially important implication of locally overabundant or expanding populations of native wild animals (Garrott et al., 1993). The success of native species that have benefited from anthropogenic habitat changes can cause problems when they threaten economically valuable or rarer species. A good example in Britain is evident in the overgrazing by red deer *Cervus elaphus*, which has been shown to have a significant detrimental impact on the regeneration of both native woodlands and commercial forestry plantations (Clutton-Brock and Albon, 1989), and in predation by foxes *Vulpes vulpes*, which take domestic livestock as well as the eggs and chicks of ground-nesting birds (Green and Etheridge, 1999).

Such conflicts have frequently led to the implementation of management procedures aimed at reducing the density or spatial distribution of the undesirable species (Feare, 1991). In most cases this has involved the large scale culling of breeding adults, or the targeted removal of so-called "rogue" individuals (Bateson, 1997; Guillemette and Brouddeau, 2001). Although a detailed investigation of interspecific interactions should underpin these targeted species management strategies, this is rarely the case; most management decisions are based on the assumption that the overabundant species must have a detrimental impact on other species, and that removal of the "offenders" will relieve the problem. The need for sound scientific research on which to base management decisions has been highlighted by situations in which the so-called "pest" species is in itself of conservation interest (Jewell and Holt, 1981). Recent examples in Britain include hen harrier *Circus cyaneus* predation on commercial grouse moors and the spread of tuberculosis to livestock from wild badger *Meles meles* populations (Gallagher and Clifton-Hadley, 2000; Thirgood et al., 2000). Given the increasing anthropogenic effects on the countryside and the restriction of wildlife to limited spaces with artificial boundaries, such conflicts are likely to become more common in the future. The need for active management of wild animal populations will therefore become an increasingly important issue for conservation biologists.

An interesting example of a conflict of conservation priorities concerns the management of large gull populations. During the middle of the last century, the populations of many large gulls (*Larus* spp.) increased dramatically world-wide, probably due to anthropogenic effects such as reduced persecution and changes in food supplies (Spaans and Blokpoel, 1991). In Britain, herring gull *L. argentatus*, lesser black-backed gull *L. fucus* and great black-backed gull *L. marinus* populations increased to such an extent that they soon became regarded as pest species (Hagemeijer and Blair, 1997). In addition to posing a risk to human health through aircraft strikes and the pollution of water sources (e.g. Benton et al. 1983), expanding and colonising gull populations were thought to have deleterious effects on the breeding performance of other birds (Monaghan, 1983). Gulls frequently predate eggs, chicks and adults of other bird species and also kleptoparasitise their food loads (Oro & Martinez-Vilalta, 1994; Stenhouse &

Montevecchi, 1999). Gulls can also compete for breeding sites with other ground-nesting species (Quintana & Yorio, 1998).

The perceived adverse effects of increasing gull numbers on seabird communities led to the implementation of a widespread gull culling programme throughout Europe and North America. Between 1972 and 1987, 100 000 herring and lesser black-backed gulls were killed in Britain as part of an extensive culling programme (Coulson, 1991). However, although the occurrence of interactions between gulls and other species has been well documented (Gonzales-Solis et al., 1997; Regehr and Montevecchi, 1997), few studies have been carried out to determine whether removing gulls does indeed benefit the species targeted for protection (but see Harris and Wanless, 1997; Guillemette and Brousseau, 2001). More recently, gull populations have stabilised and have even shown large declines in some areas (Lloyd et al., 1991; Hagemeijer and Blair, 1997). This has lead to an increase in the conservation status of both herring and lesser black-backed gulls, which have now been designated as being of medium conservation concern (Gibbons et al., 1996). It is now no longer acceptable to base management decisions on the assumption that gulls invariably have deleterious effects on the breeding performance of other birds and should be removed. When formulating management programmes, it is important to quantify the actual impact of gulls on the species targeted for protection to ensure that any future control programmes implemented are both necessary and effective.

This thesis focuses on the interactions between large gulls and the Atlantic puffin *Fratercula arctica,* which is thought to be particularly at risk as it frequently nests in close proximity to gulls. Puffins are expected to be adversely affected by gulls since gulls kleptoparasitise adult birds as they return to the colony with fish and also predate puffin chicks (Harris, 1984). This work was carried out on the Isle of May, in the Firth of Forth, southeast Scotland (Fig. 1.1). This is an ideal system in which to undertake a study of the interactions between gulls and puffins as the gull population has been actively managed for the last 30 years.

The island therefore offers in effect an experimental situation, with artificially created variation in gull nest density across the island.

By acting as both competitors and predators, the presence of gulls is expected to have a significant influence on the breeding location of other birds by reducing the attractiveness of an area as a potential breeding site. ***Chapter two*** of this thesis investigates the influence of gulls on the recruitment patterns of immature puffins to the breeding colony. Following this, ***chapter three*** quantifies the actual impact of gulls on the foraging economics and reproductive performance of puffins.

Although the control of gull populations is widespread, few studies have been carried out to assess the effectiveness of different management options. The findings of an experimental manipulation to test the effectiveness of (a) maintaining gull-free areas and (b) delaying gull breeding as potential management strategies to reduce kleptoparasitism risk for puffins are reported in ***chapter three***. The impact of the delayed breeding on the reproductive output of gulls is discussed in ***chapter seven***.

Despite the often considerable loss of food to kleptoparasites, most studies investigating the impact of kleptoparasitism on the reproductive performance of the host species have found no significant reduction in the growth or survival of chicks. ***Chapter four*** investigates the possibility that adults may compensate for food loads lost to kleptoparasites by increasing foraging effort. Under such circumstances, the costs of kleptoparasitism are likely to be borne by the adult rather than transferred to the chick. ***Chapter five*** therefore assesses the impact of kleptoparasitism by gulls on the body condition of breeding adult puffins. The relationship between adult puffin body condition and reproductive performance is discussed in ***chapter six***.

In long-lived species, such as seabirds, with a high probability of survival, but low annual fecundity, even a small change in adult survival can have a significant impact on population size. ***Chapter eight*** quantifies the current level of predation of adult puffins by great black-backed gulls and uses simple population models to explore the potential impact of gull predation on breeding puffins over the next 20 years.

It is of course not just other animals that affect the status of vulnerable species. Humans can also have a direct effect. In ***chapter nine***, I consider an increasingly important threat to many wild animal population, that of visitor disturbance. In areas where visitor pressure is high, a conflict arises between the benefits of people visiting, for example due to educational and fundraising purposes, and the possible direct detrimental impact of human disturbance on the animals themselves. ***Chapter nine*** investigates the impact of visitors on adult puffin colony attendance and chick provisioning rates.

In the final discussion (***chapter ten***), the importance of behavioural research for species management and conservation is discussed.

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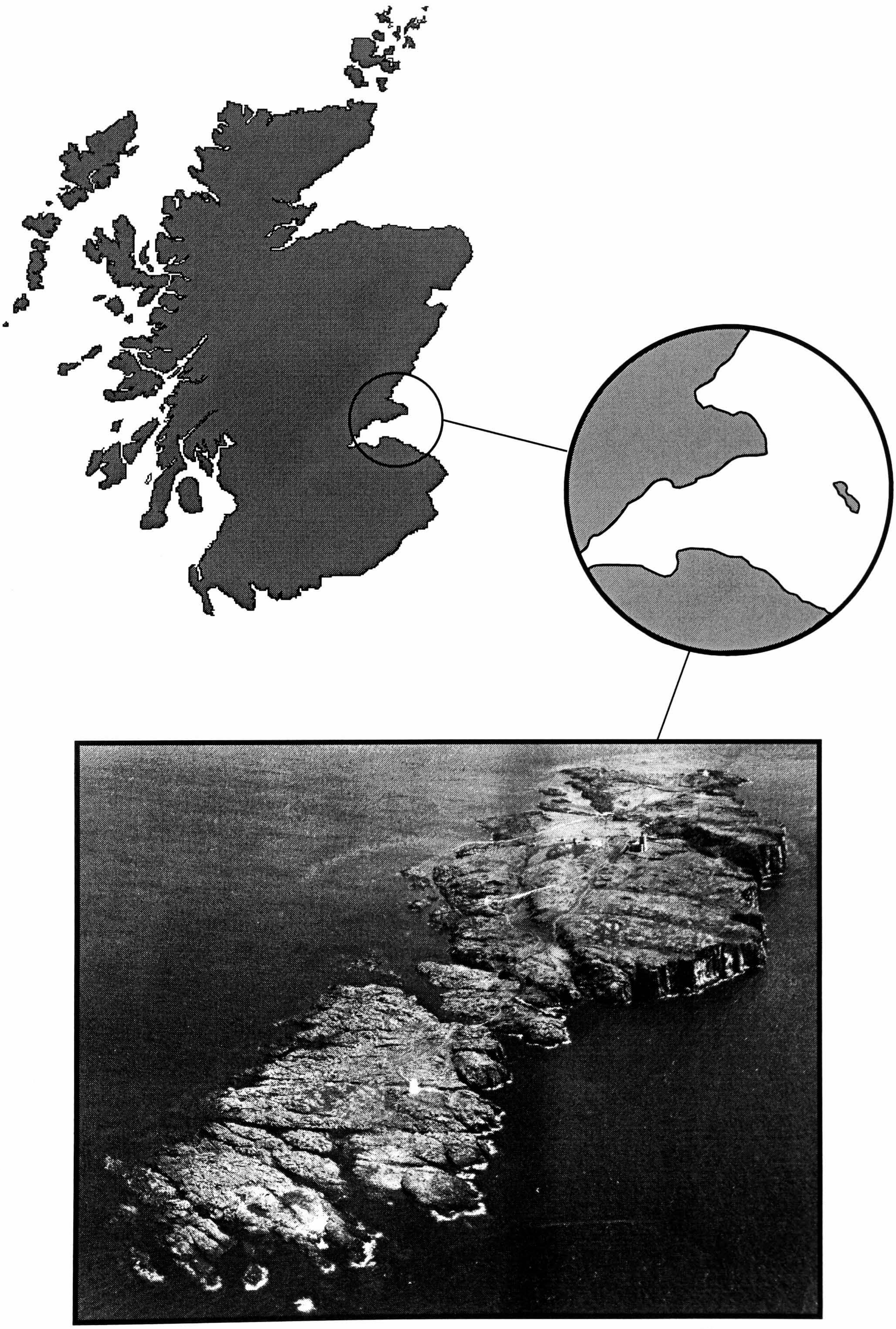
Figure 1.1: The Isle of May study site



Aerofilms Ltd, 1963

Chapter 2

Reducing the density of breeding gulls leads to enhanced recruitment of immature Atlantic puffins *Fratercula arctica* to a breeding colony.

Suzanne K. Finney, Michael P. Harris, Lukas F. Keller, David A. Elston, Pat Monaghan and Sarah Wanless. 2002. Submitted.

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Abstract

By acting as both competitors and predators, gulls (*Larus* spp.) are generally considered to significantly reduce the attractiveness of an area as a potential breeding site for other birds. This perceived threat posed by gulls to other breeding birds has led to the implementation of gull control procedures at many seabird colonies. However, the extent to which reducing gull numbers does indeed benefit other species has received little rigorous scientific investigation. During a gull control programme (1972-1989), gull nest density on the Isle of May was reduced by between 30% and 100% in different sections of the island. Following termination of the original programme in 1989, several sections were maintained as gull-free by repeated removal of nests. We used data collected over a 23 year period to determine the extent to which the spatial distribution of puffin recruitment was influenced by changes in the density and spatial distribution of breeding gulls resulting from the control programme. The presence of breeding gulls significantly affected the pattern of recruitment of puffins to the colony. Puffin recruitment rate was highest in the sections of the island where gull nest density was low. Gull density explained 21% of the variation in puffin recruitment rate. These results suggest that the reduction in the number of breeding gulls substantially increased the attractiveness of the colony as a potential breeding site for puffins and is thus likely to have played an important role in the pattern of expansion of the puffin population on the island. Following a recent increase in the conservation status of both herring and lesser black-backed gulls, there has been a move to make management decisions more objective. This has highlighted the need for studies such as this, aimed at assessing the impact of gulls and their removal on other breeding birds, to ensure that any future control programmes implemented are both necessary and effective.

Introduction

Finding a suitable place to breed is a key component of animal reproductive strategies. In highly mobile organisms such as birds, individuals are capable of covering large distances and thus can encounter and sample a wide range of potential breeding locations. Birds commonly use a variety of physical and biotic cues to assess habitat suitability such as topography (Donázar et al., 1993), vegetation cover (Probil, 1998) and food availability (Sherman, 1984; Tjernberg, 1984; Bollmann et al., 1997). The presence of other individuals can also have a strong influence on breeding location. In colonially breeding species for example, individuals often prefer to breed in close proximity to conspecifics as this can provide protection against predation (Hagelin and Miller, 1997; Larsen and Grundetjern, 1997; Danchin et al., 1998). However, the presence of other individuals is not always beneficial. Both inter and intraspecific competition for breeding sites or territories in preferred areas can force some individuals to breed in less favourable habitat (Wallace et al., 1992). The presence of a predator can also substantially reduce the attractiveness of a potential breeding site (Madsen et al., 1992; Morris et al., 1992; Howes and Montevecchi, 1993). For example, in a study of Brent geese *Branta bernicla* breeding in northern Russia, Spaans et al. (1998) found that most birds bred on small offshore islands where predation by foxes was lower than on the mainland. Birds preferentially bred on these islands despite food availability being poor compared to suitable breeding locations on the mainland.

At seabird breeding colonies, gulls (*Larus* spp.) are common predators of adults, eggs and young of other birds and may also kleptoparasitise food carrying adults (Oro and Martinez-Vilalta, 1994; Ratcliffe et al., 1997; Stenhouse and Montevecchi, 1999). Furthermore, gulls often compete for breeding sites with other ground-nesting species (Quintana and Yorio, 1998). By acting as both competitors and predators, the presence of gulls is expected to have a significant influence on the breeding distribution of other birds. Indeed, the abandonment of traditional nesting areas by terns (*Sterna* spp.) in response to the encroachment of breeding gulls has already been demonstrated in a number of studies (Wanless, 1988; Morris et al., 1992; Howes and Montivecchi, 1993). The apparent adverse effect of gulls on other breeding birds has led to the implementation of gull control procedures at many colonies. However, very few attempts have been made to determine whether the removal of breeding gulls does indeed benefit other species (but see Morris et al., 1992; Harris and Wanless, 1997; Guillemette and Brousseau, 2001). In areas where gull control measures are implemented, it is often tacitly assumed that any subsequent increase in the population size of the species targeted for protection is a direct result of the reduction in the number of breeding gulls. As this has rarely been tested explicitly, it is generally not possible to rule out the possibility that other factors may have been responsible for the population increase. It is this assumption, that removing breeding gulls leads to enhanced recruitment of other species, that we aimed to test in this study.

The population data were collected on the Isle of May, southeast Scotland. The island was designated as a National Nature Reserve in 1956 due to its large populations of breeding seabirds (Ratcliffe, 1977). Herring gulls *L. argentatus* and lesser black-backed gulls *L. fuscus* first colonised the island in 1907 and 1930 respectively, after which the numbers of both species increased rapidly, reaching a combined population size of almost 18,000 breeding pairs by the early 1970's (Eggeling, 1960; Coulson et al., 1982). At this point, a decision was made to reduce gull numbers due to the heavy predation by gulls on other resident birds (Wanless and Kinnear, 1988). During the period from 1972 to 1989, the population of herring and lesser black-backed gulls nesting on the island was reduced to 2,500 breeding pairs by the culling of adult birds and destruction of nests (Coulson, 1991; Fig. 2.1a). The control programme was terminated in 1989 and the population of herring and lesser black-backed gulls has since increased to 4,100 breeding pairs in 1998 (Harris et al., 2000). Over the same period (1975-1998), the population of Atlantic puffins breeding on the island increased from 3,000 breeding pairs to over 42,000 breeding pairs (Harris et al., 2000; Fig. 2.1b). Although there is no direct competition between gulls and puffins for breeding sites, gulls frequently predate young puffins and kleptoparasitise adult birds as they return to the colony with fish (Harris, 1984; Finney et al., 2001). The presence of gulls would therefore be expected to reduce the attractiveness of an area as a potential breeding site for puffins. The aim of this study was to determine the extent to which the removal of breeding gulls influenced the recruitment of Atlantic puffins *Fratercula arctica* to the Isle of May breeding colony.

Gulls predominantly target puffins that breed in close proximity to them (Finney et al., 2001). As such, if the reduction in the number of breeding gulls influenced puffin recruitment to the island, we would expect this to be reflected in the local patterns of recruitment within the colony. We would predict puffin recruitment rate to be highest in the areas of the colony where gull nest density is low. The Isle of May provided an ideal system in which to test this prediction as the extent to which gull nest density was reduced varied spatially across the island with management effort being focused in particular areas. In some sections of the island gulls were removed completely, while in others gull nest density was reduced to a much lesser extent (Wanless and Kinnear, 1988). The island therefore represented an experimental situation, with artificially created variation in gull density both between plots and within plots through time. In this study, we were able to use this spatial and temporal variation in gull nest density on the island to determine if the removal of large numbers of breeding gulls influenced the pattern of recruitment of puffins to the colony.

Methods

The Isle of May (56°11'N, 2°33'W) is 57 hectares in size with 50 m high cliffs along its west and south west sides. Elsewhere on the island the ground slopes gently down to the sea. 12 plots were used for comparison in this study (Fig. 2.2). These plots were selected as they were the same as those used to delineate areas differing in the intensity of gull management effort during the gull control programme. Management effort was focused on areas where gull density was particularly high or where gulls nested in close proximity to terns (Wanless and Kinnear, 1988). Four sections of the island, where gull numbers were reduced during the original control programme, have since been maintained as gull-free areas as part of the current management regime (areas 6-8 and 10 shown in Fig. 2.2).

Counts of the number of occupied puffin burrows (as indicated by fresh digging, faeces or regular wear) in each study plot were made at the end of April in 1975, 1984, 1989, 1992 and 1998. Counts of the number of gull nests in each study plot were made annually at the end of May. All gull nests containing eggs were counted and empty nests, if well-built, were also included since these were likely to involve late breeders (full details in Wanless et al., 1996). Gull nest density was calculated by dividing the number of nests counted in each plot by the total area of the plot. In the calculations of puffin burrow density, the area of exposed bedrock in each study plot was subtracted from the total area of the plot as it was unavailable to puffins as breeding habitat. All 12 plots contained suitable breeding habitat for colonising puffins in terms of soil depth and vegetation cover.

As puffins usually return to the same burrow each year to breed (Harris, 1984), an increase in burrow density reflects first-time breeders recruiting to the colony rather than a change in the location of established breeding individuals. Changes in puffin burrow density between years can therefore be used as a measure of recruitment rate. One limitation of this method is that the measurement of puffin recruitment rate could be influenced by changes in adult mortality, as unoccupied burrows can be re-used by recruiting individuals. However, the annual survival rate of adult puffins decreased during the study period from a mean of 97.5% between 1973 and 1980 to a mean of 92.4% between 1981 and 1993 (Harris et al., 1997). The increase in puffin recruitment rate recorded during this time is therefore a conservative estimate. Furthermore, in addition to being low, adult mortality is also likely to be uniform across the colony since it occurs mainly outside of the breeding season. We were therefore able to assess the impact of gull removal on the spatial distribution of puffin recruitment by comparing the rate of change in puffin burrow density between plots that differed in the density of breeding gulls.

Statistical analysis

Puffin recruitment rate was calculated separately for each plot and was expressed as the mean number of new burrows per hectare per year between successive puffin counts. Gull density was taken as the mean nest density during the period between successive puffin counts. The relationship between gull density and puffin recruitment rate was analysed in a linear mixed model using REML (Restricted maximum likelihood; Patterson and Thompson, 1971; SAS, 1996). This technique allowed repeated measurements within plots through time to be accounted for by including "plot" as a random effect. The model had a repeated measures design for time within plot and an unstructured covariance matrix. For each fitted model, the mean of the four diagonal elements was calculated and this was used as a measure of unexplained variance. Fixed effects included in the models were puffin density at the beginning of each time period studied, time period and gull density. The interactions between gull density and time period and gull density and puffin density were also included. Denominator degrees of freedom for F-tests for inclusion of fixed effects were calculated using Satterthwaite's approximation (Sattherthwaite, 1946). Means are presented ± one standard error.

Results

Puffin recruitment rate

Puffin recruitment rate differed significantly among the four time periods studied (Fig. 2.3). Mean recruitment rate for the island as a whole ranged from 8 to 62 burrows/hectare/year. The variation between plots in puffin recruitment rate also differed between time periods, being lowest during the period 1975-1984 (range 2 to 82 burrows/hectare/year) and greatest during the period 1992-1998 (range -59 to 240 burrows/hectare/year). The trends in recruitment rate were similar in the different study plots. There was a significant positive relationship between the mean annual recruitment rate during each time period and puffin burrow density at the beginning of the time period (Fig. 2.4). Having included time period in the model as a fixed effect, puffin density at the beginning of the time period explained 11% of the remaining variance in puffin recruitment rate. Puffin density was retained in the model as a covariate when analysing the relationship between puffin recruitment rate and gull nest density.

Relationship between gull nest density and puffin recruitment rate

In 1975, gulls nested over much of the island although nest density differed markedly between the study plots, ranging from 7 to 192 nests/hectare. The gull control programme resulted in a substantial reduction in the number of breeding gulls. However, this decrease was not uniform across the island; the extent to which gull nest density was reduced varied from 30% to 100% among the study plots, with management effort being focused in particular areas. The control programme was terminated in 1989 and by 1998, eight of the twelve study plots had shown an increase in gull nest density. The remaining four plots were actively maintained as gull-free by repeated removal of nests.

The impact of nesting gulls on puffin recruitment rate differed significantly among the four time periods studied (interaction between gull nest density and time period, $F_{3,12}=3.62$, $P<0.05$, Fig. 2.5). There was no significant relationship between puffin recruitment rate and gull density during the two periods spanning 1975-1989, the time when culling took place. However, during the two periods spanning 1989-1998 (i.e. following termination of the gull control programme), puffin recruitment rate was significantly lower in the areas of the island where gull nest density was relatively high. The interaction between gull nest density and puffin burrow density at the beginning of the time period was also significant ($F_{1,7}=13.5$, $P<0.008$), the impact of gulls on puffin recruitment rate increasing as puffin density increased. Having already included time period and puffin burrow density in the model, gull nest density explained a further 21% of the variance in puffin recruitment rate. The final model explained 72% of the variance in puffin recruitment rate on the Isle of May.

Discussion

The results from this study support the prediction that the presence of breeding gulls reduces the attractiveness of an area as a potential breeding site for puffins. The recruitment rate of immature puffins to the breeding colony was significantly lower in the areas of the island where gull nest density was high. However, this effect was not evident in all years. The negative relationship between gull nest density and puffin recruitment rate was only significant during the period 1989 to 1998, after the gull control programme had terminated. During the period 1975 to 1989, there was no detectable effect of gulls on the recruitment rate of immature puffins to the colony, despite gull density being higher at this time. There are several possible explanations for these findings.

First, the impact of gulls on puffin recruitment rate was highest when puffin burrow density was high and, in all sections of the island, puffin burrow density was higher during the latter part of the study period. The reason for the greater impact of gulls in areas where puffins were breeding at high density is unclear but may be related to changes in the extent to which gulls target breeding puffins as a food source. In a previous study of puffins in Newfoundland, Rice (1987) found that gulls were sensitive to the pay-off from kleptoparasitism and that the frequency at which gulls attacked returning puffins was significantly higher when there were many puffins returning to an area with fish compared to when there were few. Kleptoparasitism by gulls may therefore represent a greater threat when puffins are breeding at high density. A second potential explanation relates to changes in the level of human disturbance on the island during the study period. Throughout the gull control programme, the amount of human disturbance on the island was very high. However, the level of disturbance in each of the study plots varied in intensity and also differed between years depending on the particular section of the gull colony that was being targeted at that time (Wanless and Kinnear, 1988). The impact of gulls on puffin recruitment only became apparent after 1989, which coincided with the termination of the control programme and a dramatic reduction in the level of disturbance at the colony. Prior to 1989, human disturbance may have had a stronger influence than gull nest density on the patterns of puffin recruitment to the island.

The negative relationship between gull nest density and puffin recruitment rate observed in this study is in contrast to the results of Pierotti (1983), who found that Atlantic puffins breeding on Great Island, Newfoundland, preferentially nested in areas of high herring gull nest density. One explanation given was that the puffins may have gained protection from the reaction of herring gulls to other, more serious predators such as great black-backed gulls *L. marinus* and ravens *Corvus corax* (Pierotti, 1983). On the Isle of May, great black-backed gulls are the only resident predators of adult puffins. The number breeding on the island increased from zero to 14 pairs during the course of this study (Scottish Natural Heritage unpublished accounts) and, given the large size of the puffin population, the risk of predation to adult birds was therefore relatively low. The potential benefits that adult puffins may have gained by breeding in areas occupied by herring and lesser black-backed gulls may not have been sufficient to outweigh the costs of increased kleptoparasitism risk and predation of chicks. The results from this study do however demonstrate that the pattern of recruitment of immature puffins to the colony was significantly affected by the location of other breeding puffins. Recruitment rate was higher in the areas of the colony where puffins were breeding at high density compared to the areas where puffin density was low. Preferential selection of high density areas in which to breed is common amongst colonially breeding birds and has been linked to increased reproductive performance in a number of species, including puffins (Harris, 1980; Gilchrist, 1998; Massaro et al., 2001).

The expansion of the puffin population on the Isle of May appears to have involved immigration of puffins to the island, in addition to natal recruits. This is evident from a simple population model. If we assume (a) an annual adult survival rate of 98.9%, (b) an annual breeding success of 93% and (c) that 37% of fledged chicks return to the colony to breed when five years old (the maximum values ever recorded at this colony: Harris 1985, Harris et al. 1997), then the maximum possible rate of increase of the puffin population would be 10.7% year^{-1}. The actual mean rate of increase during the study period was 12% year^{-1} indicating that there was substantial immigration of puffins to the Isle of May colony from elsewhere. Thus, the population expansion involved an enhanced recruitment rate, rather than being simply a consequence of improved puffin breeding success following gull control.

In conclusion, we found that puffins recruiting to the Isle of May breeding colony avoided nesting in close proximity to gulls. The evidence from this study therefore suggests that, by reducing both the density of breeding gulls and restricting the area where gulls were allowed to nest, the control programme substantially increased the attractiveness of the island as a potential breeding site for puffins and is thus likely to have influenced the pattern of recruitment of puffins to the island over the last 25 years. Management programmes aimed at controlling the numbers of breeding gulls have been commonplace in both Europe and North America over the past 30 years, but until recently, very few were accompanied by detailed monitoring to determine if gull removal did indeed benefit the species targeted for protection (but see Harris & Wanless 1997; Guillemette & Brousseau 2001). In the past, gulls were regarded as pest species and this was often considered sufficient justification for the implementation of control procedures. However, in a recent review of the conservation status of British birds, both herring and lesser black-backed gulls were designated as being of medium conservation interest (Gibbons et al. 1996). In light of this review, decisions regarding the management of breeding gulls must now be assessed more objectively. This has highlighted the need for studies aimed at assessing both the impact of gulls on other species and the effectiveness of different gull management strategies. Studies such as this will ensure that any future control programmes implemented are both necessary and effective.

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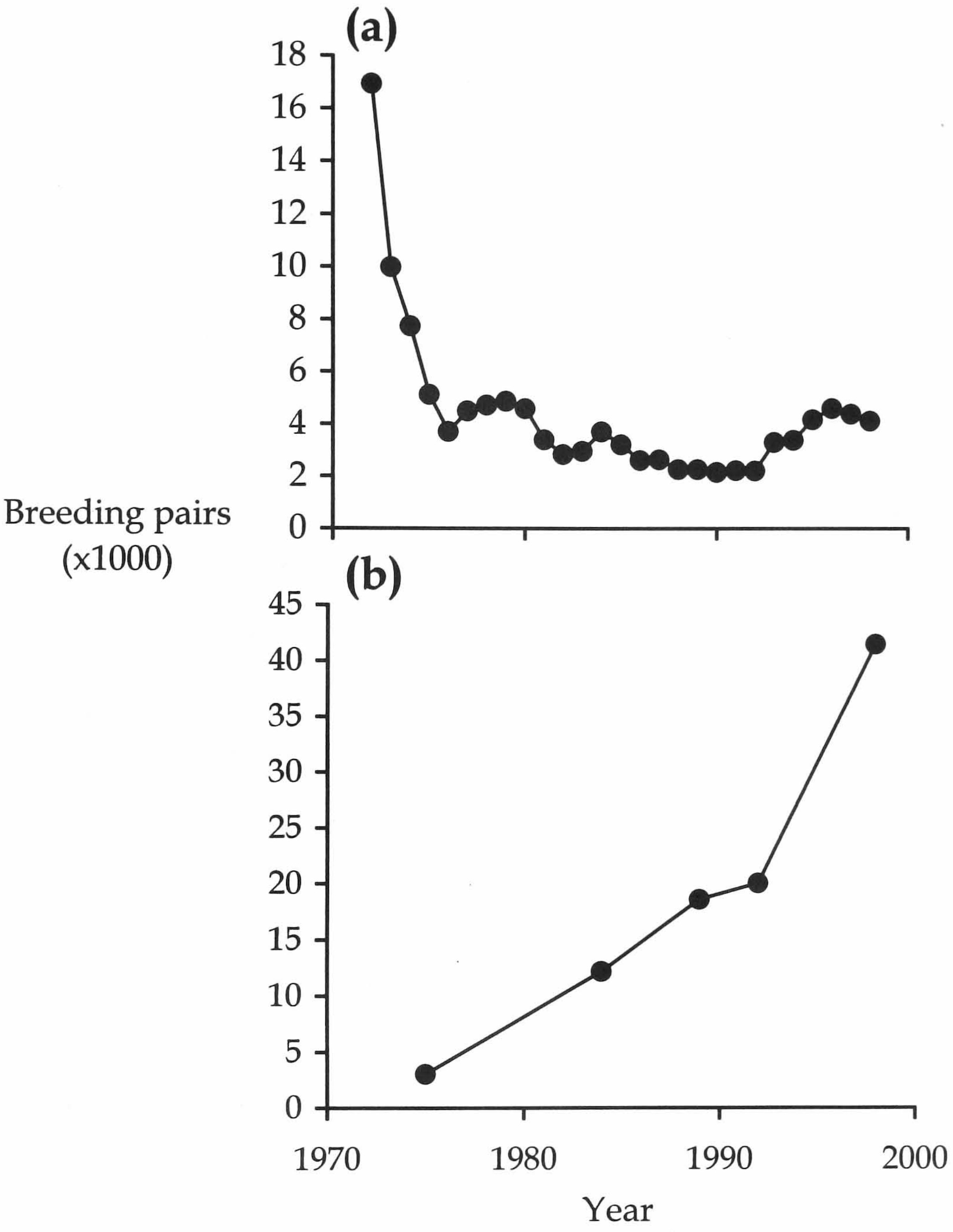

Figure 2.1: Population size of (a) herring and lesser black-backed gulls and (b) Atlantic puffins breeding on the Isle of May.

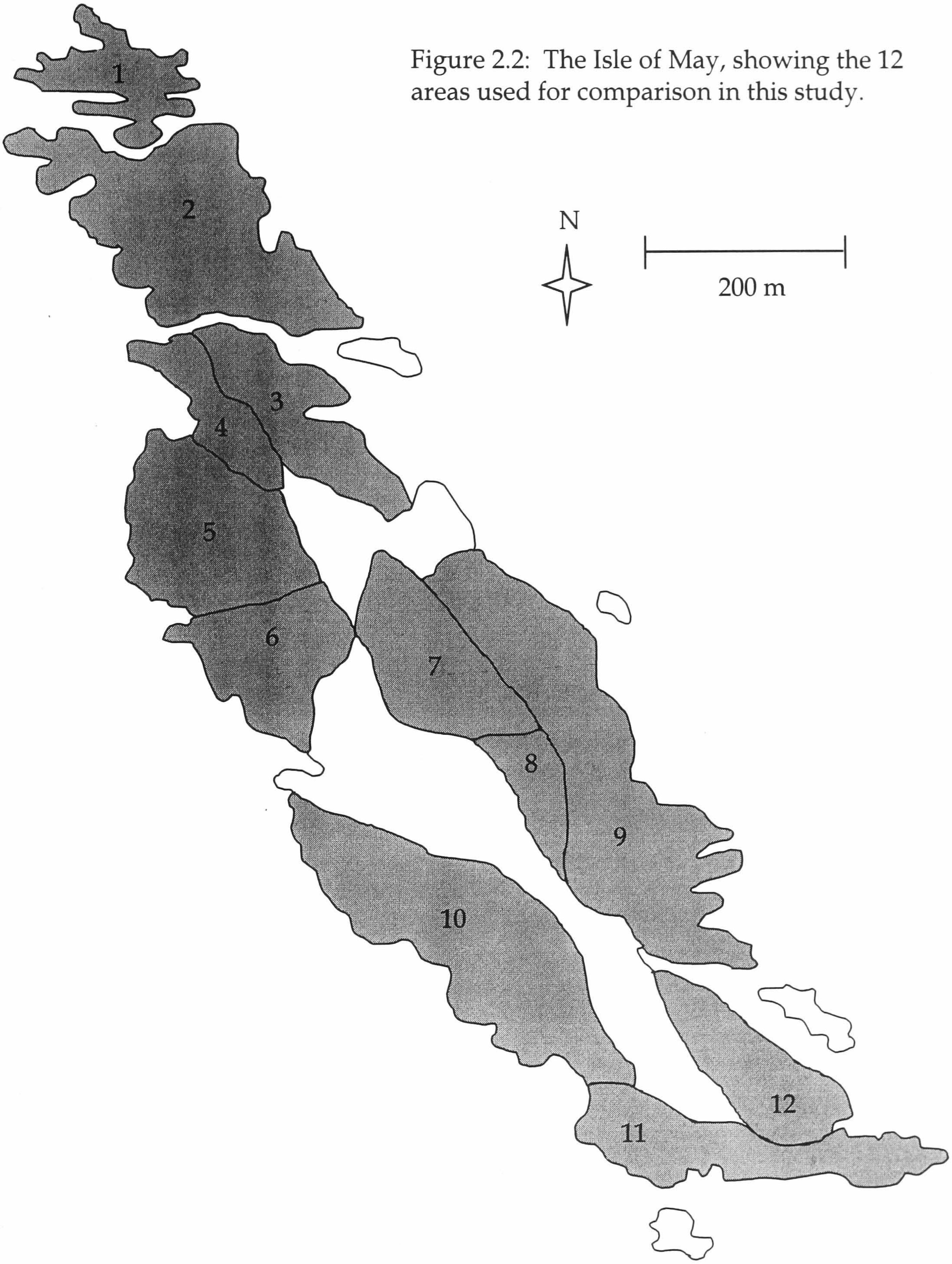

Figure 2.2: The Isle of May, showing the 12 areas used for comparison in this study.

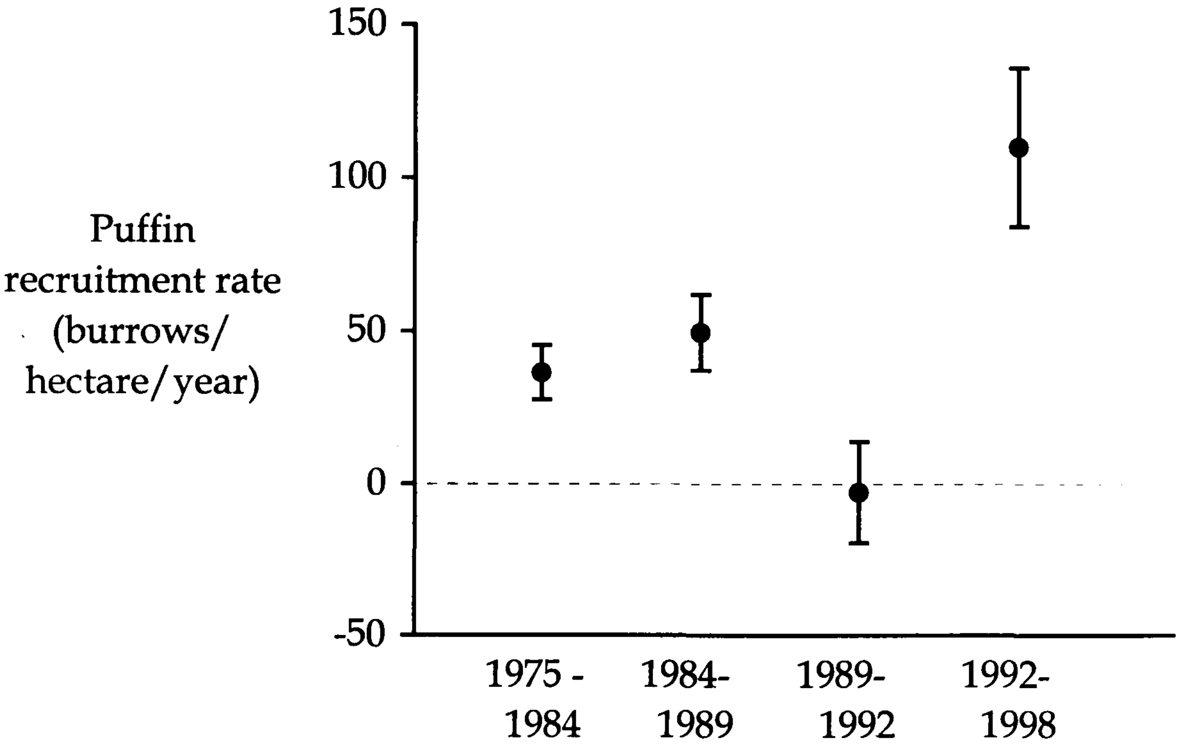

Figure 2.3: Mean (+/- one standard error) puffin recruitment rate on the Isle of May measured during four time periods between 1975 and 1998. There was a significant difference among time periods in puffin recruitment rate (Results from linear mixed model with a repeated measures design: $F_{3,13}$=6.91, P <0.006).

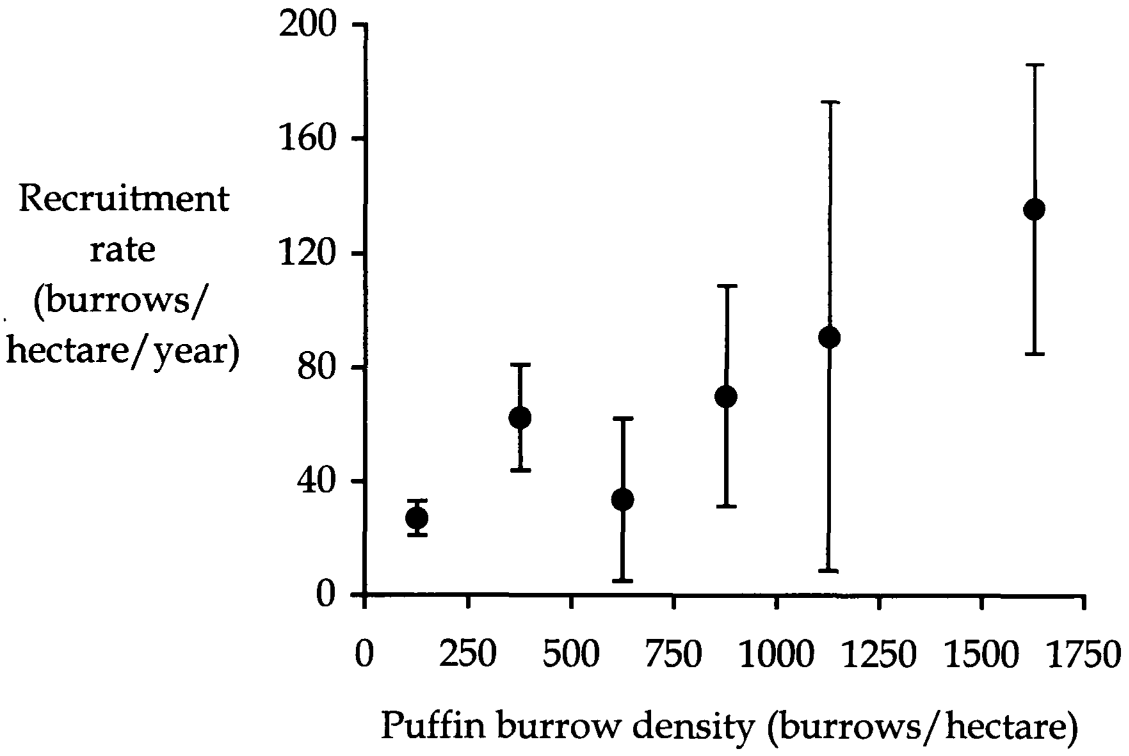

Figure 2.4: Relationship between puffin burrow density at the beginning of each time period studied and the mean annual recruitment rate of puffins during that time period (Results from linear mixed model with a repeated measures design: $F_{1,7}$=97.99, P<0.0001). For clarity, means (+/- one standard error) at intervals of 250 burrows/hectare are shown.

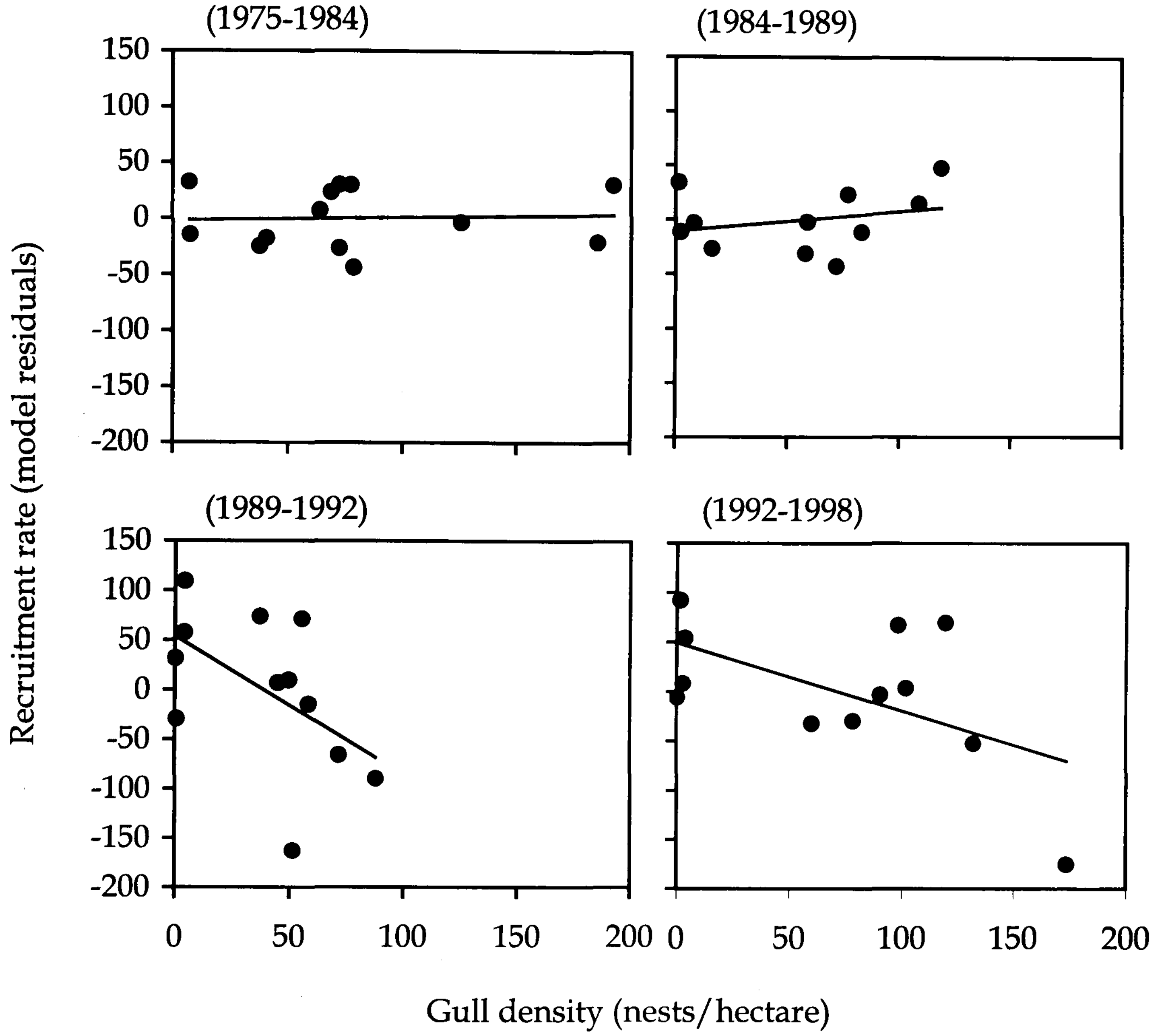

Figure 2.5: Relationship between puffin recruitment rate and gull-nest density on the Isle of May during four time periods between 1975 and 1998. Residuals from a linear mixed model with a repeated measures design, having controlled for the significant effects of time period and puffin burrow density at the beginning of each time period, are shown. Trendlines fitted using least-squares regression.

Chapter 3

The impact of gulls on puffin reproductive performance: an experimental test of two management strategies

Suzanne K. Finney, Sarah Wanless, Michael P. Harris, Pat Monaghan. 2001. Biological Conservation 98, 159-165.

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Abstract

Gulls frequently predate eggs and young and kleptoparasitise other seabirds during the breeding season. This has lead to the implementation of gull control programmes at many colonies. However, few studies have been carried out to assess the effectiveness of different management options. We investigated the impact of (a) maintaining gull-free areas and (b) delaying gull breeding, on the foraging economics and breeding success of puffins. Puffins breeding in gull-free habitat provisioned their chicks at a higher rate and had a lower risk of kleptoparasitism than puffins breeding in gull-occupied habitat. However, there was no significant difference between gull-free and gull-occupied habitat in puffin chick growth or survival. Delaying gull breeding by approximately three weeks had no impact on mean kleptoparasitism risk or the rate at which adult puffins provisioned their chicks. In line with these results, we found that delaying gull breeding had no impact on puffin chick growth or survival. Our results suggest that, under current conditions, gulls do not have an immediate negative impact on puffin reproductive performance.

Introduction

Many populations of birds show high annual variation in breeding success (Ainley and Boekelheide, 1990; Newton, 1999). The most dramatic fluctuations are often the result of stochastic phenomena such as adverse weather conditions (Elkins, 1983; Cucco et al., 1992) or changes in food supplies (Martin, 1987; Barrett and Krasnov, 1996). However, reproductive success can also be affected by more predictable events such as interactions with other breeding birds. Both interspecific and intraspecific interactions during the breeding season can affect reproductive success directly, through the predation of eggs and chicks (Grant et al., 1999), or indirectly through competition for nest space (Howes and Montevecchi, 1993) or kleptoparasitism (Brockmann and Barnard, 1979; Furness, 1987).

Much work on interspecific interactions has focused on gulls (*Larus* spp.), which frequently predate eggs and chicks and kleptoparasitise other birds during the breeding season. Concern regarding the possible detrimental impact of gulls on the breeding success of other species increased when gull populations in Europe and North America expanded rapidly during the second half of the last century (Spaans and Blokpoel, 1991; Hagemeijer and Blair, 1997). The apparent adverse effect of gulls on other seabirds resulted in the implementation of gull control programmes at many colonies. One of the most common gull management strategies used was the removal of gulls from specified areas, usually through systematic culling of adult birds or repeated destruction of nests (Morris et al., 1992; Bosch, 1996). The latter is now most frequently used, and assumes that preventing gulls nesting in close proximity to the target species will relieve the problem. More recently, gull populations have stabilised and are even beginning to decline in some areas and there has been a move to make management decisions more objective and to investigate alternatives to gull removal. However, although the occurrence of interactions between gulls and other breeding birds has been well documented (Osorno et al., 1992; Gonzales-Solis et al., 1997), few studies have quantified the impact of gull management programmes on the reproductive success of the species targeted for protection (but see Harris and Wanless, 1997). One species selected for protection is the Atlantic puffin (*Fratercula arctica*), which may be particularly vulnerable as it frequently nests in close proximity to gulls.

Puffins are highly colonial, burrow-nesting auks that lay a single egg clutch. The chick is brooded and fed by both members of the pair and remains in the burrow for 38-44 days (Cramp, 1977). Adult puffins provision their chick with loads of several fish that are carried cross-wise in the bill. Gulls frequently patrol puffin nesting areas apparently looking for displaced eggs and chicks or dropped fish. However, the most common interaction between gulls and puffins is kleptoparasitism, gulls attacking adult puffins as they return to the colony with fish. Gulls can attack puffins in the air but most attacks occur on the ground as a puffin lands near its burrow with food for the chick (Grant, 1971; Harris, 1984). Kleptoparasitism has the potential to affect the reproductive success of puffins both directly, through the loss of food for the chick and indirectly, as a result of increased energetic costs to adults associated with avoidance and escape behaviours.

We carried out a detailed investigation into the effects of herring gulls (*L. argentatus*) and lesser black-backed gulls (*L. fuscus*) on the foraging economics and breeding success of puffins and carried out experimental manipulations to test the effectiveness of two different gull management strategies. We evaluated the effectiveness of maintaining gull-free areas as a management procedure by comparing kleptoparasitism risk and reproductive performance of puffins breeding in gull-occupied habitat with that of puffins nesting in areas kept free of breeding gulls. Furthermore, it is likely that kleptoparasitism risk will be highest when gulls and puffins have synchronous breeding periods, as the peak energy demand of gull chicks will coincide with the maximum rate of food delivery to puffin chicks (Harris, 1984; Drent et al., 1992). We experimentally delayed gull breeding and monitored kleptoparasitism risk and puffin reproductive performance to assess the effectiveness of altering the relative timing of breeding as an alternative management strategy.

Methods

Study site

The study was carried out on the Isle of May, Firth of Forth, Scotland (56°11'N, 2°33'W) during the 1999 breeding season. The island supports over 42000 breeding pairs (bp) of puffins and is the largest colony on the east coast of Scotland. During the period from 1972 to 1989 the population of herring and lesser black-backed gulls nesting on the island was reduced from 18000 to 2000 bp, by culling adult birds and destruction of nests, as part of a gull control programme (Coulson, 1991). With the exception of 1994, when approximately one-third of pairs on the island were prevented from rearing chicks (Wanless et al., 1996), no further attempt was made to control breeding. The population has since increased to 4200 bp in 1999 (Scottish Natural Heritage unpublished accounts). There is a high degree of overlap in the spatial distribution of breeding gulls and puffins on the island. The current management regime involves maintaining gull-free areas by repeated removal of gull nests.

Experimental design and sampling procedure

Data were collected from 24 (8 m x 8 m) study plots, containing active puffin burrows, distributed across the island in the main gull and puffin breeding areas. The gull and puffin breeding colonies were mapped in detail in 1998 and this information was used to select the locations of the study plots used in the 1999 experiments. Eight plots were in areas where there were no breeding gulls (gull-free; no breeding gulls within a 50 m radius of the centre of the study plot) and 16 plots were in areas with breeding gulls (five or more breeding pairs of gulls within a 10 m radius of the centre of the study plot). In eight of the 16 plots with breeding gulls, gulls were left to breed normally (gull-normal); in the remaining eight plots, gull breeding was experimentally delayed by removal of the first clutch (gull-delayed). Plots assigned to the gull-normal and gull-delayed treatment groups had a similar density of gull nests (gull-normal, mean 0.026 ± 0.004 nests/m^2; gull-delayed, mean 0.032 ± 0.005 nests/m^2; t_{14}=0.85, n.s.), and all three treatment groups (gull-normal, gull-delayed and gull-free) had a similar density of active puffin burrows (ANOVA: $F_{2,21}$=0.02, n.s.; overall mean 0.44 ± 0.03 burrows/m^2). Plots from the three groups were interspersed across the island to minimise potential biases caused by intracolony differences in puffin breeding performance (Harris, 1980). The physical plot characteristics such as slope angle, aspect and distance from the sea were similar in the treatment groups, as was the level of background disturbance by tourists. Disturbance by researchers was also similar as all plots were visited daily to monitor gull laying and hatching dates and to remove eggs.

Systematic observations of puffin and gull activity were carried out twice daily, from 0500-0700 and 1915-2115 BST to coincide with the two peaks of puffin feeding activity (Harris, 1984). Observations were made from a temporary hide situated *c.* 3 m from the study plot. Watches were carried out either by an observer or by using a video recording system. Hides were erected at least 5 hours before the start of each watch. The puffin feeding rates observed during this study did not differ significantly from those recorded in a long-term study plot in the same year where there was a permanent hide; this suggests that the presence of the hide did not alter puffin feeding behaviour. However, the kleptoparasitism rate recorded by an observer was consistently lower than that obtained using the video, possibly due to observer inaccuracy or, more likely, because gulls were aware of the presence of an observer in the hide. The video data were therefore considered more reliable and the subsequent analyses of kleptoparasitism risk were carried out using only data recorded from the video. When a puffin with fish landed in the study plot the following data were recorded: time, whether the bird was attacked and, if attacked, the species of gull involved and the outcome of the interaction. A kleptoparasitic attack was defined as a gull making a direct, rapid movement towards a puffin that had just landed with fish. In practice, identification of an attack was simple as there were very few ambiguous interactions. Kleptoparasitism risk was calculated as the percentage of puffins landing with fish that were attacked. Success rate was calculated as the percentage of attacks that were successful. An attack was counted as being successful if the puffin lost some or all of its load. Six 2 hour watches were carried out at each plot; watches spanned the chick rearing period.

In order to examine whether the risk of kleptoparasitism from gulls caused puffins to alter the food brought back to the chicks, puffin food loads were compared in areas with and without breeding gulls. To minimise disturbance in the main study plots, these food loads were collected from two additional study areas, one within the gull colony and a second in a nearby gull-free area. To ensure that complete food loads were collected, specially designed tubes were made which fitted into the burrow entrance and temporarily blocked parental access to the chick. Adult birds returning with food entered the tubes, dropped the fish and flew away; handling of adult puffins was therefore not necessary. A hide was used to watch for puffins arriving with loads. Dropped loads were collected immediately and stored in sealed plastic bags. All samples were collected between 0500-0630 BST from 12 June to 14 July. Each food load was weighed and the species and length of each fish was recorded. Calorific values were estimated using equations from Harris and Hislop (1978) and Hislop et al. (1991).

Puffin breeding parameters

During incubation, 300 burrows with eggs were marked and checked again approximately 8 weeks later. Burrows in which fresh faeces or a large chick were present were considered to have fledged successfully (Harris, 1980). Breeding success was calculated as the percentage of burrows with eggs that fledged a chick. Approximately 10 burrows in each plot were selected for detailed monitoring. Burrows containing incubating adults were checked every 12 days until the egg hatched or was lost. Each chick was then weighed and measured (maximum wing chord) every four days initially and then every day towards fledging. Fledging date was taken as the day the chick was first recorded as absent.

Adult puffins are very sensitive to disturbance during incubation and the first few days of brooding (Harris, 1984), and so hatching dates could not be obtained directly. Hatching dates were therefore estimated by comparing wing lengths of study birds with those from a sample of known age chicks. Equations fitted to growth curves were based on the logistic equation (Ricklefs, 1967) but were adapted to have a fixed intercept [Eq.1]. The growth constant (k) is proportional to the maximum growth rate and can be used to make comparisons between chick growth curves fitted with the same equation. Only growth curves from chicks that fledged were used in the analyses.

$$w = \frac{a}{1 + [(\frac{a-i}{i}) * (e\hat{}(-k * age))]} \qquad \text{[Eq.1]}$$

where *w* is wing length or weight, *a* is the asymptote, *i* is the intercept and *k* is the maximum growth rate. The intercept was set at 20 mm for wing length and 40 g for weight following Harris (1984).

Statistical analyses

Differences between treatment groups in kleptoparasitism risk and breeding success were analysed using a generalised linear model with binomial errors and a logit link function. Differences between treatment groups in provisioning rate were analysed using a generalised linear model with poisson errors and a log link function. Group and time of day were included in the initial model. Parameters were retained in the final model if their deletion lead to a significant increase in deviance; significance was examined using the F-distribution and the chi-squared distribution (see Crawley, 1993). Data were corrected for overdispersion when necessary. Differences between treatment groups in hatching date and fledging period were analysed using a Kruskal-Wallis test on the means for each plot. Nested ANOVA was used to test for differences between treatment groups in all other breeding parameters. Means are presented ± one standard error.

Results

Maintaining gull-free areas

Kleptoparasitism risk was significantly lower in gull-free plots than in gull-normal plots (Fig. 3.1). There was no difference between herring and lesser black-backed gulls in the success of these attacks, which was 18% (19/103) and 12% (6/51) respectively (*G*-test: df=1, *G*=1.13, n.s.). The proportion of attacks carried out by herring and lesser black-backed gulls was consistent with the proportions in which the two species were found on the island (67% (103/154) herring gull attacks, 67% (3115/4634) herring gulls on island; *G*-test: df=1, *G*<0.01, n.s.). Puffin chick feeding rate was significantly higher in the morning than in the evening as is typical of this species (Harris, 1984; Fig. 3.2) but kleptoparasitism risk did not vary with time of day (GLIM: $F_{1,13}$=1.45, n.s.). However, while there was no significant difference between gull-free and gull-normal plots in feeding frequency in the evening, puffins in gull-free plots brought food to their chicks at a substantially higher rate in the morning than did puffins breeding in gull-normal habitat (Fig. 3.2). Since these frequencies do include loads subsequently lost to gulls, they represent a real difference in the rate at which parents attempted to provision their chicks. Overall breeding parameters for puffins in the gull-normal and gull-free plots are shown in Table 3.1. There was no significant difference between gull-normal and gull-free plots in breeding success or any of the other breeding parameters measured.

Puffins brought back a wide range of food items during the breeding season. Out of a total of 59 loads collected, 69% contained the lesser sandeel (*Ammodytes marinus*), 49% contained clupeids (herring *Clupea harengus* or sprat *Sprattus sprattus*), 12% contained cod (*Gadus morhua*) and 7% rockling (*Ciliata septentrionalis*). There was no evidence for a significant difference in food loads brought in by puffins breeding in gull-free habitat compared to gull-normal habitat in the number of fish per load (gull-normal, mean 15.2 ± 1.3 fish/load; gull-free, mean 13.2 ± 1.6 fish/load; t_{51}=1.00, n.s.), species composition (*G*-test: df=4, *G*=4.27, n.s.), weight (gull-normal, mean 9.50 ± 0.86

g; gull-free, mean 10.46 ± 0.51 g; t_{41}=0.95, n.s.) or total energy content (gull-normal, mean 51.6 ± 7.6 kJ; gull-free, mean 45.8 ± 2.9 kJ; t_{29}=0.71, n.s.).

Delaying gull breeding

Removal of the first clutch delayed peak hatching of gull chicks by *c*. 3 weeks in the experimental plots, with the median hatching date being 12 June for gull-normal plots and 4 July for gull-delayed plots; the median puffin hatching date was 27 May. Chick rearing periods were from 23 May to 24 August and from 24 June to 27 August for the gull-normal and gull-delayed plots respectively; the puffin chick rearing period was from 18 May to 20 August. While there was no evidence of a difference between gull-normal and gull-delayed plots in the mean number of chicks produced per nest (overall mean 1.44 ± 0.13 chicks/nest; t_{12}=0.83, n.s.), the mean density of gull chicks in the study plots was lower for the gull-delayed group (mean 0.024 ± 0.006 chicks/m^2) than for the gull-normal group (mean 0.039 ± 0.006 chicks/m^2). This was because not all pairs that had their first clutch removed laid a second clutch.

The mean hourly feeding frequency of puffin chicks was again significantly higher in the morning (0.50 feeds/chick/hour) than in the evening (0.32 feeds/chick/hour; GLIM: df=1, χ^2=5.61, $P<0.05$) but there was no significant difference in feeding frequency of puffin chicks between gull-normal and gull-delayed plots (GLIM: df=1, χ^2=2.49, n.s.). The risk of puffins bringing food to their chicks being kleptoparasitised was not affected by delaying the breeding of the gulls (37% risk in gull-normal plots, 31% in gull-delayed plots; GLIM: $F_{1,14}$=0.90, n.s.), nor was there a difference in the temporal pattern of risk (time of day, GLIM: $F_{1,14}$=0.002, n.s.). Moreover, kleptoparasitism risk did not differ significantly between treatment groups in either June (when hatching had not begun in the delayed plots) or July (Fig. 3.3), suggesting that the need to feed chicks was not a primary determinant of gull kleptoparasitic behaviour. The success rate of the kleptoparasitic attacks was also similar between the gull treatments, 14% (25/183) and 15% (27/180) for gull-normal and gull-delayed plots respectively (*G*-test: df=1, *G*<0.01, n.s.). Overall breeding parameters for puffins in the gull-normal and gull-delayed plots are shown in Table 3.1. There was no significant difference between the two treatment groups in breeding success or any of the other breeding parameters measured.

Discussion

The results from this study demonstrate that maintaining gull-free areas as a management strategy was effective at reducing the frequency at which puffins were attacked by gulls. Kleptoparasitism risk was 37% in gull-normal habitat compared to only 5% in gull-free habitat. These results also indicate that gulls predominantly attacked puffins that bred in close proximity to them and did not move outwith the main gull breeding areas to attack puffins elsewhere on the island. However, although puffins breeding in gull-normal habitat had a high risk of being attacked, the success of both herring and lesser black-backed gull attacks was relatively low, being between 10 and 20% for both species. This was lower than that reported by Nettleship (1972) and Pierotti (1983) for glaucous-winged gull (*L. glaucescens*) attacks on tufted puffins (*F. cirrhata*) on Great Island, Newfoundland, where 30% of gull attacks were successful, but was similar to previous studies of kleptoparasitism on the Isle of May (Harris, 1984; Wilson and Harding, 1997). The low success rate suggests that puffins were able to effectively avoid gull attacks and previous studies have demonstrated that puffins show a range of behavioural responses to avoid kleptoparasitism by gulls (Harris, 1984; Rice, 1987).

The mean feeding frequency of puffins breeding in gull-normal habitat was significantly lower than that of puffins breeding in gull-free areas. The feeding frequency calculated included loads subsequently lost to gulls and therefore indicates a real difference in the attempted provisioning rate. Previous studies have shown that puffins provisioning chicks in areas where gulls were breeding circled above the colony before landing, waited for more puffins to join them and then landed synchronously, swamping the gulls

(Merkel et al., 1998). The probability of an individual puffin being kleptoparasitised was thus reduced (Pierotti, 1983; Harris, 1984). In a detailed study of the behavioural adaptations of puffins to kleptoparasitism, Rice (1987) found that in areas of high gull density, puffins with food aborted more landings and took longer to complete a foraging trip. The increased time spent circling above the colony prior to landing reduced the frequency with which puffins were able to return with fish for their chicks and may explain the differences in feeding rates observed in this study. Moreover, we found no evidence that puffins breeding in gull-normal habitat compensated for the lower feeding frequency by altering the type of food load carried back for the chick. Food loads brought in by puffins breeding in gull-free and gull-normal habitat did not differ significantly in species composition, weight or total energy content.

The lower provisioning rate coupled with the higher kleptoparasitism risk resulted in puffins breeding in gull-normal habitat delivering 44% fewer food loads to their chicks in the morning and 25% fewer in the evening compared to puffins breeding in gull-free areas. Despite this difference, we found no evidence for a significant reduction in puffin breeding success. In both gull-normal and gull-free habitat, 75% of burrows with eggs fledged a chick successfully. This was unexpected given the markedly different rates of food delivery. However, previous studies of puffin chick growth have found that under conditions of low or reduced food availability chicks show a reduced growth rate (Øyan and Anker-Nilssen, 1996), which in turn can lead to an increase in the length of the fledging period (Barrett et al., 1987). We compared a range of other breeding parameters including chick growth rates, fledging weight and the length of the fledging period but again found no evidence for a significant difference between gull-free and gull-normal habitats. There are several possible explanations for these findings. Puffin chicks in gull-normal habitat may receive less food as a result of kleptoparasitism but the reduction may not be sufficient to detect a measurable limitation in growth. However, similar reductions in food intake have previously been found to cause a significant reduction in the growth rate of puffin chicks in both laboratory (Øyan and Anker-Nilssen, 1996) and field studies (Barrett and Rikardsen, 1992). Another possibility is that a disproportionate number of attacks were directed towards only a few individual puffins, making it more difficult to detect an effect of kleptoparasitism when testing for differences at the plot level. Alternatively, adult puffins may have compensated for the lower rate of food delivery during the morning and evening peaks of feeding activity by increasing foraging effort in the middle of the day, a time when provisioning rates are normally low, or by extending the period of the day used for foraging. Kleptoparasitism pressure would therefore be expected to have a greater impact on adults than chicks through energetic costs associated with increased time spent flying and foraging. Clearly, further work on the daily patterns in provisioning rate and the effect of reduced food intake on puffin chick growth is needed.

Removing the first clutch of eggs resulted in two changes in the gull population; firstly, peak hatching of gull chicks was delayed by *c.* 3 weeks and secondly, the mean density of gull chicks decreased as not all pairs that had their first clutch removed laid a second clutch. Both effects were expected to cause a reduction in kleptoparasitism risk, particularly during June, when gulls in the delayed plots were not provisioning chicks. However, we found no evidence that delaying gull breeding had a significant impact on the mean frequency or success of kleptoparasitic attacks. There are several possible explanations for these findings. Gulls may not have kleptoparasitised puffins solely to provide food for their chicks, adults may have also stolen fish to meet their own energy requirements. Alternatively, the attacks may have been carried out by gulls moving into the study plots from adjacent areas where breeding had not been delayed. The majority of gulls in our study colony were unmarked and it was therefore not possible to determine if this was the case; however, this seems unlikely as gulls actively defend their breeding territories from other birds (Tinbergen, 1956; Burger, 1984). Moreover, the differences between the gull-normal and gull-free plots suggest that there is little movement of gulls from the main breeding territories into the gull-free areas of the island. In addition, delaying gull breeding did not affect the rate at which puffins brought back food for their chicks. It is possible that the presence of gulls elicited the same behavioural response from puffins, discussed above, regardless of the presence or absence of gull chicks. In line with these results, we found no difference between gull-normal and gull-delayed plots in any of the puffin breeding parameters measured.

In conclusion, we found that delaying gull breeding had no impact on mean kleptoparasitism risk or the rate at which puffins brought back food for their chicks. However, the current management practice of maintaining gull-free areas was found to be effective at reducing the risk of kleptoparasitism. In addition, puffins breeding in gull-free areas brought back food for their chicks at a higher rate than puffins breeding in gull-normal habitat. Nevertheless, this did not lead to a significant increase in puffin chick growth or survival, which suggests that gulls did not have an immediate negative impact on puffin reproductive performance. These results are important given the changing population trends of gulls in Britain and Europe. In the past, when gull populations were expanding, the assumed threat of gulls to other breeding birds was considered sufficient justification for the implementation of control procedures. More recently, the stabilisation and even decline in gull populations in some areas (Hagemeijer and Blair, 1997) has lead to an increase in the conservation interest of herring and lesser black-backed gulls. It is now no longer acceptable to base management decisions on the assumption that gulls invariably have deleterious effects on the breeding performance of other birds. When formulating management programmes, it is important to quantify the actual impact of gulls on the species targeted for protection before beginning any control procedure and to assess the effectiveness of alternative management strategies to culling.

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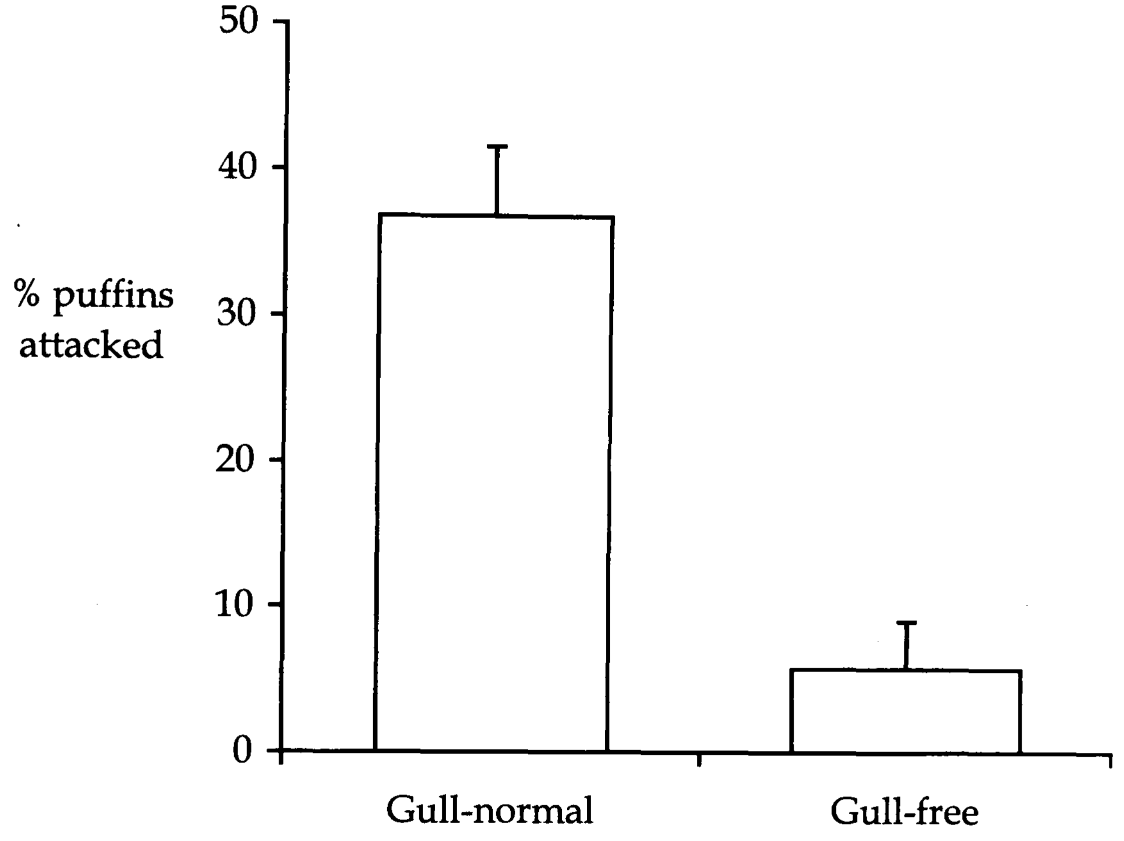

Figure 3.1: Mean (+/- one standard error) kleptoparasitism risk for puffins breeding in eight areas with (gull-normal) and eight areas without (gull-free) breeding herring and lesser black-backed gulls (difference between treatment groups, GLIM: $F_{1,14}=25.93$, $P<0.0005$).

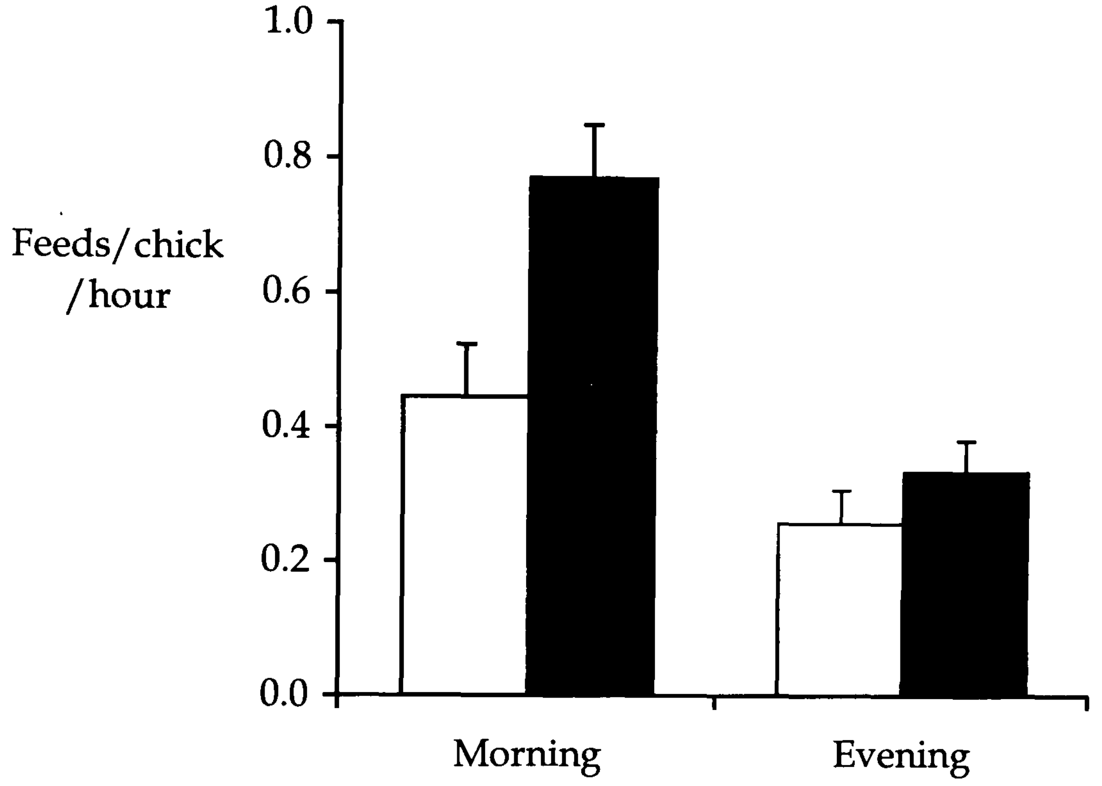

Figure 3.2: Mean (+/- one standard error) feeding frequency of puffins breeding in areas with breeding herring and lesser black-backed gulls (white bars) and gull-free areas (black-bars) in the morning and evening (difference between times of day, GLIM: d.f.=1, χ^2=22.84, P <0.001. There was a significant interaction between time of day and treatment group: difference between treatment groups, GLIM: morning d.f.=1, χ^2=10.35, P <0.01; evening d.f.=1, χ^2=2.38, n.s.).

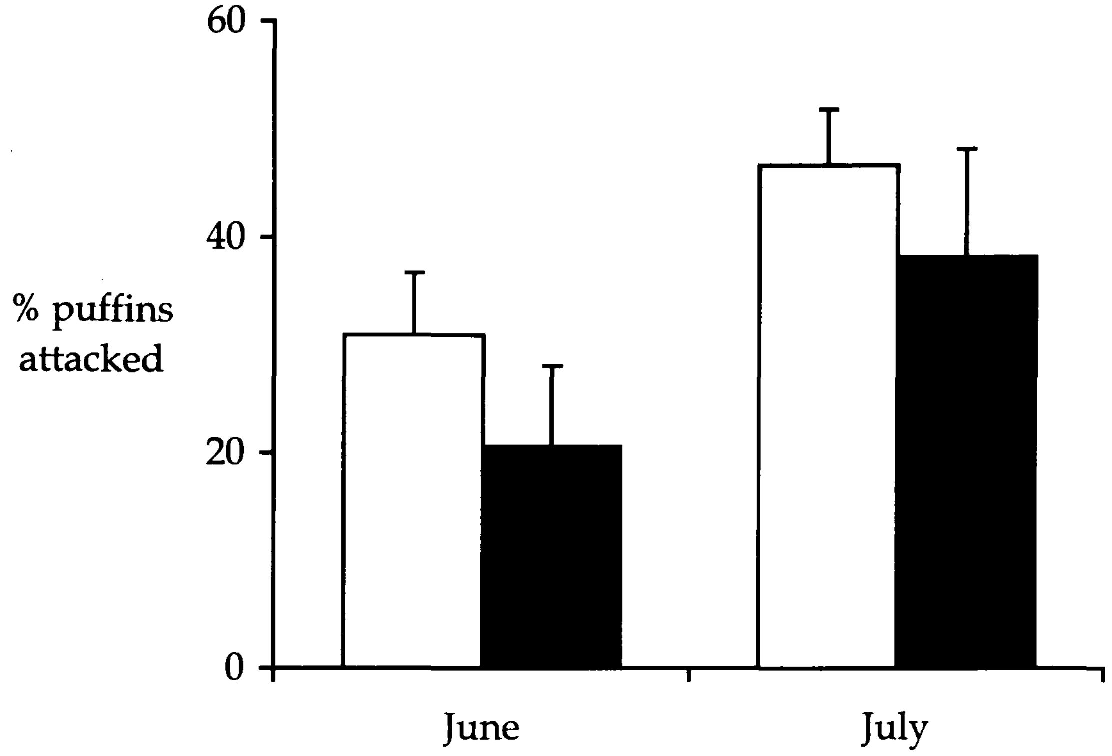

Figure 3.3: Mean (+/- one standard error) kleptoparasitism risk of puffins breeding in eight areas where herring and lesser black-backed gulls were breeding normally (gull-normal, white-bars) and in eight areas where gull breeding had been experimentally delayed (gull-delayed, black bars) (difference between treatment groups, GLIM: June $F_{1,13}$=0.26, n.s.; July $F_{1,13}$=1.46, n.s.)

Table 3.1: Breeding parameters of puffins in different treatment groups. Mean and standard error given (*median and interquartile range).

Parameter	Gull-free	Gull-normal	Gull-delayed
[1]Breeding success (% fledged)	73 (2.72)	70 (6.07)	81 (3.15)
[2]Hatching date (Julian day)*	144 (142,154)	147 (143,155)	148 (144,158)
[3]Peak weight (g)	292 (3.21)	288 (2.95)	293 (3.50)
[4]Wing growth rate (k)	0.090 (0.001)	0.093 (0.001)	0.092 (0.001)
[5]Weight growth rate (k)	0.126 (0.005)	0.131 (0.006)	0.129 (0.004)
[6]Fledging wing length (mm)	135 (0.55)	137 (0.61)	137 (0.59)
[7]Fledging weight (g)	261 (2.83)	260 (3.20)	261 (3.21)
[8]Fledging period (days)*	46 (44,48)	46 (44,49)	47 (44,49)

Maintenance of gull-free areas	[1] df=1, x^2=0.24, n.s.; [2] n=15, W=75, n.s.; [3] $F_{1,13}$=0.62, n.s.; [4] $F_{1,13}$=4.35, n.s.
(gull-free/gull-normal)	[5] $F_{1,13}$=0.96, n.s.;[6] $F_{1,13}$=1.88, n.s.; [7] $F_{1,13}$=0.11, n.s.; [8] n=15, W=71, n.s.
Delaying gull breeding	[1] df=1, x^2=2.67, n.s.; [2] n=16, W=76, n.s.; [3] $F_{1,14}$=0.84, n.s.; [4] $F_{1,14}$=0.28, n.s.
(gull-normal/gull-delayed)	[5] $F_{1,14}$=0.71, n.s.; [6] $F_{1,14}$=0.01, n.s.; [7] $F_{1,14}$=0.07, n.s.; [8] n=16, W=73, n.s.

Chapter 4

The impact of kleptoparasitism risk on the foraging behaviour of breeding Atlantic puffins *Fratercula arctica*

Abstract

Puffins breeding in close proximity to breeding gulls return with food for their chicks at a significantly lower rate during the morning peak of feeding activity and lose a significantly greater proportion of food loads to kleptoparasitic gulls compared to puffins breeding in areas free of breeding gulls. Despite this food loss, there is no evidence for a significant reduction in the growth or survival of puffin chicks in the gull-occupied areas. The aim of this study was to investigate two possible mechanisms by which adult puffins may compensate for food losses due to kleptoparasitism and thus prevent their chicks being adversely affected: (a) that adults compensate by increasing chick provisioning rate later in the day or (b) that adults compensate by altering the type of prey loads delivered to chicks. Both the daily pattern of food deliveries and the size, prey composition and energy content of food loads delivered to chicks were compared between puffins breeding in gull-occupied and gull-free areas. We found no evidence that puffins breeding in gull-occupied habitat increased the frequency or energy content of food loads delivered to chicks compared to puffins breeding in gull-free areas. Possible explanations for the apparent discrepancy between the energy intake and growth rate of puffin chicks are discussed.

Introduction

Kleptoparasitism or food stealing is common among birds (Brockmann and Barnard, 1979). It is particularly prevalent among seabirds, which generally breed in dense colonies and therefore offer a predictable source of large numbers of potential hosts (Furness, 1987). Under such conditions, kleptoparasitism rates can be very high. For example, on Teuri Island, Japan, 40% of Rhinoceros auklets *Cerorhinca monocerata* returning to the colony at dusk with fish for the chicks were successfully kleptoparasitised by black-tailed gulls *Larus crassirostris* (Watanuki, 1990). In a study at Punta Leon, Patagonia, Quintana and Yorio (1999) found that 11% of fish brought in to the colony by Royal terns *Sterna maxima* were lost to kelp gulls *L. dominicanus.*

However, despite the often considerable loss of food to kleptoparasites, most studies investigating the impact of kleptoparasitism on the reproductive performance of the host species have found no significant reduction in the growth or survival of chicks (Fuchs, 1977; Pierotti, 1983; Rice, 1985; Wilson, 1993; Quintana and Yorio, 1999; Finney et al., 2001; but see also Stienen et al., 2001). Such studies therefore often conclude that kleptoparasitism does not have a significant negative impact on the host species. However, to date, no study has investigated the possibility that adult birds may compensate for food loads lost to kleptoparasites by increasing foraging effort, and that the costs of kleptoparasitism may be borne by the adult rather than transferred to the chick. In this study we investigated the impact of kleptoparasitism risk on the foraging behaviour of adult Atlantic puffins *Fratercula arctica,* which are frequently kleptoparasitised by herring *L. argentatus* and lesser-black backed gulls *L. fuscus* during the chick-rearing period.

Puffins are highly colonial, burrow-nesting auks that lay a single egg clutch. The chick is brooded and fed by both members of the pair and remains in the burrow for 38-44 days (Cramp, 1977). Adult puffins provision their chick with loads of several fish carried cross-wise in the bill. Gulls do attack puffins in the air, but most attacks occur when a puffin lands near its burrow with food for the chick (Grant, 1971; Nettleship, 1972; Harris, 1984). Gulls grab the puffin by the tail or neck and shake the bird violently until it either drops its fish or escapes.

In a previous study at this colony, we found that almost 40% of puffins bringing fish to young in gull-occupied habitat were attacked by gulls compared with only 5% of puffins breeding in gull-free areas; approximately 12% of these attacks were successful (Finney et al., 2001). Furthermore, during the morning peak of feeding activity, the rate at which adults returned with food for the chick was 42% lower in gull-occupied habitat compared to gull-free areas (for details see Finney et al., 2001; *Chapter 3*). Assuming that there were no other differences in foraging behaviour, then the lower chick provisioning rate in the mornings coupled with the higher kleptoparasitism risk resulted in puffins breeding in gull-occupied habitat delivering approximately 18% less food loads per day to their chicks compared to puffins breeding in gull-free areas. Despite this difference, we found no evidence for a significant reduction in the growth or survival of chicks (Finney et al., 2001). This was unexpected as both laboratory and field studies have found that similar reductions in food intake caused a significant negative impact on puffin chick growth (Barrett and Rikardsen, 1992; Øyan and Anker-Nilssen, 1996). These results therefore suggest that adult puffins breeding in gull-occupied habitat may compensate for the apparent lower rate of food delivery to chicks by altering their foraging behaviour.

The aim of this study was to investigate two possible mechanisms by which adult puffins may compensate for food losses due to kleptoparasitism: (a) that adults compensate by increasing chick provisioning rate later in the day or (b) that adults compensate by increasing the energy content of prey loads delivered to chicks. Both the daily pattern of food deliveries and the size and species composition of food loads delivered to chicks were therefore compared between puffins breeding in areas of high and low kleptoparasitism risk.

Methods

This study was carried out on the Isle of May, Firth of Forth, Scotland (56°11'N, 2°33'W) during the 2000 and 2001 breeding seasons. The island supports over 42,000 breeding pairs of Atlantic puffins and is the largest colony on the east coast of Scotland. Approximately 4,200 pairs of herring and lesser black-backed gulls also breed on the island each year (Harris et al., 2000).

Data on puffin provisioning rates were collected from 12 (8 m x 8 m) study plots, containing active puffin burrows, that were distributed across the island in the main gull and puffin breeding areas. Six plots were in areas where gull breeding was prevented by nest removal as part of the island management strategy (gull-free; no breeding gulls within a 50 m radius of the centre of the study plot) and six plots were in areas where breeding gulls were present (gull-occupied; five or more breeding pairs of gulls within a 10 m radius of the centre of the study plot). Systematic observations of puffin activity were made from a temporary hide situated approximately 3 m from the edge of the study plot. A total of six paired feeding watches were carried out. Watches were paired (gull-free and gull-occupied plots being observed simultaneously, using two observers) to control for daily variation in puffin feeding behaviour. Each plot was observed for a total of 9 hours during the day (0430-0700, 1000-1200, 1400-1600 and 1900-2130 BST). For each puffin that landed with fish in the study plot the following data were recorded: time, whether the bird was attacked and, if attacked, the outcome of the interaction. Kleptoparasitism risk was calculated as the percentage of puffins landing with fish that were attacked. Success rate was calculated as the percentage of attacks where the puffin lost some or all of its food load. In practice, a successful attack usually resulted in puffins losing their entire food load. Calculations concerning the amount of food lost to kleptoparasites are therefore based on the assumption that the entire food load was lost in a successful attack.

In order to examine whether kleptoparasitism by gulls caused puffins to alter the size or quality of food loads brought back to the chick, food loads were collected from two additional study areas, one within the gull colony and another in a nearby gull-free area. The gull-free and gull-occupied areas were sampled on the same days to control for daily variation in food load composition. Mist-nets were erected in the morning (0500-0700) and in the evening (1900-2100) to catch puffins returning to the colony with food for the chick. All food loads dropped were collected immediately and stored in sealed plastic bags. Each food load was subsequently weighed and the species and length of each fish was recorded. The energy value of each fish was estimated from its length using relationships given in Harris and Hislop (1978).

Results

Chick provisioning rate

The frequency of food deliveries to chicks was highest in the early morning, as is typical of this species (Harris, 1984). Consistent with our previous study of kleptoparasitism at this colony (Finney et al., 2001), puffins breeding in gull-occupied habitat returned with food loads for chicks at a significantly lower rate during the morning peak of feeding activity compared to puffins breeding in gull-free areas (Fig. 4.1).

As expected, kleptoparasitism risk was significantly higher in gull-occupied habitat (21.6 ± 3.9%) compared to gull-free habitat (2.8 ± 0.6%; t-test, df=5, t=4.75, P<0.006). The mean success rate of these attacks was 33 ± 8.3%. The percentage of puffins returning with fish that lost their load to gulls was therefore 1.0% and 7.1% in gull-free and gull-occupied areas respectively.

The greater proportion of food loads lost to gulls and the lower chick provisioning rate meant that puffins breeding in gull-occupied habitat delivered approximately 30% less food to their chicks during the morning peak of feeding activity compared to puffins breeding in gull-free areas. However, we found no evidence that puffins breeding in gull-occupied habitat compensated by increasing provisioning rate later in the day. The rate at which adults returned with food for the chick did not differ significantly between puffins breeding in gull-free and gull-occupied areas at any other time of day (Fig. 4.1). Puffins breeding in gull-occupied habitat therefore delivered approximately 15% less food loads per day to their chicks compared to puffins breeding in gull-free areas.

Quality of food loads

Puffins brought back a wide range of food items during the breeding season. Out of a total of 169 loads collected, 80% contained the lesser sandeel (*Ammodytes marinus*), 43% contained clupeids (herring *Clupea harengus* or sprat *Sprattus sprattus*) and 12% contained gadoids (cod *Gadus morhua* or rockling *Ciliata septentrionalis*). The species composition of food loads brought in by puffins breeding in gull-occupied and gull-free habitats did not differ significantly either in the morning (G-test: df=4, G=0.43, n.s.) or in the evening (df=4, G=0.22, n.s.). There was also no significant difference between puffins breeding in gull-occupied and gull-free habitat in the load weight or the number of fish per load (Fig. 4.2). In line with these results, there was no significant difference between puffins breeding in gull-free and gull-occupied habitats in the energy content of food loads delivered to chicks (Fig. 4.3). We therefore found no evidence that puffins breeding in gull-occupied habitat compensated for the reduced number of food loads delivered to chicks by altering the nature of their food loads.

Discussion

Puffins breeding in areas occupied by breeding gulls provisioned their chicks at a significantly lower rate during the morning peak of feeding activity and lost a significantly greater proportion of food loads to gulls compared to puffins breeding in gull-free areas. This amounted to a 30% reduction in the number of food loads delivered during the morning peak of feeding activity compared to puffins breeding in gull-free areas. Surprisingly, we found no evidence that adult puffins compensated for this lower rate of food delivery to chicks by altering their foraging behaviour. Neither chick provisioning rate later in the day nor the quality of food loads delivered to chicks differed significantly between puffins breeding in gull-free and gull-occupied areas. There are several possible explanations for our findings.

Firstly, if puffins were already working at the maximum rate possible in order to raise their chicks, then an increase in provisioning rate would not be expected. However, several experimental studies have already demonstrated that adult puffins are able to adjust the frequency with which they deliver food loads to the chick. Johnsen et al. (1994) swapped young and old puffin chicks between burrows to experimentally increase or decrease the energy demands placed on the adults by their young and found that adults rapidly adjusted the frequency of food deliveries in response to the changing needs of the chick. Furthermore, adult puffins have been shown to increase feeding frequency in response to an experimental increase in chick begging calls, suggesting that unmanipulated adults were not providing food as frequently as they were able (Harris, 1983). Puffins therefore appear to have the capacity to increase the frequency with which they bring back food for their chicks, although such a behavioural response was not evident in this study.

Secondly, an increase in the size of food loads brought back to chicks may not be possible due to the physical constraints of carrying a larger load. Flapping fight is energetically expensive, particularly in the auks (Alcidae), which have the highest wing loading of any family (Nettleship and Birkhead, 1985). As the metabolic requirements for flight increase exponentially with body mass (Witter and Cuthill, 1993), even relatively small changes in the mass of the load carried could have a large impact on flight efficiency and hence energy expenditure i.e. adult puffins may already have been working at their maximum capacity. Furthermore, kleptoparasitism risk may even select against increases in the size of food loads. Larger food loads would be more conspicuous to gulls and could potentially impair flying ability by decreasing speed and manoeuvrability (Witter et al., 1993), thus rendering the puffin more vulnerable to kleptoparasitic attacks. Individuals would therefore face a trade-off between the size of the prey load carried and the probability of successfully delivering it to the chick. Several previous studies of sandwich terns *Sterna sandvicensis* have indeed found that individuals carrying larger fish were preferentially targeted by black-headed gulls *L. ridibundus* (Fuchs, 1977; Ratcliffe et al., 1997; Stienen et al., 2001). However, due to the multiple prey loads carried and the speed with which returning puffins enter their burrows, it has not yet been possible to assess reliably whether puffins carrying larger loads are preferentially targeted by gulls.

Finally, if gulls targeted particular individuals repeatedly, then using mean values of food load composition and provisioning rates from a sample of adult puffins breeding within a gull-occupied area, may not reflect any impact of kleptoparasitism since the majority of individuals would be unaffected. This was not the case however, as within the gull-occupied areas, puffin burrows were targeted in direct proportion to the number of food loads that were delivered (Finney, unpublished data).

To summarise, we found no evidence that puffins breeding in gull-occupied habitat compensated for the lower chick provisioning rate in the mornings and the greater proportion of food loads lost to gulls by increasing their foraging effort. As a result, puffin chicks in gull-occupied habitat received approximately 15% less food per day than puffins breeding in gull-free areas (gull-occupied, 253 kJ/day; gull-free, 297 kJ/day). It was therefore surprising that no significant impact on chick growth or survival was found (Finney et al., 2001). There are several possible explanations for this. Chicks in gull-occupied habitat may have altered their behaviour in order to reduce energy expenditure. Most studies of chick behaviour in response to changes in food availability have focused on multi-chick broods (Drummond, 2001). For example, in a study of black guillemots *Cepphus grylle*, Cook et al. (2000) found that the frequency of aggressive interactions between siblings increased when food supply was experimentally reduced. The only study of puffin chick behaviour in relation to food availability found that chicks with experimentally reduced food intake spent more time outside the nest chamber near the burrow entrance, where they were at greater risk from predation by gulls (Nettleship, 1972). Empirical data on both egg quality and the energy expenditure of puffin chicks under different feeding regimes is clearly needed to investigate this further. Alternatively, although no immediate impact on chick growth was detected, nutritional deprivation during the fledging period may have longer term consequences for future survival and fecundity. Again, data on post-fledging survival and reproductive performance would be needed to investigate this further.

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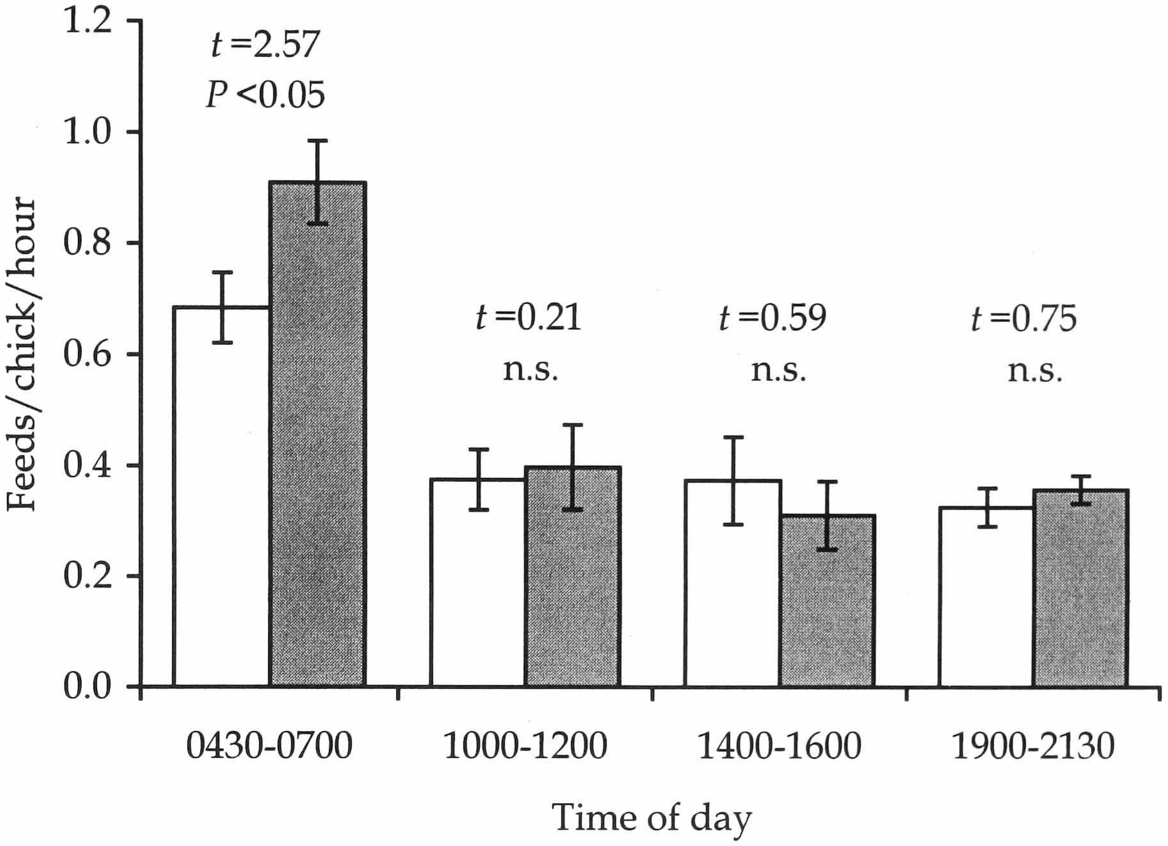

Figure 4.1: Mean (+/- one standard error) provisioning rate of puffins breeding in areas occupied by herring and lesser black-backed gulls (white bars) and gull-free areas (grey bars). Results of paired t-tests used to examine differences in feeding frequency between gull-occupied and gull-free areas are given (in all cases, df=5).

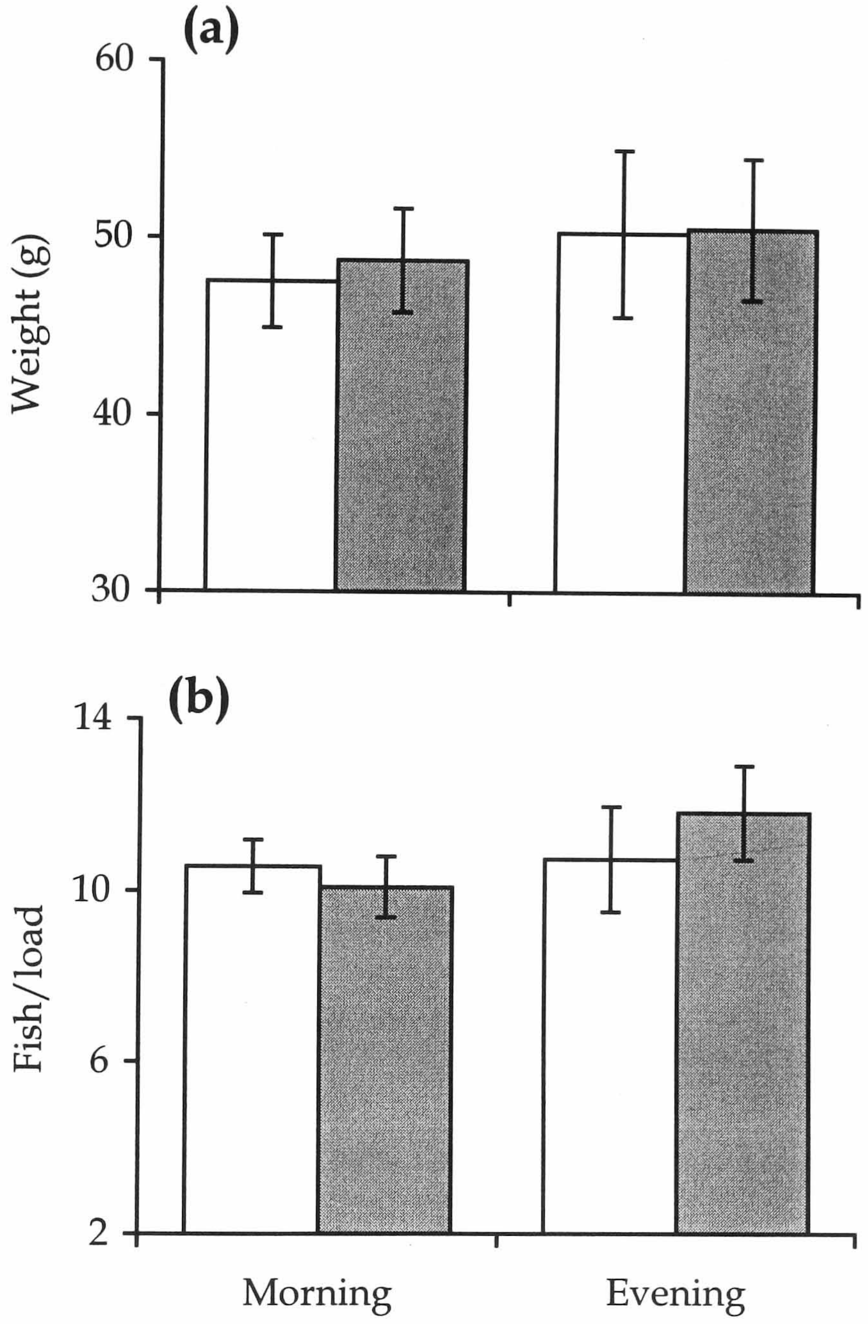

Figure 4.2: Comparison of food loads carried by puffins breeding in areas occupied by breeding herring and lesser black-backed gulls (white bars) and in gull-free areas (grey bars). Mean (+/- one standard error) (a) load weight and (b) number of fish per load are shown. (Difference between gull-occupied and gull-free areas: t-tests, (a) Morning, df=91, t=0.08, n.s.; Evening, df=74, t=0.76, n.s., (b) Morning, df=91, t=0.51, n.s.; Evening, df=74, t=0.66, n.s.).

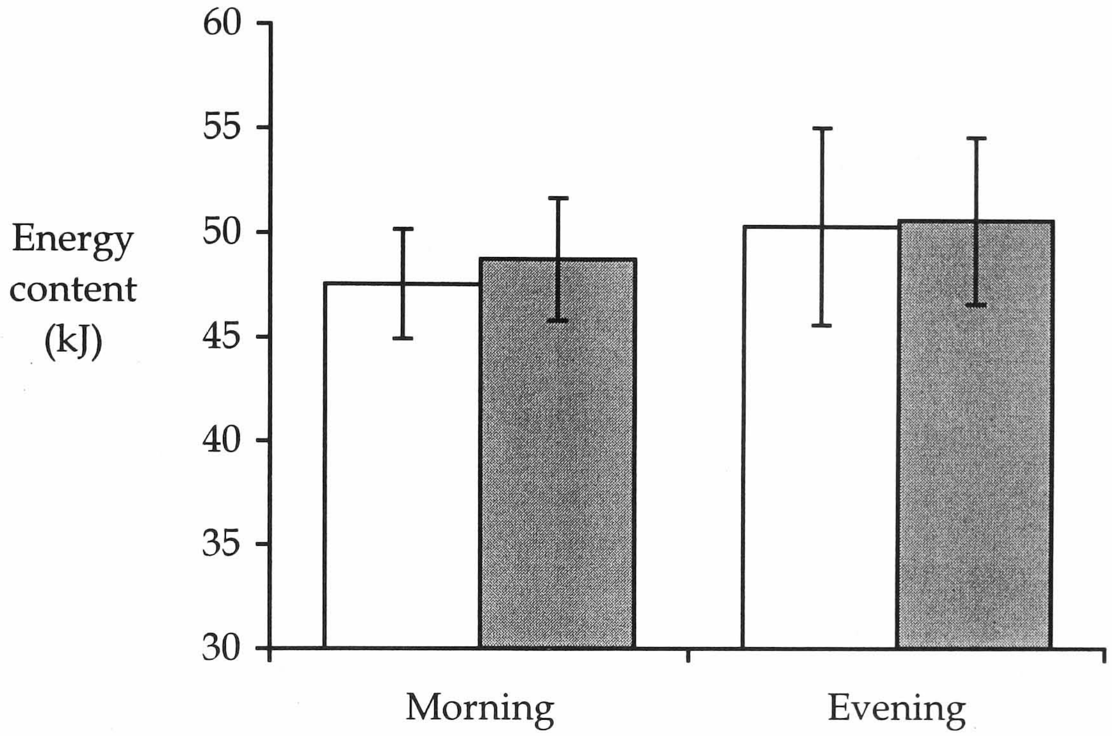

Figure 4.3: Mean (+/- one standard error) energy content of food loads brought in by puffins breeding in areas occupied by breeding herring and lesser black-backed gulls (white bars) and in gull-free areas (grey bars). (Difference between habitat types: t-test, Morning, df=91, *t* =0.31, n.s.; Evening, df=74, *t* =0.05, n.s.).

Chapter 5

The impact of kleptoparasitism risk on body condition in breeding adult Atlantic puffins *Fratercula arctica*: implications for gull management

Presented at the British Ecological Society Winter Meeting, Birmingham (January, 2001).

Abstract

Large gulls (*Larus* spp.) frequently kleptoparasitise other birds during the breeding season. To date, most studies investigating the impact of kleptoparasitism on the host species have focused entirely on the direct impact on chick growth and survival, usually finding no significant effect. No work has yet been undertaken to assess the potentially more subtle effects of kleptoparasitism such as effects on the body condition of adult birds, which may have important consequences for future survival and reproduction. We investigated the impact of kleptoparasitism on the body condition of breeding adult Atlantic puffins *Fratercula arctica,* which are frequently kleptoparasitised by herring *L. argentatus* and lesser black-backed gulls *L. fuscus* during the chick-rearing period. Body mass, haematocrit and mean corpuscular volume of puffins breeding in areas of high kleptoparasitism risk were compared with those of puffins breeding in areas where kleptoparasitic attacks were rare. There was no evidence that the increased stress or energy expended by adult puffins in response to kleptoparasitic attacks by gulls had a significant negative impact on their body condition.

Introduction

Kleptoparasitism or food stealing is common among birds (Brockmann and Barnard, 1979). It is particularly prevalent among seabirds, which generally breed in dense colonies and therefore offer a large and predictable return of food-carrying hosts to a specific area (Furness, 1987). Most studies investigating the impact of kleptoparasitism by gulls on the reproductive performance of the host species have focused entirely on the direct impact on the growth and survival of chicks, usually finding no significant effect (Fuchs, 1977; Pierotti, 1983; Rice, 1985; Wilson, 1993; Quintana and Yorio, 1999; Finney et al., 2001). However, to date, no study has assessed the potentially more subtle effects of kleptoparasitism risk on adult birds, which could have important consequences for future survival and reproduction if body condition is negatively affected. The increased stress or energy expended by adults in response to kleptoparasitic attacks may have a significant impact on body condition, particularly if adults increase their foraging effort to compensate for lost food loads. The body condition of host species may also alter as a strategic response to increased kleptoparasitism risk, for example to improve flight performance and manoeuvrability (Gosler et al., 1995; Lilliendahl, 1997; Veasey et al., 1998), which under certain circumstances may increase the probability of successfully evading a kleptoparasitic attack. It is therefore important to look at a range of body condition measures.

One species that is particularly at risk from kleptoparasitism is the Atlantic puffin *Fratercula arctica*, which frequently nests in close proximity to gulls. By experimentally altering the workload of adult puffins during the chick-rearing period, Wernham and Bryant (1998) demonstrated a link between parental energy expenditure and both the over-winter survival of adults and breeding performance in the following year. Such results suggest that additional stress or effort expended by breeding puffins during the chick-rearing period, such as that associated with kleptoparasitic attacks, could have important consequences for adult survival and future reproductive success.

Puffins are highly colonial, burrow-nesting auks that lay a single egg clutch. The chick is brooded and fed by both members of the pair and remains in the burrow for 38-44 days (Cramp, 1977). Adult puffins provision their chick with loads of several fish carried cross-wise in the bill. Gulls do attack puffins in the air, but most attacks occur when a puffin lands near its burrow with food for the chick (Grant, 1971; Nettleship, 1972; Harris, 1984). Gulls grab the puffin by the tail or neck and shake the bird violently until it either drops its fish or escapes. In a previous study at this colony, we found that almost 40% of puffins bringing fish to young in gull-occupied habitat were attacked by gulls compared to only 5% of puffins breeding in gull-free areas; approximately 12% of these attacks were successful (Finney et al., 2001). While we found no evidence that kleptoparasitism had a significant negative effect on the growth or survival of puffin chicks (Finney et al., 2001), the impact on adult birds has not yet been assessed. Accordingly, in this study, we investigated the impact of kleptoparasitism by herring and lesser black-backed gulls on the body condition of breeding adult Atlantic puffins.

Methods

Body condition measurements

Three different body condition measurements were taken from breeding puffins; body mass index (mass corrected for structural size), haematocrit and mean corpuscular volume (Jones, 1983; Morton, 1994; Bearhop et al., 1999). Body mass index is frequently used as an indicator of condition as fat storage can have important implications for survival and future reproduction (Monaghan and Metcalfe, 1986; Witter and Cuthill, 1993; Golet et al., 1998). Haematocrit, or packed cell volume, reflects the extent and efficiency of oxygen uptake and transfer to tissues (Ots et al., 1998). There is evidence that an increase in haematocrit levels may arise as a result of elevated oxygen consumption during periods of increased workload (Saino et al., 1997; Hõrak et al., 1998). A deficiency in the amount of oxygen reaching the tissues stimulates an increase in the production of red blood cells and their release into the circulation. Furthermore, studies of mammals and fish have found that an individual suffering a stressful event, such as pursuit or capture, can show a sympathetically-mediated release of red blood cells into the circulation. Although this has not yet been demonstrated in birds, it is possible that adult puffins repeatedly pursued and attacked by gulls may have elevated haematocrit levels as a result of this stress response (Wesson et al., 1979; Inversen et al., 1998). However, as the haematocrit measurement is dependent on both cell density and cell size, different combinations of these can produce similar haematocrit values while not reflecting similar physiological conditions. Mean red blood cell size (mean corpuscular volume, MCV) has therefore been proposed as an alternative indicator of condition (Bearhop et al., 1999). In birds, immature erythrocytes are slightly larger than mature erythrocytes; in a healthy individual, most erythrocytes are mature but a small percentage of immature cells is expected, indicating normal replenishment from the bone marrow. However, under conditions of increased workload, MCV may be elevated as the blood contains a greater proportion of the larger, immature cells that have been released into the circulation to increase oxygen transport. MCV would also be increased if immature red blood cells were released into the circulation as part of a stress response to pursuit or capture by gulls.

If the increased stress or energy expended by adults in response to kleptoparasitic attacks had a significant impact on their body condition, then we would expect puffins breeding in areas of high kleptoparasitism risk to have a lower body mass, higher haematocrit levels and a higher MCV than puffins breeding in areas where kleptoparasitism risk was low. Furthermore, as kleptoparasitism only occurs during the chick-rearing period, we expect any impact on adult condition to be most evident at this time.

Study site

The study was carried out on the Isle of May, Firth of Forth, Scotland during the 2000 breeding season. The island supports over 42,000 breeding pairs of Atlantic puffins. Approximately 4,200 pairs of herring and lesser black-backed gulls also breed on the island each year (Harris et al., 2000). Both the conservation status of herring and lesser black-backed gulls at this site and the management plan for the island are currently under review with a view to assessing whether the current level of the gull population poses any threats to other species.

There is a high degree of overlap in the spatial distribution of gulls and puffins on the island. However, there are also several areas that are actively maintained as gull-free, by repeated removal of nests, as part of a long-term management policy. The island therefore presents an experimental situation with control (gull-occupied) and treatment (gull-free) areas. Four plots (approximately 25 m by 25 m) were set up in the main puffin breeding areas in the 2000 breeding season. Two were in gull-occupied habitat (five or more active gull nests within 10 m of the edge of the study plot) and two were in gull-free habitat (no breeding gulls within 30 m of the edge of the study plot). Study plots were selected to minimise differences between gull-occupied and gull-free plots in the density of breeding puffins and in physical characteristics such as slope angle, aspect and distance from the sea.

Sampling procedure

A total of 235 individual adult puffins were captured between 0500-1000 B.S.T. during the incubation and chick-rearing periods (April to July). Of these, 59 were caught both during incubation and during the chick rearing-period (mean interval between captures, 48 ± 1.48 days). During incubation, adults were removed from the burrows by hand. Burrows were left completely undisturbed for three weeks during the peak hatching period as this is when puffins are considered to be most sensitive to disturbance (Harris, 1984). Adults were then captured during chick-rearing by placing small nets in the entrance to the burrows. A temporary hide was erected approximately 5 m away. When a puffin returned with food for the chick, it entered the burrow and became caught in the net. An observer was present at all times and birds were removed from the nets immediately.

A blood sample was taken within 3 minutes of capture (under Home Office Licence) by venepuncture of the brachial vein. Blood was drawn into a syringe containing EDTA (ethylene diamine tetra-acetic acid 1.6mg/ml blood) and mixed. Blood samples were taken back to the laboratory and processed within 5 hours of collection using standard haematological techniques (Campbell, 1988). Total erythrocyte counts were made using an improved Neubauer haemocytometer. Two counts were made from each sample (correlation, $r=0.70$, $n=201$, $P<0.001$, mean % difference=10%); the mean for each individual was used in the calculations of mean corpuscular volume (MCV). In addition, two microhaematocrit capillaries were filled from each individual sampled. These were centrifuged and the volume of red blood cells (haematocrit) was measured. The mean of these two measurements (correlation, $r=0.87$, $n=201$, $P<0.001$, mean % difference=3%) was used in the calculation of MCV. MCV was calculated using the following equation (Campbell, 1988):

$$\text{MCV}\ (\mu\text{m}^3) = \left[\frac{\text{haematocrit}\ (\%)}{\text{total erythrocyte count}\ (10^6 / \mu\text{L})} \right] \times 10 \qquad \text{[Eq.1]}$$

It was not possible to obtain usable blood samples from every bird so the sample sizes in the analyses vary. The bird was weighed and the wing length (maximum wing chord) and head plus bill measurements were recorded. To control for differences between individuals in structural size, body mass was first calculated as the residual of mass regressed against structural size. Structural size was taken as the PCA score of wing and head plus bill size. The relationship between mass and structural size differed between the sexes and therefore sex-specific regression analyses were used to calculate residuals. A total of 118 female and 117 male adult puffins were caught and measured; the sex-ratio of birds sampled did not differ significantly between the gull-free and gull-occupied areas (df=1, χ^2=1.23, n.s.). In the analyses, the residuals were expressed as a percentage of the predicted value (body mass index), which allowed comparisons to be made of the relative condition of individuals of different body sizes (Blem, 1990; Bolton et al., 1993). The birds were sexed using DNA from the blood sample taken (Griffiths et al., 1998).

Results

Body mass

Seasonal changes in body mass index were examined using measurements from all 235 individual puffins caught between April and July. For those caught twice (n=59), only the first measurement was used in this analysis. Measurements of individuals from all four study plots were pooled; approximately the same number of individuals were sampled in each plot. A regression analysis showed that the body mass index of adult puffins declined significantly as the breeding season progressed (Fig. 5.1). That this represented a real seasonal decline within individuals, rather than reflecting a bias in the sample of adults measured, was corroborated by examination of the sub-sample of individuals caught twice, once during incubation and again during chick-rearing; this analysis showed a significant seasonal decline in mass within individuals (Fig. 5.2). The rate of mass loss was 0.43 ± 0.06 g/day. There was no significant difference between males and females in body condition ($F_{1,232}$=0.003, n.s.) or in the rate of mass loss at the individual level (df=57, t=0.82, n.s.).

The impact of kleptoparasitism risk on adult body mass index was tested using a nested ANOVA, which allowed any variation between plots within each treatment (gull-occupied and gull-free) to be taken into account in the analysis.

Data from the incubation and chick-rearing periods were analysed separately. Based on our sample sizes and the variation in body mass index between individuals within the gull-free and gull-occupied areas, our analyses were capable of detecting a 3% difference in body mass index between puffins breeding in gull-occupied and gull-free areas with a power of over 90% (GPOWER, Faul & Erdfelder, 1992). We found no evidence of a significant difference in body mass index between puffins breeding in gull-occupied and gull-free habitat during incubation (Fig. 5.3a), a period when there were no kleptoparasitic attacks by gulls. However, there was also no evidence of a significant difference in body mass index between puffins breeding in gull-occupied and gull-free habitat during chick-rearing (Fig. 5.3b), the time when puffins breeding in gull-occupied habitats were subject to frequent kleptoparasitic attacks by gulls. In line with these results, the rate of mass loss during the breeding season did not differ significantly between puffins breeding in gull-occupied and gull-free habitats (nested ANOVA based on changes within the sub-sample of 59 individuals caught twice, n in gull-free = 28, n in gull-occupied = 31, $F_{1,2}$=0.26, n.s.).

Blood parameters

Seasonal changes in haematocrit and MCV were examined using measurements from a sample of 201 individual puffins caught between April and July. As above, measurements of individuals from all four study plots were pooled for this analysis. Regression analysis showed no evidence of a consistent seasonal change in haematocrit or MCV (Fig. 5.4). That this result did not reflect a bias in the sample of adults measured was again confirmed by analyses of the sub-sample of individuals caught twice, once during incubation and again during chick-rearing; this analysis also showed no evidence of a significant seasonal change within individuals in haematocrit (paired t-test: df=44, *t*=1.32, n.s.) or MCV (paired t-test: df=42, *t*=0.39, n.s.). Mean haematocrit and mean MCV were 47.8 % (± 0.003) and 166.4 μm^3 (± 1.32) respectively. There was no significant difference between males and females in either of these blood parameters (haematocrit, $F_{1,198}$=1.47, n.s.; MCV, $F_{1,198}$=0.0001, n.s.).

As with body mass index, the impact of kleptoparasitism risk on physiological condition was tested using a nested ANOVA, with the incubation and chick-rearing periods being analysed separately. We found no evidence of a significant difference between puffins breeding in gull-occupied and gull-free habitat in haematocrit or MCV during incubation or chick-rearing (Fig. 5.5).

Discussion

The 2000 season was a typical year for puffins breeding on the Isle of May; adult survival, breeding success and diet were comparable to those recorded in previous years (Harris, unpublished data). Adult puffins showed a significant decline in mass as the breeding season progressed. Mass loss during breeding is shown by many bird species and is thought to occur either as a result of an increase in energy expenditure or as an adaptation to reduce flight costs when provisioning young (Jones, 1994; Hillström, 1995; Golet and Irons, 1999). However, a number of studies have demonstrated a link between mass loss in breeding birds and reduced survival and future reproductive success (Monaghan and Metcalfe, 1986; Monaghan et al., 1989; Golet et al., 1998). A reduction in body mass of just 5% below normal has been shown to cause a significant reduction in adult survival in both glaucous-winged gulls (Reid, 1987) and kittiwakes (Jacobsen et al., 1995). Additional stresses on adult birds during the breeding season, such as kleptoparasitism, could therefore have important consequences for survival and future reproductive performance if body condition is negatively affected.

In this study however, we found no evidence that puffins breeding in gull-occupied habitat had a lower body mass index than puffins breeding in gull-free habitat during incubation or during the chick-rearing period. This was unexpected as puffins breeding in gull-occupied habitats were subject to frequent kleptoparasitic attacks by gulls as they returned to the colony with fish (Finney et al., 2001). Puffins breeding in areas of high kleptoparasitism risk were expected to have a lower mass either as a result of increased energy expenditure (resulting from avoidance and escape behaviours, increased foraging effort or elevated heart rate as part of a stress response), or as an adaptation to improve flight performance and manoeuvrability, which may have increased the likelihood of escape. There are several possible explanations for our findings.

Firstly, a reduction in body mass, and the potential improvements in flight performance, may not have been beneficial in terms of an increase in the probability of escape from a kleptoparasitic attack. Previous studies that have demonstrated mass-dependent predation risk have focused on passerines, which typically escape by taking-off and flying into cover (Gosler et al., 1995; Cresswell, 1998; Veasey et al., 1998). Gulls do not usually chase puffins in flight and, if they do, their effectiveness is very low as puffins can easily outpace them (Harris, 1984). Most kleptoparasitic attacks occur on the ground as a puffin lands near its burrow with food for the chick. Puffins usually land at the burrow entrance and dive directly in and, if caught, rarely try to take-off again. Instead they hang on to their fish and attempt to pull free and escape down the burrow. For these reasons, the potential increase in flight velocity, manoeuvrability and take-off speed resulting from a reduction in mass would be unlikely to increase the probability of escape. When kleptoparasites attack host species in flight, such as gulls kleptoparasitising terns (*Sterna* spp.), strategic regulation of body mass by the host species in response to kleptoparasitism risk could play a more important role.

Secondly, the additional energetic costs associated with avoidance and escape behaviours in response to kleptoparasitic attacks by gulls may have been insignificant at a time when adults were already working hard to meet the demands of raising young. In their experimental alteration of the work rate of adult puffins, Wernham and Bryant (1998) were only able to examine the mass of six birds and thus it is not possible to assess from their study whether additional mass loss is associated with increased work rate. However, flapping fight is energetically expensive, particularly in the auks (Alcidae), which have the highest wing loading of any bird (Nettleship and Birkhead, 1985). Foraging for the chick therefore places considerable energetic demands on the adults with feeding trips lasting several hours (Harris, 1984) and adult birds may therefore have already reached their lowest mass level. The additional energy expenditure resulting from avoidance and escape behaviours in response to kleptoparasitic attacks when returning to the colony may therefore not represent a significant additional demand on adults. These findings also suggest that adult puffins do not increase foraging effort to compensate for food loads lost to kleptoparasites.

An increase in haematocrit is considered to be an adaptive response to enhance the uptake and efficiency of oxygen transfer to the tissues during periods of increased muscular activity (Hõrak et al., 1998). Alterations to the oxygen-carrying capacity of the blood can also be made by more subtle means than changes in haematocrit, such as alterations in the volume and number of erythrocytes (Breuer et al., 1995). We found no consistent seasonal change in the haematocrit levels or MCV of adult puffins during the breeding season. The lack of adjustment of blood oxygen-carrying capacity between incubation and chick-rearing suggests that either the demand on aerobic metabolism did not increase at that time or that oxygen delivery was enhanced through other mechanisms. Furthermore, we found no significant difference in haematocrit levels or MCV between puffins breeding in areas of high kleptoparasitism risk and those breeding in areas where kleptoparasitic attacks were rare. This suggests that the increased muscular activity resulting from avoidance and escape behaviours in response to kleptoparasitic attacks was not sufficient to cause significant adjustments in the oxygen-carrying capacity of the blood.

The similarity in both haematocrit and MCV between puffins breeding in gull-occupied and gull-free habitat also suggests that kleptoparasitic attacks by gulls did not induce a significant release of red blood cells into the circulation as part of a stress response. Studies of deer and fish however, have shown that stress caused by handling during blood sampling can also induce a release of red blood cells into the circulation (Wesson et al., 1979; Inversen et al., 1998). If such an effect occurred in puffins, any differences in haematocrit or MCV caused by kleptoparasitic attacks may have been swamped due to the bird exhibiting a more chronic stress response. However, a previous study of stress responses in guillemots *Uria aalge* found that although hormone levels increased rapidly, haematocrit and MCV did not change significantly during handling (Wanless and Maxwell, 2001). Finally, if gulls targeted particular individuals repeatedly, then a comparison of mean values of body condition measurements, taken from a sample of adult puffins breeding within a gull-occupied area, may not reflect any impact of kleptoparasitism since the majority of individuals would be subjected to little stress. This was not the case however, as within the gull-occupied areas puffin burrows were targeted in direct proportion to the number of food loads that were delivered (Finney, unpublished data).

In conclusion, we found no evidence that the current level of kleptoparasitism by gulls had a significant negative impact on the body condition of adult puffins. Previous work at this colony also found no detectable impact of gulls on the growth or survival of chicks (Finney et al., 2001). These results add to the increasing evidence that gulls do not invariably have a negative impact on the reproductive performance of other birds. However, this study was carried out at a time when the number of gulls breeding on the island had been dramatically reduced as part of a gull control programme (Harris et al., 2000). The mean density of breeding gulls during the study period was only one quarter of that prior to the cull. If gull numbers were to increase, the impact of kleptoparasitic attacks on breeding puffins could be far greater.

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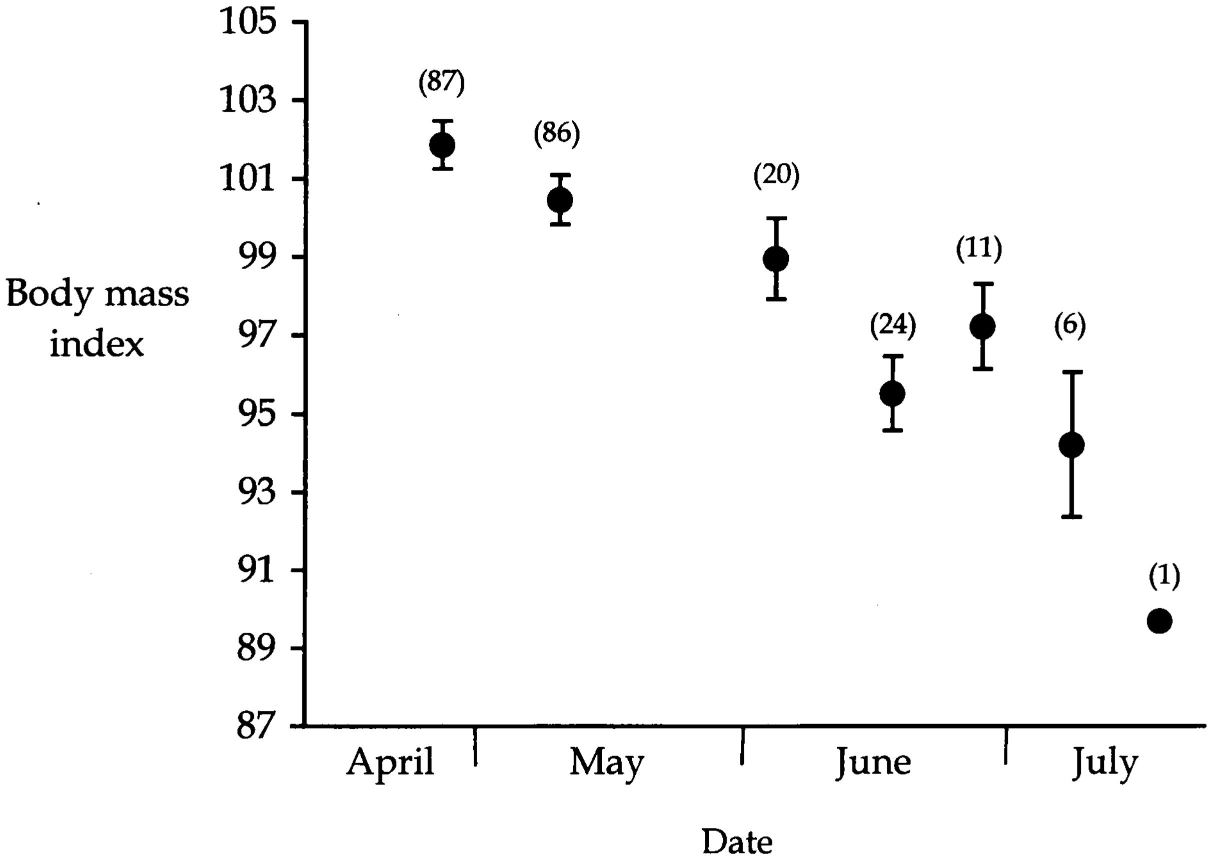

Figure 5.1: Body mass index (mass corrected for structural size) of adult puffins during the breeding season. For clarity, means (+/- one standard error) at 10 day intervals are shown. Sample sizes are given in parentheses. Regression equation based on all 235 individuals, y = 114 - 0.101*date (date = days from 1st January), $F_{1,233}$=35.95, P <0.001.

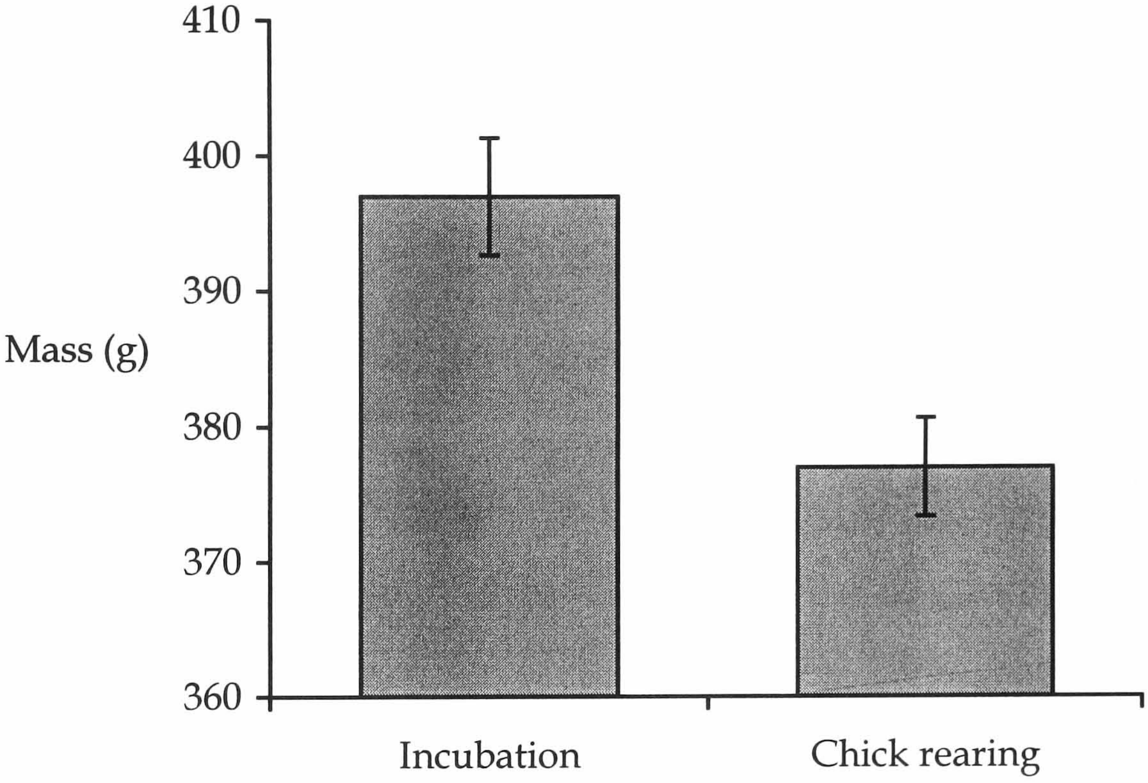

Figure 5.2: Mean (+/- one standard error) body mass of adult puffins caught during incubation and again during chick rearing (mean difference between incubation and chick rearing = 20.2 +/- 2.88 g; paired t-test, df=58, t =6.99, P <0.001).

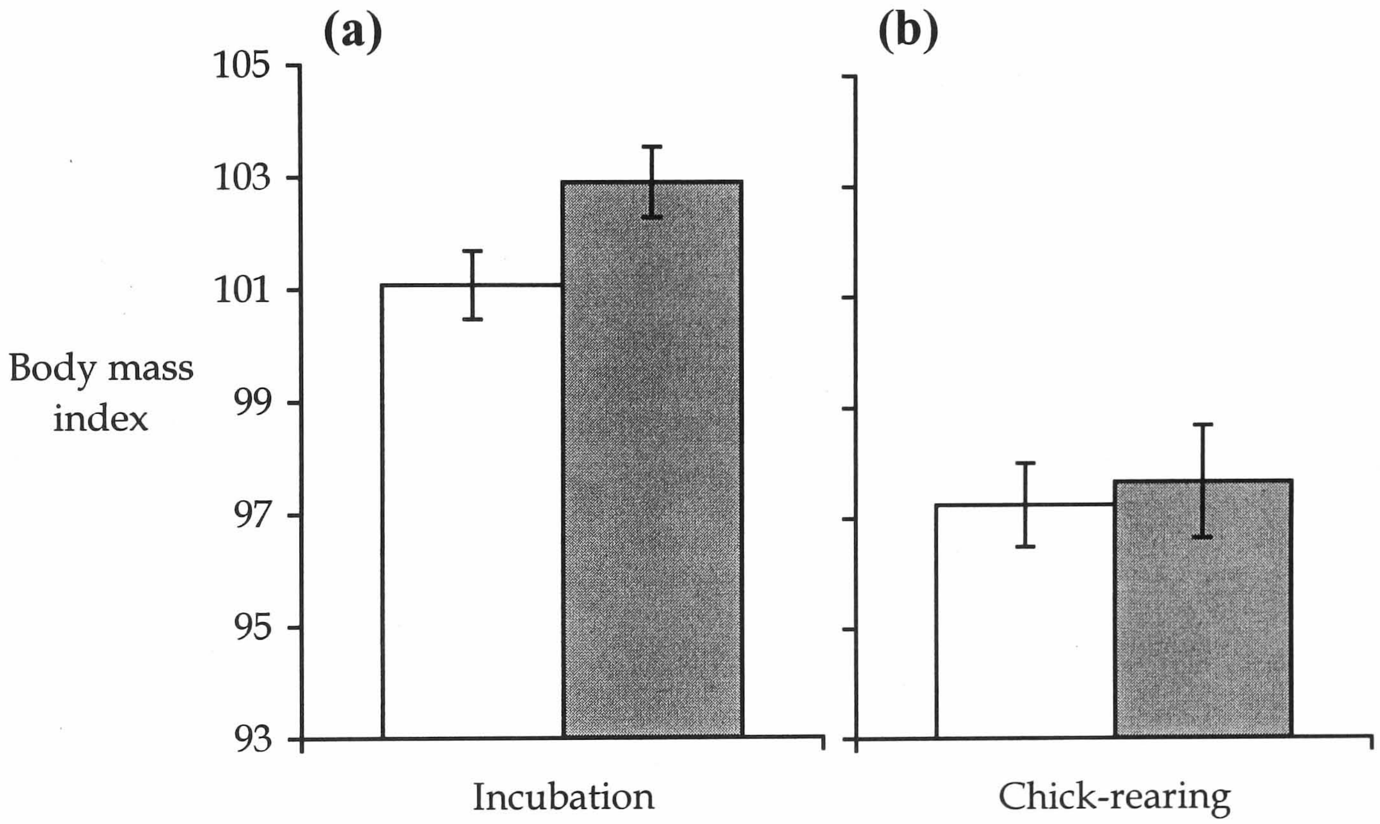

Figure 5.3: Body mass index (mass corrected for structural size) of puffins breeding in gull-occupied (white bars) and gull-free areas (grey bars) during (a) incubation and (b) chick rearing. Means are presented +/- one standard error (difference between gull-occupied and gull-free areas: (a) n=173, $F_{1,2}$=0.39, n.s., (b) n=62, $F_{1,2}$=0.06, n.s.).

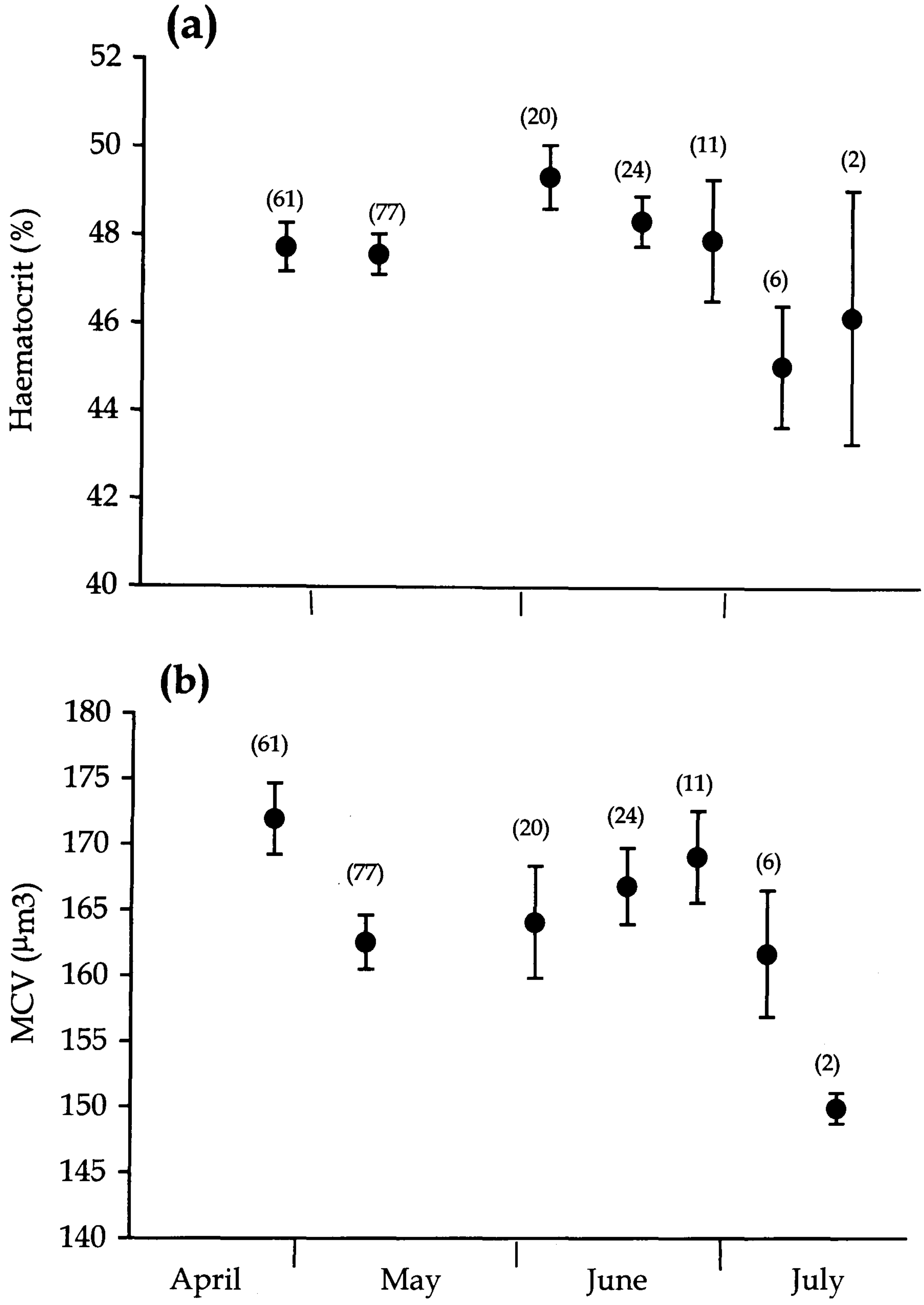

Figure 5.4: (a) Haematocrit and (b) mean corpuscular volume of adult puffins during the breeding season. For clarity, means (+/- one standard error) at 10 day intervals are shown. Sample sizes are given in parentheses. Regression analysis based on all 201 individuals showed no significant seasonal trend in haematocrit ($F_{1,199}$=0.49, n.s.) or MCV ($F_{1,199}$=0.74, n.s.).

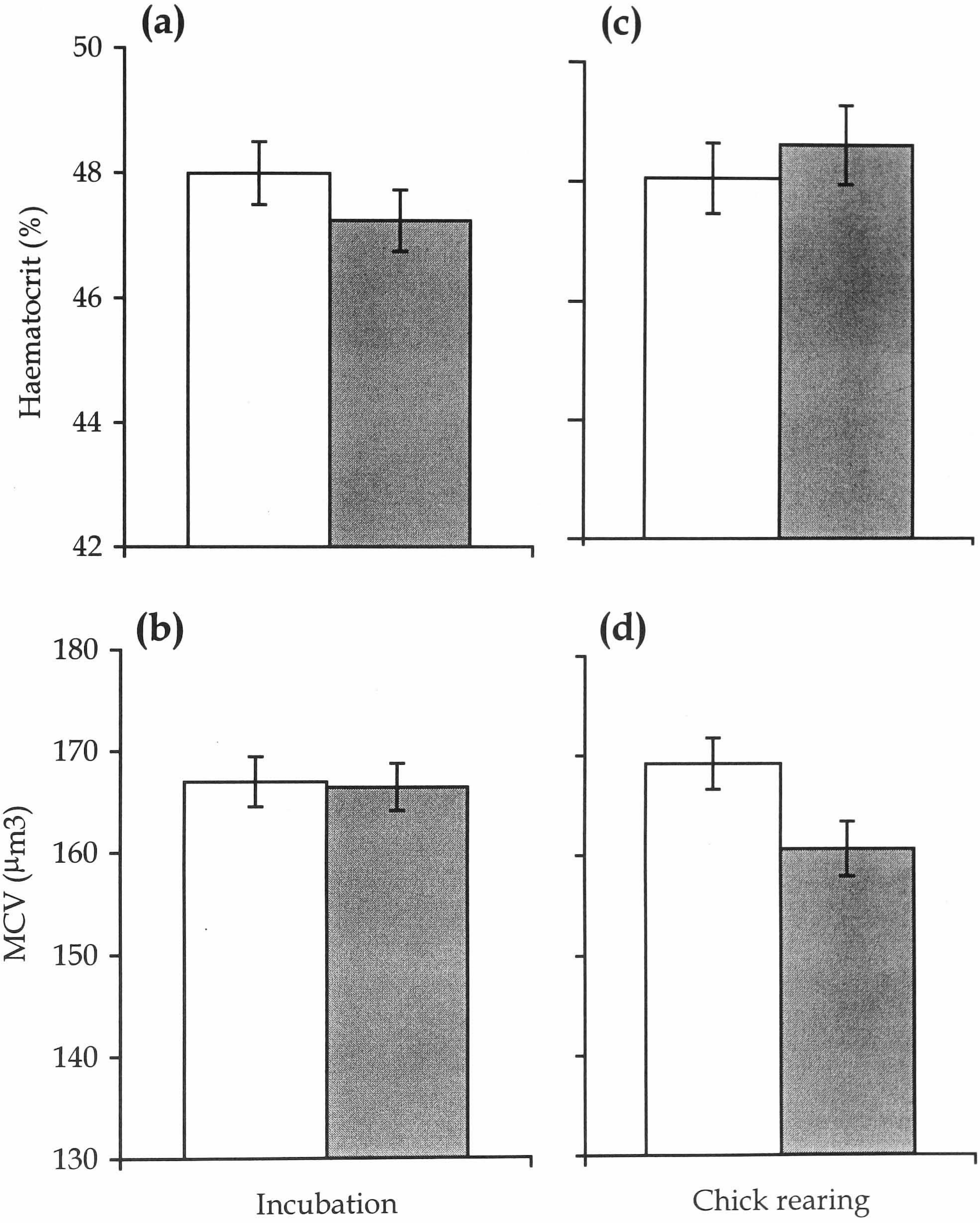

Figure 5.5: Comparison of haematocrit and mean corpuscular volume of puffins breeding in gull-occupied (white bars) and gull-free areas (grey bars) during incubation and chick rearing. Means are presented +/- one standard error (difference between gull-occupied and gull-free areas: (a) n=138, $F_{1,2}$=0.02, n.s., (b) n=138, $F_{1,2}$=0.004, n.s., (c) n=63, $F_{1,2}$=0.23, n.s. and (d) n=63, $F_{1,2}$=2.08, n.s.)

Chapter 6

Adult body condition and reproductive performance in the Atlantic puffin *Fratercula arctica*

Abstract

Adult body condition has been shown to have a strong influence on reproductive performance in a number of species. Body condition can affect both the probability that a breeding attempt will be made and the number and quality of offspring produced. In this study we investigated the relationship between body condition during incubation and reproductive performance in the Atlantic puffin *Fratercula arctica.* Body condition was expressed as mass corrected for structural size, which provides an estimate of an individual's energy reserves. Adult puffins whose breeding attempt failed during incubation were significantly lighter for their size compared to individuals who hatched a chick successfully. Furthermore, the body mass index of females whose chicks died was lower than that of females who fledged a chick successfully. However, of the females that fledged a chick successfully, individuals that had a high body mass index during incubation had chicks that grew at a significantly slower rate than individuals with a lower body mass index. There was no relationship between paternal body mass index and chick growth or survival to fledging. Possible explanations for these findings are discussed.

Introduction

Adult body condition has been shown to have a strong influence on reproductive performance in a number of species (Clutton-Brock, 1988). Body condition can affect both the probability that a breeding attempt will be made and the number and quality of offspring produced. In birds, body condition is often expressed as mass corrected for structural size, which provides an estimate of an individual's energy reserves (Blem, 1990; Brown, 1996). Results from several recent studies have found a positive relationship between a birds body condition at the beginning of the breeding period and its reproductive performance. For example, Wendeln and Becker (1999) found that the body condition of adult common terns *Sterna hirundu* during incubation was positively correlated with chick growth rates and breeding success. Similarly, in a study of lapwings *Vanellus vanellus* and black-tailed godwits *Limosa limosa,* Hegyi and Sasvari (1998) found a positive correlation between the body condition of females and both hatching success and the probability of laying a replacement clutch. It has been suggested that individuals with larger body reserves at the beginning of the breeding period are able to invest more energy in reproduction, without compromising their own future survival or fecundity, compared to initially lighter individuals (Monaghan et al., 1992).

However, there are disadvantages as well as benefits to carrying large body reserves due to the negative impact of increased body mass on flight efficiency and performance (Hedenstrom, 1992). Flapping flight is energetically expensive and the metabolic requirements for flight increase exponentially with body mass (Witter and Cuthill, 1993). Individuals with large body reserves will therefore expend more energy during flight compared to lighter individuals. High body mass can also reduce take-off speed and manoeuvrability, which may lead to a greater risk of predation (Gosler, 1995; Metcalfe and Ure, 1995). Body mass at the beginning of the breeding period may therefore represent a trade-off between the benefits of carrying large reserves, in terms of increased potential for parental investment and reduced risk of starvation, and the benefits of being light, in terms of greater flight efficiency and reduced predation risk. The relationship between body mass and reproductive performance within a given species or population will therefore depend on the relative importance of the various costs and benefits of carrying large body reserves.

In this study we investigated the relationship between body condition and reproductive performance in the Atlantic puffin *Fratercula arctica*, a highly colonial, burrow-nesting auk that lays a single egg clutch. Puffins are long-lived seabirds, with an average life-expectancy of 25 years (Harris, 1984). Males and females are similar in appearance and both are involved in incubation and chick-rearing. Auks (Alcidae) have the highest wing loading of any bird family, making flapping flight very energetically expensive (Nettleship and Birkhead, 1985; Witter and Cuthill, 1993). Puffins are therefore an interesting species in which to study the relationship between body condition and reproductive performance as the disadvantages of carrying large body reserves, in terms of increased energy expenditure during flight, are relatively high. To date, there has been no detailed published study of the relationship between body condition and reproductive performance in auks. The only previously reported data on parental condition and reproduction in puffins showed no evidence that parental body reserves affected breeding success, however only a small number of birds were measured (Wernham and Bryant, 1998). In this study we investigated the relationship between parental body condition and the hatching success, growth rate and survival to fledging of chicks in a population of Atlantic puffins breeding in southeastern Scotland.

Methods

Study site

The study was carried out on the Isle of May, Firth of Forth, Scotland (56°11'N, 2°33'W) during the 2000 breeding season. The island currently supports a population of over 42,000 breeding pairs of Atlantic puffins. For this work, 160 accessible burrows distributed across the island were marked with canes and numbered. These burrows were then used for all subsequent measurements of adult body condition and chick growth and survival.

Chick growth and survival

During incubation, the maximum length and width of eggs were measured to the nearest 0.1mm using callipers. Egg volume was calculated using the equation $V = 0.476 \times \text{length} \times \text{width}^2$ (Harris, 1964). Burrows were then checked at the beginning of the chick-rearing period and scored as being active (chick or intact egg) or inactive. Burrows containing an egg were checked every 12 days until the egg hatched or was lost. Each chick was then weighed and measured (maximum wing chord) every four days initially and then every day towards fledging. Blood samples were collected (under Home Office Licence) and used to sex the chicks (Griffiths et al., 1998).

Adult puffins are very sensitive to disturbance during laying and hatching (Harris, 1984), and so laying and hatching dates could not be obtained directly. Hatching dates were estimated by comparing wing lengths of our study birds with those from a sample of known age chicks; laying date was taken as being 40 days prior to hatching (Harris, 1984). For this reason, laying and hatching dates were only available for eggs that successfully hatched. Equations fitted to growth curves were based on the logistic equation (Ricklefs, 1967) but were adapted to have a fixed intercept [Eq.1]. The growth constant (*k*) is proportional to the maximum growth rate and can be used to make comparisons between chick growth curves fitted with the same equation.

$$m = \frac{a}{1 + [(\frac{a-i}{i}) * (e^\wedge(-k * age))]} \qquad \text{[Eq.1]}$$

where m is mass, a is the asymptote, i is the intercept and k is the maximum growth rate. The intercept was set at 40 g following Harris (1984). Growth curves could only be fitted to data from chicks that fledged as insufficient measurements were available for chicks that died. Thus, to enable all chicks to be included in the analysis, chicks were divided into three groups, (1) hatched successfully but later died, (2) fledged successfully but grew slowly (below average growth rate) and (3) fledged successfully and grew quickly (above average growth rate). These three categories, referred to as chick growth and survival, were then used as the response variable in the analyses.

Adult body mass index

A total of 225 individual adult puffins (of which 59 were caught twice) were captured from 0500-1000 B.S.T. between 27 April and 21 July 2000. During incubation, adults were removed from the burrows by hand. Burrows were left completely undisturbed for three weeks during the peak hatching period as this is when puffins are considered to be most sensitive to disturbance (Harris, 1984). Adults were then captured during the chick-rearing period by placing small nets in the entrance to the burrows. A temporary hide was erected approximately 5 m away. When a puffin returned to the burrow it became caught in the net. An observer was present at all times and birds were removed from the nets immediately.

After capture, the bird was weighed and the wing length (maximum wing chord) and head plus bill measurements were recorded. To reduce the influence of structural size and seasonal variation on body mass, body mass index was expressed as the residual from a multiple linear regression of mass on structural size and measuring date. Structural size was taken as the PCA score of wing and head plus bill size. The regression analyses were carried out for males and females and for the incubation and chick-rearing periods separately. Although time since laying would have been a more accurate correction factor than measuring date, laying date was not known for all individuals (see above). Based on a sub-sample of individuals for which measuring date and laying date were available, we found that the body mass indices calculated using the two dates were highly correlated (df=178, *r*=0.97, *P*<0.001). There was a consistent, but very small difference between the two (paired t-test: df=178, *t*=3.91, *P*<0.001). The use of measuring date was therefore considered to give a reliable condition index and was used for all individuals. Blood samples were collected (under Home Office Licence) and used to sex the birds following the procedure in Griffiths et al. (1998).

Statistical analysis

The relationship between parental body mass index and hatching success was analysed using a generalised linear model with binomial errors and a logit link function. This type of analysis was chosen as it is robust when dealing with binary response variables. Significance was tested using the chi-squared distribution (for details see Crawley, 1993). A multinomial linear regression was used to test the relationship between the growth and survival of chicks and laying date, chick sex, egg volume, parental body mass index and the rate of adult mass loss during the breeding period. Laying date was $\log_{10}$ transformed to make the data conform to a normal distribution. Other tests used are described in the appropriate section of the results. Means are presented ± one standard error.

Results

Parental body mass index

Seasonal change in mass was analysed using measurements from the 59 individuals (24 males and 35 females) that were caught twice, once during incubation and again during the chick-rearing period. Adult puffins lost approximately 5% of their body mass between the incubation and chick-rearing periods (Fig. 6.1). The mean rate of mass loss was 0.43 ± 0.06 g/day and did not differ significantly between males and females (df=55, *t*=0.57, n.s.). There was a positive relationship between body mass index during incubation and the rate of mass loss in both sexes. Individuals with a high body mass index during incubation lost mass at a significantly faster rate than individuals with a low body mass index (Fig. 6.2). There was no significant correlation between the body mass index of males and females within a pair (df=40, r=-0.13, n.s.).

Parental body mass index and reproductive performance

The relationship between parental body mass index and reproductive performance was analysed using measurements from 170 individual adult puffins, 87 males and 83 females, caught during the incubation period. As above, body mass index refers to the measurement of body mass having corrected for time of season and body size. There was no significant relationship between body mass index during incubation and laying date in either sex (Regression: females, $F_{1,58}$=0.01, n.s.; males, $F_{1,53}$=3.05, n.s.). There was a significant, but weak, positive relationship between female body mass index during incubation and egg volume ($F_{1,81}$=4.46, *P*=0.038); maternal body mass index accounted for only 5% of the variation in egg volume.

The overall breeding success of the study birds was 58% (92/160). Of those that failed, 71% failed during incubation and 29% failed after the chick had hatched. There was a significant positive relationship between the body mass index of males during incubation and hatching success. Males whose breeding attempt failed during incubation had a lower body mass index compared to males whose chick hatched successfully (Fig. 6.3a). Females showed the same trend although the relationship was not significant (Fig. 6.3b).

There was no evidence that chick growth and survival to fledging was related to either egg volume (df=2, χ^2=1.65, n.s.) or chick sex (df=2, χ^2=0.05, n.s.). However, there was a significant relationship between laying date and chick growth and survival (df=2, χ^2=6.05, *P*<0.05). Laying date was therefore included as a covariate when testing the relationship between parental body mass index and chick growth and survival to fledging. There was a significant relationship between maternal body mass index during incubation and chick growth and survival to fledging (Fig. 6.4). Post-hoc analyses showed that females who fledged a chick with a below average growth rate had a significantly higher body mass index than both females whose chicks died (df=1, Wald=5.53, *P*=0.019) and females who fledged a chick with an above average growth rate (df=1, Wald=4.47, *P*=0.035). There was however, no significant difference in body mass index between females who fledged a chick with an above average growth rate and females whose chicks died (df=1, Wald=0.96, n.s.).

There was no significant relationship between chick growth rate and paternal body mass index during incubation (df=2, χ^2=1.19, n.s.). There was also no direct relationship between the rate of mass loss in adults and the growth or survival of their chicks (females, df=2, χ^2=2.14, n.s.; males, df=2, χ^2=1.20, n.s.).

Discussion

There was a significant relationship between parental body mass index and reproductive performance. Adult puffins whose breeding attempt failed during incubation were significantly lighter for their size compared to individuals who hatched a chick successfully. Monaghan et al. (1992) proposed that the mechanism whereby adult mass influences reproductive decisions and performance may operate via a critical threshold, which may alter seasonally, and below which individuals will not allow their body mass to fall due to an increased mortality risk. Adults with low reserves would be expected to abandon a breeding attempt rather than compromise their probability of survival. For long-lived species, such as seabirds, any reduction in adult survival would have a dramatic impact on average life expectancy and thus lifetime reproductive success (Wooler et al., 1992). The results from this study therefore suggest that puffins with low reserves abandon the breeding attempt rather than suffer an increased mortality risk, a behaviour that has already been demonstrated in a number of seabird species (Chaurand and Weimersirch, 1994; Olsson, 1997).

The relationship between body mass index and hatching success was stronger in males than in females. The reasons for this are unclear but may be related to the different roles played by the two sexes during the incubation period. In comparison to females, males spend a greater proportion of their time engaged in energetically costly activities such as burrow maintenance and defence (Wernham, 1993). Males with low reserves may be unable invest sufficient energy in these activities and would thus be more likely to abandon the breeding attempt. Similar results were found in a study of blue petrels *Halobaena caeruelea* on Mayes Island, Antarctica (Chastel et al., 1995). After laying, male blue petrels incubate the egg continuously for 12 days while the female forages at sea. Chastel et al. (1995) found that males with low reserves at the beginning of the incubation period were more likely to abandon the egg than heavier individuals. The body mass index of female blue petrels had no significant influence on hatching success.

There was a significant relationship between maternal body mass index and fledging success. The body mass index of females whose chicks died was lower than that of females who fledged a chick successfully. These results are in accordance with the high energetic expenditure associated with raising young. Individuals with low reserves would be more likely to reach their critical mass threshold, and thus abandon the breeding attempt, compared to initially heavier individuals. These results are consistent with those from several previous studies of fledging success in relation to adult body mass in seabirds. For example, Monaghan et al. (1992), found that the length of time that adult Arctic terns continued to feed young was related to their body reserves at the time of hatching. Parents with low reserves at the time of hatching were the first to abandon the breeding attempt. In puffins however, the relationship between body mass index and chick survival was only evident in females. This was most likely due to the greater role played by females during the chick-rearing period. Females provision the chick significantly more frequently than males, particularly in the first few weeks after hatching (Wernham, 1993). It follows therefore that maternal body mass index will have a stronger influence on fledging success than that of males.

Females with a low body mass index were therefore more likely to have chicks that died compared to heavier individuals. However, of the females that fledged a chick successfully, individuals that had a high body mass index during incubation had chicks that grew at a significantly slower rate than individuals with a lower body mass index. These results are in contrast to several previous studies, which found that parents with the largest body reserves during incubation had faster growing chicks and, in terns, a larger clutch size (Monaghan et al., 1992; Lorentsen, 1996; Wendeln and Becker, 1999). The interpretation of this relationship was that individuals with large reserves could afford to lose more mass than initially lighter individuals and that this energy could then be allocated to the offspring, resulting in higher breeding success (Norberg, 1981). In this study, individuals that were heaviest during incubation also lost the most mass, but did not have a higher reproductive performance. There are several possible explanations for these findings.

In a study of Blue tits *Parus caeruleus*, Gebhardt-Henrich et al. (1998) also found that females that were heavy during incubation lost more mass than initially lighter individuals but had a lower reproductive performance (measured in terms of fledgling condition). The authors proposed that body reserves at the beginning of the breeding period was used as insurance by those females that would lose more mass during the rearing of young due to factors such as poor foraging ability or a low quality territory (Gebhardt-Henrich et al., 1998). These "lower quality" females were therefore heavier during incubation but had chicks that fledged in poorer condition. Alternatively, heavier individuals may simply have had greater foraging costs than initially lighter individuals. A further explanation is that differences in chick growth rates may have been related to differences in egg volume and/or quality, which has been demonstrated to a significant impact on chick growth and survival (Bolton, 1991). Although we found a weak positive relationship between maternal body mass index and egg size, female puffins that were lighter during incubation may still have invested more resources in the egg in terms of its composition. A significant correlation between egg composition and chick development has already been demonstrated in a number of studies (Williams, 1994; Royle et al., 1999; Eising et al., 2001). Data on both maternal body mass index during the pre-laying period and egg composition would be needed to examine this further.

The data presented in this study suggest that the relationship between body condition and reproductive performance in puffins is complex. Although puffins with the lowest body mass index during incubation were more likely to have a failed breeding attempt, there were also disadvantages to carrying large body reserves; heavier females had chicks that grew at a significantly slower rate than initially lighter individuals (Fig. 6.4). Slow growing chicks are at a disadvantage for two main reasons. Firstly, they have a longer fledging period than faster growing chicks (Finney, unpublished data), which increases the length of time that the chicks are most vulnerable to predation by gulls. Secondly, slow growing and thus lighter chicks are at greater risk of starvation during periods of unpredictable food supply. The evidence from this study therefore suggests that females with an intermediate body mass index had a higher reproductive performance than heavier individuals. However, individuals with limited reserves are also at greater risk from additional unpredictable stresses during the breeding season. An increase in energy expenditure, resulting from factors such as reduced food availability or increased disturbance, may cause birds with already limited reserves to abandon their breeding attempt. Clearly, an experimental study of the impact of body mass on reproductive performance would be needed to investigate this further.

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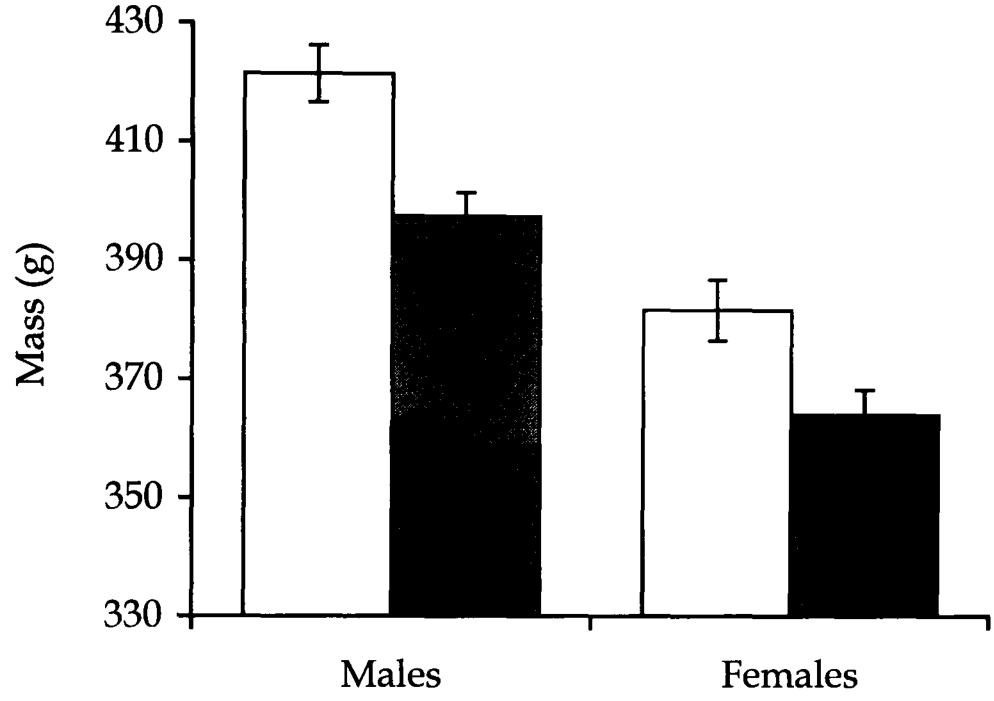

Figure 6.1: Mean (+/- one standard error) body mass of male and female adult puffins during incubation (white bars) and during the chick-rearing period (grey bars). (Mean percentage loss of mass between the incubation and chick-rearing periods: males, 5.6 +/- 0.01%, n=24; females, 4.3 +/- 0.01%, n=35).

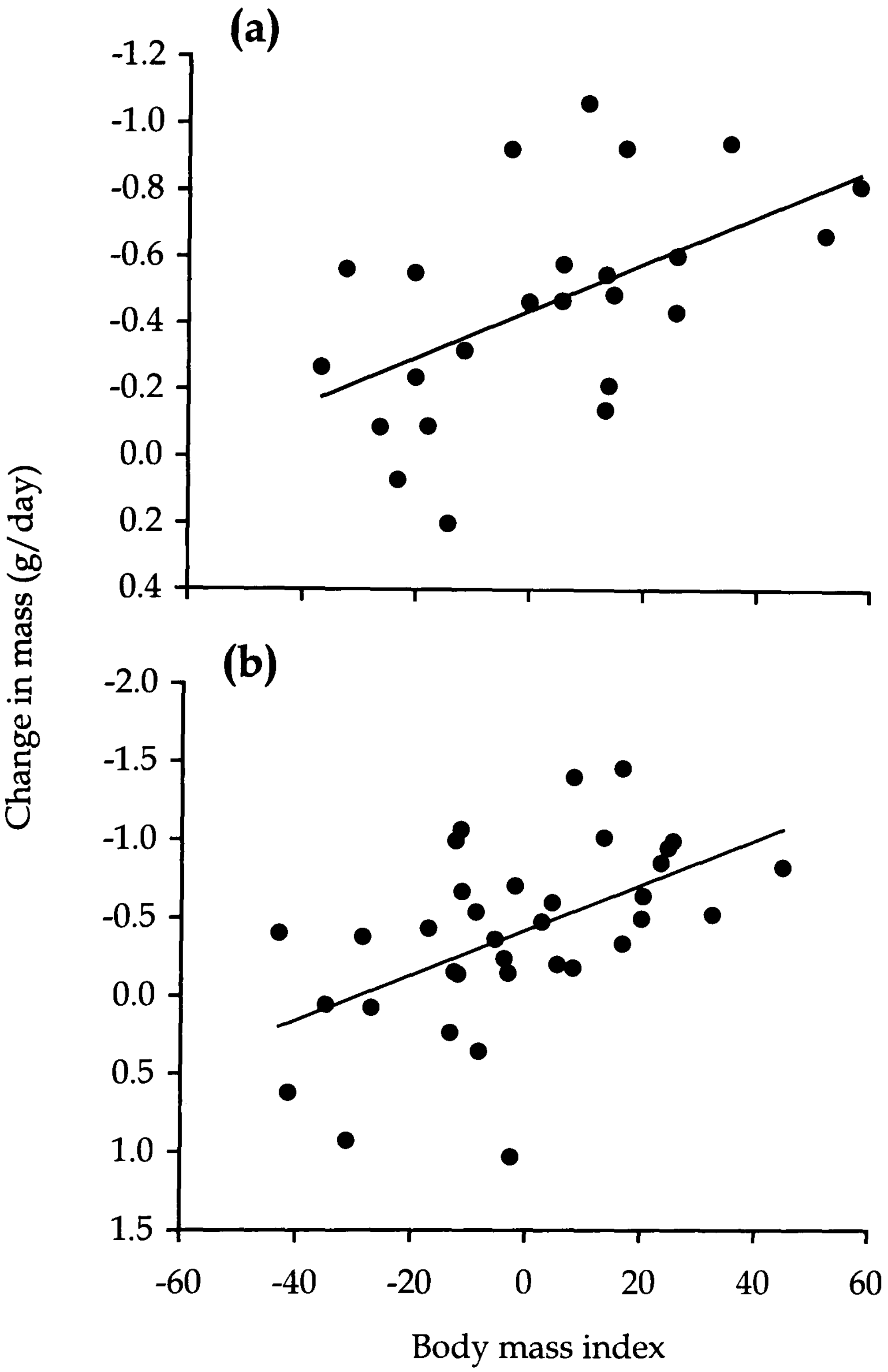

Figure 6.2: Relationship between body mass index during incubation and the rate of mass loss in (a) male and (b) female breeding Atlantic puffins (Regression: males, $F_{1,22}$=9.28, P=0.006; females, $F_{1,33}$=12.97, P=0.001).

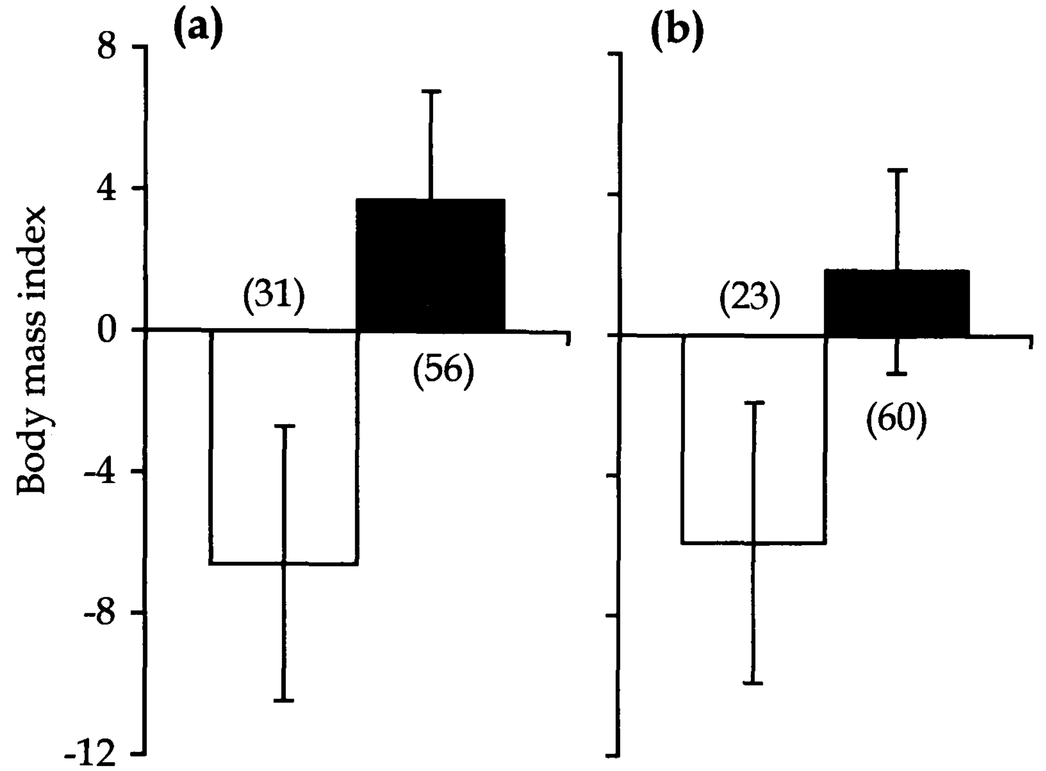

Figure 6.3: Mean (+/- one standard error) body mass index of (a) male and (b) female breeding Atlantic puffins during incubation. Data shown for individuals whose breeding attempt failed during incubation (white bars) and for individuals whose chick hatched successfully (grey bars). Relationship between adult body mass index and hatching success, GLIM: males, df=1, χ^2=4.07, P <0.05; females, df=1, χ^2=2.14, n.s.

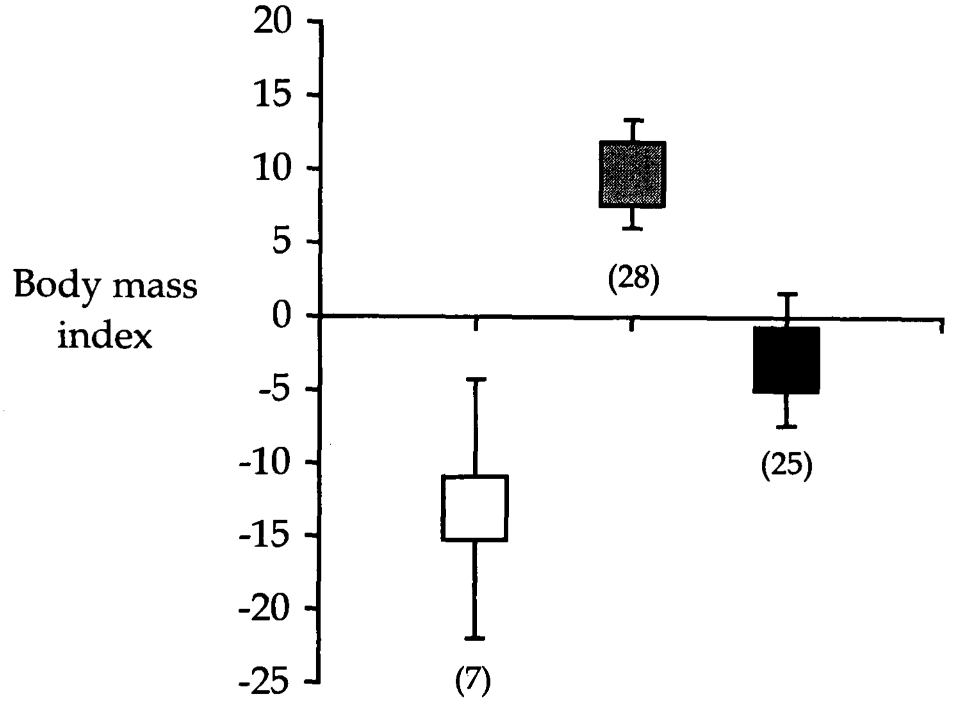

Figure 6.4: Mean (+/- one standard error) body mass index of breeding female Atlantic puffins during incubation. Data shown for individuals whose chicks died (white box), whose chicks fledged but grew at below average growth rate (grey box) and those whose chicks fledged and grew at above average growth rate (black box). Results of a multinomial linear regression testing the relationship between body mass index and chick growth and survival: df=2, χ^2=8.51, P =0.014). Sample sizes are given in parentheses.

Chapter 7

Replacement egg laying in herring and lesser black-backed gulls: implications for management

Abstract

An important decision faced by many birds during the breeding season is whether or not to relay following clutch loss. Replacement clutches have the potential to make an important contribution to an individuals life-time reproductive success, particularly in species or populations where clutch loss is common. In this study we investigate the relaying capacity of herring gulls *Larus argentatus* and lesser black-backed gulls *L. fuscus*, two species that regularly suffer egg loss as a result of predation. First clutches were removed and the proportion of pairs that relaid and the number and size of eggs laid in the replacement clutch were recorded. Approximately 50% of pairs relaid following egg removal. There was a significant seasonal decline in the probability of a replacement clutch being laid. Furthermore, both clutch size and egg volume were lower in replacement clutches compared to first laid clutches. The implications of these findings for gull management strategies are discussed.

Introduction

An important decision faced by many birds during the breeding season is whether or not to relay following clutch loss. In iteroparous species, parents face a trade-off between the benefits of relaying, in terms of the chance to produce offspring within the same season, and the potential costs of increased parental investment in terms of reduced survival and future fecundity (Clutton-Brock, 1988; Stearns, 1992). Previous studies have identified several factors that influence both the probability of relaying and the number and size of eggs laid in the replacement clutch. These include intrinsic factors such as parental age, experience or body condition (Hegyi and Sasvari, 1998; Hipfner et al., 1999) and also extrinsic factors such as lateness in the season or the length of time that the first clutch had been incubated (Parsons, 1971; Wooler, 1980).

In long-lived species with low annual reproductive output, such as seabirds, life-time reproductive success is determined more by adult survival, and thus the number of breeding attempts, than by annual fecundity (Clutton-Brock, 1988). Individuals are therefore expected to invest cautiously in reproduction in any single year in order to avoid jeopardising their future reproductive potential (Stearns, 1992). However, most seabird species have the capacity to produce a replacement clutch if the first is lost (Cramp, 1977). This is thought to be an adaptation to unpredictable events such as severe weather or flooding (Storey, 1987; Brown and Morris, 1996) as well as predation. Thus, replacement clutches have the potential to make an important contribution to an individuals life-time reproductive success, particularly in the species or populations where clutch loss is most common (Martin et al., 1989).

Herring gulls *Larus argentatus* often show high rates of egg loss during the breeding season as a result of both inter and intraspecific predation (Brouwer and Spaans, 1994). However, studies that have been undertaken to quantify the relaying capacity of herring gulls (Harris, 1964; Parsons, 1971) were carried out at a time when gull populations in Britain were expanding rapidly, and thus breeding conditions were presumably favourable. More recently, herring gull populations have stabilised and in some areas numbers have declined dramatically (Hagemeijer and Blair, 1997); the ability of adults to lay replacement clutches may therefore have changed. In this study, we experimentally assess the capacity of herring gulls to relay following clutch loss at a colony where the number of breeding gulls has remained stable for the previous 5 years (Harris et al., 2000). First clutches were removed and the proportion of pairs that relaid and the number and size of eggs laid in the replacement clutch were recorded. These results are compared to those from a previous study undertaken at the same colony but which was carried out during a period when the gull population was expanding rapidly (Parsons, 1975). Data on the relaying capacity of the closely related lesser black-backed gull *L. fuscus* were also collected for comparison.

Methods

The study was carried out on the Isle of May, Firth of Forth, Scotland (56°11′N, 2°33′W) during the 2000 breeding season. During the study, around 2,800 pairs of herring gulls and 1,200 pairs of lesser black-backed gulls bred on the island (Harris et al., 2000). Approximately 2 hectares of the island where both herring and lesser black-backed gulls were breeding was selected as a study site.

The study site was visited every day between April and June. The area was systematically searched and each nest was marked with a small numbered cane as soon as the first egg was laid. The nests were also identified as belonging to herring gulls or lesser black-backed gulls at this time. Eggs were individually marked a, b or c according to their laying order. The maximum length and width of the eggs were measured to the nearest 0.1mm using callipers. Egg volume was calculated using the equation $V = 0.476 \times \text{length} \times \text{width}^2$ (Harris, 1964). Only birds that laid three eggs for their first clutch were used for comparison in this study. Eggs were removed four days after clutch completion. The laying date and size of any replacement eggs laid were recorded.

The gulls used in this study were unringed and it was therefore possible that some pairs, assumed to have failed, may have relaid outside the study area. However, as nests were left intact, it appeared that the majority of gulls relaid at, or within 1-2 metres of, their original nest-site. Furthermore, a previous study of individually colour-ringed herring gulls at this colony found that there was very little movement of nest-sites amongst gulls that had had their first clutch removed (Parsons, 1975). The small number of pairs that may have relaid elsewhere are therefore unlikely to influence the conclusions of this study.

Statistical analyses

The effect of laying date on the probability of laying a replacement clutch was analysed using a generalised linear model with binomial errors and a logit link function. Significance was examined using the chi-squared distribution (see Crawley, 1993). The effect of laying date on the number of eggs in the replacement clutch was analysed using a multinomial logistic regression. A general linear model was used to test the relationship between egg size in first and replacement clutches within individuals. Nest was included in the model as a random factor and egg (a, b or c) as a fixed effect. Other tests used are described in the appropriate section of the results. Means are presented ± standard error.

Results

Timing of breeding

The median laying date for herring and lesser black-backed gulls was 19 May and 25 May respectively. This was similar to that recorded during previous years at this colony (Scottish Natural Heritage unpublished accounts). Removing the first clutch of eggs delayed the breeding period of both species by approximately 18 days. The median laying date of replacement clutches was 7 June for herring gulls and 12 June for lesser black-backed gulls.

Probability of relaying

The mean time to relaying was 13.3 ± 0.3 days in herring gulls and 11.6 ± 0.2 days in lesser black-backed gulls and the difference between the two was statistically significant (t-test: df=34, t=4.48, P<0.001). The proportion of pairs that laid a replacement clutch did not differ between the two species (0.50 and 0.55 for herring and lesser black-backed gulls respectively; chi-squared test: df=1, χ^2=0.2, n.s.). There was a negative relationship between laying date and the probability of a replacement clutch being laid. Pairs that laid early in the season were more likely to lay a replacement clutch than pairs that laid later in the season (Fig. 7.1). Although the trend was evident in both species, it was only statistically significant for lesser black-backed gulls.

Size of the replacement clutch

The mean number of eggs laid in the replacement clutch was 2.26 ± 0.20 eggs for herring gulls and 2.72 ± 0.09 eggs for lesser black-backed gulls. In both species there was a significant difference in egg volume between the first and replacement clutch. The a-egg was significantly smaller in the replacement clutch compared to the first laid clutch (Fig. 7.2); the a-egg was smaller irrespective of the number of eggs laid in the replacement clutch. The volume of the b and c-eggs did not differ significantly between first and replacement clutches. Despite the overall decline in egg size, within individuals there was a significant positive correlation between egg size in first and replacement clutches. Individuals that laid the largest eggs in the first clutch also laid the largest eggs in replacement clutches (herring gull, $F_{1,21}$=5.12, P=0.034; lesser black-backed gull, $F_{1,58}$=15.67, P<0.001).

Discussion

Gull relaying capacity

Removing the first clutch of eggs delayed the breeding period of both herring and lesser black-backed gulls by approximately 18 days. This significantly reduced the number of individuals making a breeding attempt. Only 50% of herring gulls and 55% of lesser black-backed gulls relaid after having their first clutch removed. The low proportion of pairs that lay a replacement clutch, found in both this and other studies (e.g. Duncan, 1987; Wendeln et al., 2000), therefore suggests that the costs of relaying may be prohibitive for some individuals. Previous studies of gulls have demonstrated that the laying of just one extra egg can significantly reduce adult body mass (Monaghan et al., 1998) and that loss of mass during breeding can have important consequences for future survival (Nager et al., 2001). Increases in reproductive investment that result in a significant loss of body mass are therefore unlikely since even a small reduction in adult survival would have a large negative impact on lifetime reproductive success (Wooler et al., 1992).

There was a significant negative relationship between laying date and the probability of relaying following clutch loss. In both species, pairs that laid their first clutch early in the season were more likely to lay a replacement clutch than pairs that laid later in the season. A seasonal decline in replacement layings was also found in the previous study of herring gulls at this colony (Parsons, 1971) and has been reported in a number of other species including guillemots (Schauer & Murphy, 1996) and common terns (Wendeln et al., 2000). Several hypotheses have been proposed to explain the seasonal decline in replacement layings (Perrins, 1970). Firstly, older birds tend to breed earlier in the season than younger individuals and these more experienced breeders may have a greater capacity to relay than younger, less experienced birds. Alternatively, deteriorating environmental conditions during the season may prevent later breeding birds from relaying. Experiments aimed at separating these two hypotheses have produced conflicting results (Hipfner et al., 1999; Wiggins et al., 1994) and it is possible that both mechanisms play a role to some extent.

Clutch size was lower in replacement clutches compared to first clutches in both species. The effect was most evident in herring gulls with only 50% of replacement clutches consisting of three eggs compared to 75% in lesser black-backed gulls. In addition to laying fewer eggs, there was also a reduction in egg size between first and replacement clutches although the effect was only significant in the a-egg. These results are again consistent with those from the previous study of herring gulls at this colony; Parsons (1975) found that the smaller volume of replacement clutches was mainly due to the reduction in size of the a-egg. A reduction in egg size could have important consequences for reproductive performance as egg size has already been shown to affect the growth and early survival of chicks in a number of species, including gulls (Bolton, 1991; Williams, 1994). Chicks from small eggs grow more slowly and suffer a higher mortality risk compared to chicks hatching from larger eggs (Parsons, 1970; Hipfner and Gaston, 1999). Chicks from c-eggs laid in replacement clutches would therefore have a very low probability of survival, which may explain why there is an increase in the occurrence of two egg clutches later in the season.

The results from this study demonstrated that delaying breeding reduced the reproductive output of both herring and lesser black-backed gulls since almost 50% of pairs did not lay a replacement clutch. In the pairs that did relay, there was also a reduction in clutch size. Together, this reduced the number of eggs being incubated by 62% in herring gulls and 50% in lesser black-backed gulls. In addition to these direct effects of delayed breeding, reproductive performance was also likely to be affected indirectly through changes in egg size and in the brood-rearing capacity of adults (Monaghan et al., 1998). In an experimental study of lesser black-backed gulls, Monaghan et al. (1998)

demonstrated that the capacity of parents to rear a brood of three chicks was significantly reduced solely as a consequence of themselves having produced one extra egg. Combined with the reduction in egg size, the hatching and fledging success of the experimentally delayed pairs was likely to have been significantly reduced, although this was not measured directly in this study. Although these conclusions are based on data collected within a single breeding season, the results are comparable to those from the previous study at this colony (Parsons, 1971, 1975). This was unexpected given the marked difference in the size and status of the gull population during the two studies. The similarity in the results from the two studies suggests a consistent response of gulls to delayed breeding.

Implications for gull management strategies

Large gulls (*Larus* spp.) are common predators of the eggs and chicks of other birds during the breeding season and often compete for breeding sites with other ground-nesting species. Concern regarding the possible detrimental impact of gulls on the reproductive success of other birds increased when gull populations in Europe and North America expanded rapidly during the second half of the last century (Monaghan, 1983; Lloyd et al., 1991; Spaans and Blokpoel, 1991). The apparent adverse effect of gulls on other breeding birds has resulted in the implementation of gull control programmes at many colonies (Bruyns, 1958; Wanless et al., 1996). One of the most common management strategies used was the removal of gulls from specified areas, usually through the culling of adult birds (Morris et al., 1992; Bosch, 1996). More recently, gull populations have stabilised and have even shown marked declines in some areas (Hagemeijer and Blair, 1997). This has led to an increase in their conservation status (Gibbons et al., 1996) and has highlighted the need to consider alternative management strategies to culling.

In situations where predation and kleptoparasitism are the main threats posed by gulls to other breeding birds, altering the relative timing of breeding of gulls with respect to that of the species targeted for protection could be an alternative management strategy. The impact of gulls on other birds varies during the breeding season and is usually greatest when gulls are provisioning young, due to the high energy demands of their chicks (Oro and Martinez-Vilalta, 1994). Thus, delaying breeding such that gulls are still incubating eggs while other birds are raising young could potentially reduce the impact of gulls on the species targeted for protection while also reducing the impact of management on the gull population itself.

The results from this study showed that only 50-55% of pairs laid a replacement clutch following egg removal. The effectiveness of delaying gull breeding as a potential management strategy would therefore depend to a large extent on the movements and behaviour of the birds that did not relay. If these individuals left the colony, then delaying gull breeding may indeed reduce predation and kleptoparasitism risk. However, if these individuals were to remain in their breeding territories, then predation and kleptoparasitism risk is unlikely to be significantly reduced, and could potentially even increase since the gulls would not have to spend time incubating eggs. Clearly, further work is needed to determine how delaying breeding effects gull behaviour, and thus the interactions between gulls and other species, before its effectiveness as a viable alternative to culling can be fully assessed.

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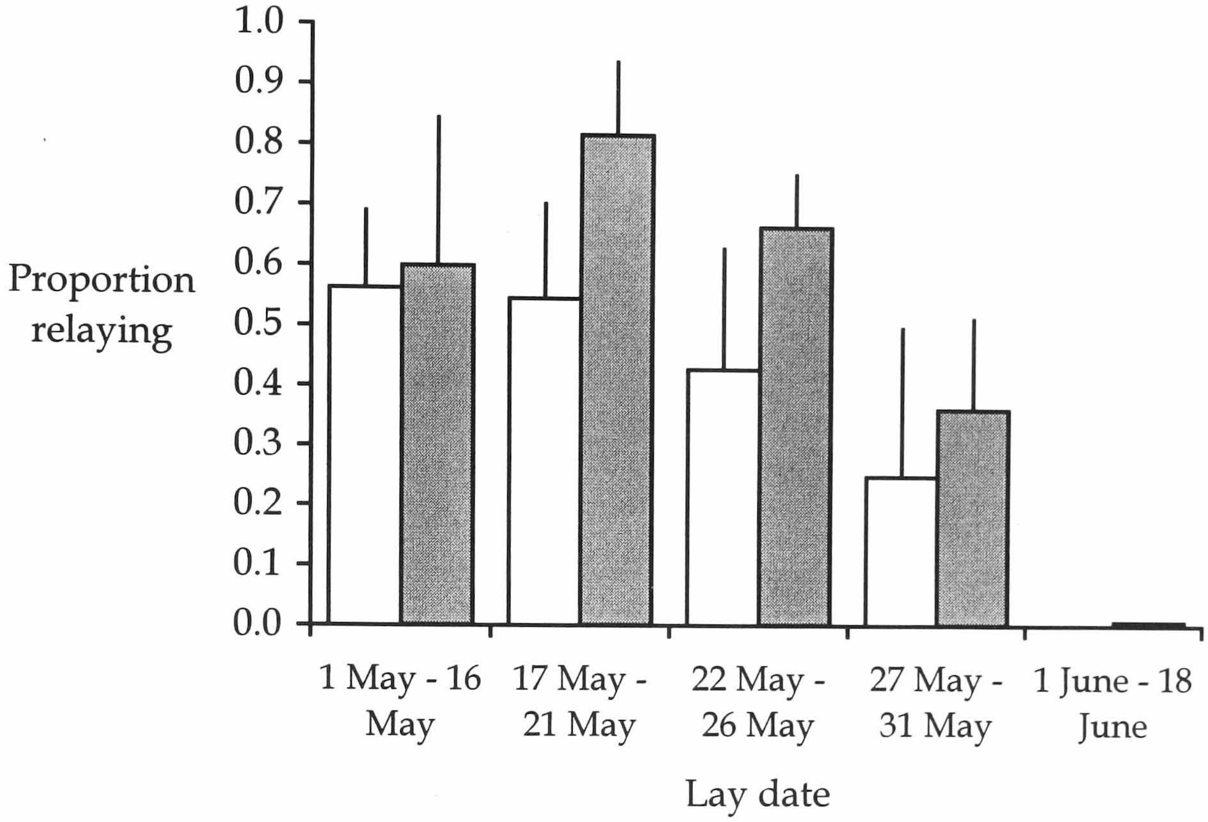

Figure 7.1: Relationship between the laying date of the first clutch and the probability of laying a replacement clutch for herring gulls (white bars) and lesser black-backed gulls (grey bars). (Seasonal trend in the probability of relaying, GLIM: herring gull, df=1, χ^2=0.05, n.s.; lesser black-backed gull, df=1, χ^2=12.13, P <0.001).

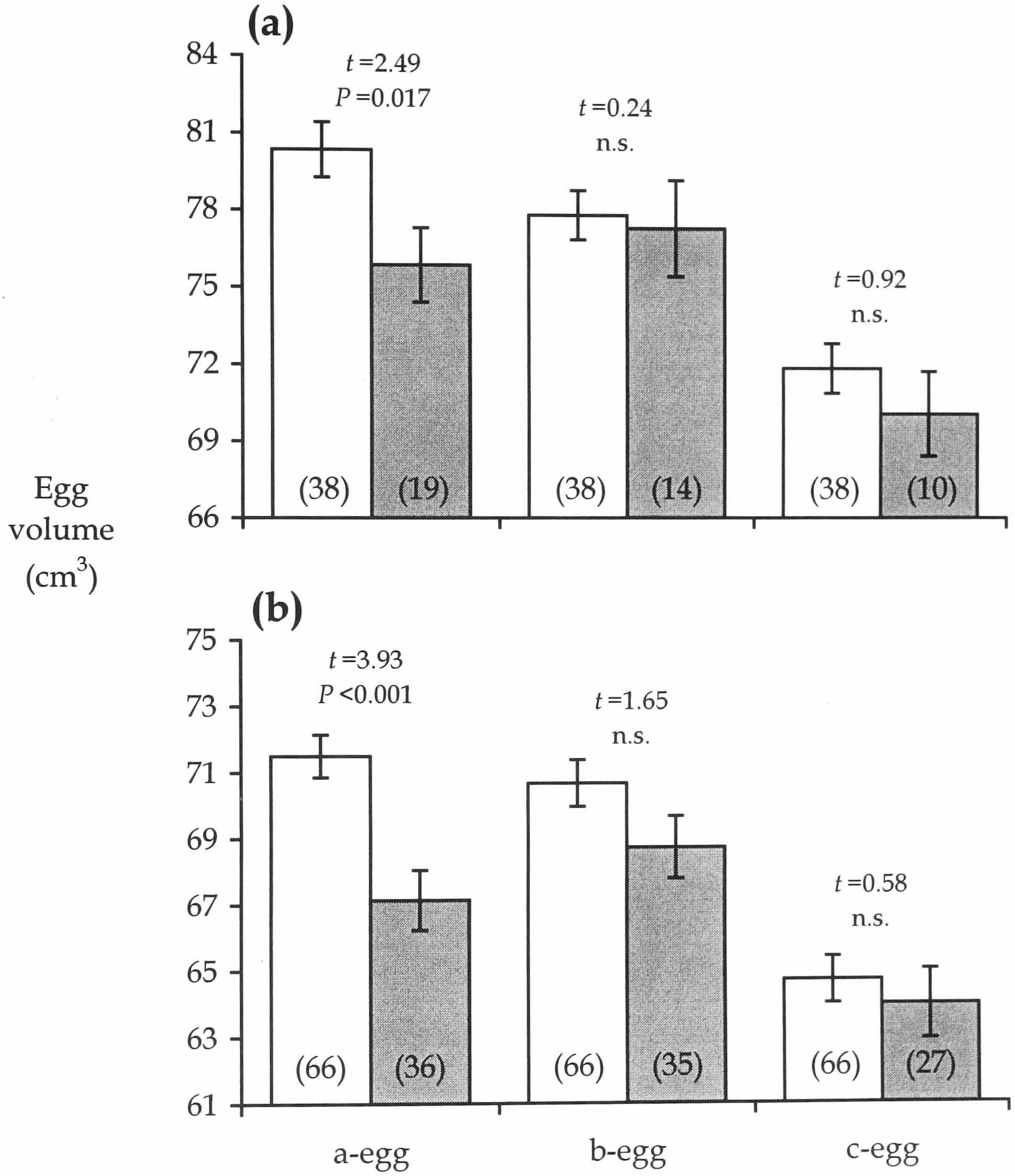

Figure 7.2: Mean (+/- one standard error) volume of eggs laid in first (white bars) and replacement clutches (grey bars) for (a) herring gulls and (b) lesser black-backed gulls. Sample sizes are given in parentheses. Results of t-tests are also shown.

Chapter 8

Great black-backed gull *Larus marinus* predation of adult Atlantic puffins *Fratercula arctica* on the Isle of May

Abstract

Predation by great black-backed gulls *Larus marinus* has been shown to have a significant negative impact on the breeding success of a number of seabird species. The rapid increase in the number of great black-backed gulls breeding on the Isle of May, southeast Scotland, therefore led to concern as to the possible impact of gulls on breeding puffins. The aim of this study was to quantify the number and breeding status of adult puffins predated by great black-backed gulls during the breeding season. Almost 200 full-grown puffins were predated by great black-backed gulls during the breeding season. The proportion of immature birds killed increased significantly as the season progressed but was in direct proportion to the number expected to be present in the colony at that time. Simple population models are used to explore the potential impact of great black-backed gull predation on breeding puffins over the next 20 years.

Introduction

There are many sources of mortality in seabird populations including disease, injury and starvation (Ortiz and Smith, 1994; Piatt and VanPelt, 1997; Kuiken, 1999). However, in some populations, predation can also be an important factor affecting the probability of survival. High rates of predation can generate strong selection pressure on behaviour (Mougeot and Bretagnolle, 2000; Whittam and Leonard, 2000) and under certain circumstances may reduce the size of the prey population (McChesney and Tershy, 1998; Phillips et al., 1999).

One of the most important predators at seabird colonies in Britain and North America is the great black-backed gull *Larus marinus*, which frequently preys upon eggs, chicks and adults of other bird species during the breeding season (Cramp, 1977; Taylor, 1982). Predation by great black-backed gulls has been shown to have a significant impact on the breeding success of a number of species (Regehr and Montevecchi, 1997). In a study on Gull Island, Newfoundland, Massaro et al. (2000) found that predation by great black-backed gulls significantly reduced the breeding success of black-legged kittiwakes *Rissa tridactyla*. Similarly, great black-backed gulls were responsible for the low productivity of common eiders *Somateria mollissima* at several colonies in the Bay of Fundy, Canada (Mawhinney et al., 1999).

The number of great black-backed gulls breeding on the Isle of May, southeast Scotland, has increased dramatically over the past 10 years (Harris et al., 2000; Scottish Natural Heritage unpublished records). This rapid increase has lead to concern as to the possible detrimental impact of predation by great black-backed gulls on other breeding birds. The management plan for the island is currently under review with a view to assessing whether the current number of great black-backed gulls breeding on the island poses any significant threats to other species. One species that may be particularly vulnerable is the Atlantic puffin *Fratercula arctica*. Great black-backed gulls frequently predate adult puffins during the breeding period, which is from late April to mid-July for both species. As puffins are long-lived birds with a high probability of survival but with low annual fecundity (Cramp, 1977), even a small reduction in adult survival could have a significant impact on population size. The aim of this study was to quantify the number and breeding status of adult puffins predated by great black-backed gulls on the Isle of May.

Methods

The Isle of May, Firth of Forth, Scotland (56°11′N, 2°33′W) was designated as a National Nature Reserve in 1956 due to its large populations of breeding seabirds (Ratcliffe, 1977). The island supports over 42,000 breeding pairs of Atlantic puffins (Harris et al., 2000). Great black-backed gulls first colonised the island in 1962 but during the period from 1972 to 1989 there was only intermittent breeding by a few pairs (Harris et al., 2000). This was most probably due to the disturbance caused by a gull control programme set up to reduce the number of herring *L. argentatus* and lesser black-backed gulls *L. fuscus* breeding on the island (Coulson, 1991). The control programme was terminated in 1989 (Wanless et al., 1996), and the population of great black-backed gulls has since increased rapidly to 27 breeding pairs in 2001 (Fig. 8.1).

Great black-backed gulls carry dead puffins back to the nest where the entrails and breast muscles are eaten, the skin turned inside out and the bones picked clean. Nests of gulls that feed on puffins are therefore often surrounded by wings or other remains (Harris, 1984). The nest sites of all great black-backed gulls breeding on the island were located and mapped in early May 2001. Remains of dead puffins from the previous years were also collected and removed at this time. During the chick rearing period, nest sites were visited every 5-6 days and all puffin carcasses were counted and removed. The number of grooves on the bill was used to classify full-grown puffins as breeders (more than two grooves), immatures (less than two grooves) or of unknown breeding status (two grooves; Harris, 1981). Clutch size and fledging success were also recorded for all great black-backed gull pairs.

Results

Great black-backed gull territories were predominantly in areas occupied by breeding puffins (Fig. 8.2). A total of twenty-seven pairs of great black-backed gulls bred on the Isle of May during the 2001 season; five pairs failed after laying and 20 pairs successfully fledged one or more chicks. The outcome of the breeding attempt for two pairs was not known and these pairs were therefore omitted from the calculation of breeding success. Mean clutch size was 2.75 ± 0.12 eggs and the overall breeding success was 1.76 ± 0.23 chicks fledged per pair.

A total of 169 carcasses of full-grown puffins were found at great black-backed gull nests during the breeding season. A further 22 corpses showing signs of predation were found in close proximity to breeding great black-backed gulls but could not be attributed to individual nests. Approximately 70% of all puffins found dead were killed in June and early July when the gulls were feeding large chicks (Fig. 8.3). The peak mortality rate was in mid-June, when an average of 4.7 puffins were killed each day. However, the number of puffins killed by each pair of great black-backed gulls varied greatly. Most pairs killed less than 10 puffins during the breeding season but three pairs had more than 20 dead puffins found at the nest-site (Fig. 8.4). Great black-backed gull pairs were considered to be puffin-specialists if more than 20 puffins were found at their nest-site. The mean number of puffins killed by specialist and non-specialist pairs during the season was approximately 32 and 4 respectively. Hence, the three specialist pairs accounted for half of all the puffins killed.

The status of puffins predated by great black-backed gulls changed during the season. The proportion of immatures birds killed increased significantly between May and July while there was a corresponding decrease in the proportion of breeding individuals taken (Fig. 8.5).

Discussion

Between May and July, the remains of almost 200 full-grown puffins were collected from around the nests of great black-backed gulls breeding on the Isle of May. All puffin carcasses found were probably the result of predation rather than scavenging since there were no other predators of full-grown puffins on the island and puffin chicks were well fed, suggesting that adult starvation was unlikely. The actual number of puffins killed during the breeding season will certainly be higher than that recorded as it is likely that some corpses were dropped in the sea by the gulls or were overlooked during collection. The estimate of the numbers of puffins killed is therefore conservative.

Of the 169 puffin corpses with heads, 74 (44%) had more than two grooves and were thus likely to be breeding individuals (Harris, 1981). This is similar to the 41% recorded by Harris (1980) for great black-backed gull predation of puffins on Dun, St. Kilda. Birds with two grooves would have been a mixture of breeders and non-breeders and birds with less than two grooves would have been immatures. If the ratio of birds with two grooves to those with more than two grooves was the same for predated puffins at is was for the breeding population, and if the age composition was the same amongst the birds found without heads, then a total of 111 breeding puffins were killed by great black-backed gulls during the season. With a current puffin population size of approximately 50,000 breeding pairs, this represented 0.1% of the breeding population, which is similar to that reported for great black-backed gull predation of puffins in Newfoundland (<1%, Pierotti, 1983; 0.1%, Rodway, cited in Russell and Montevecchi, 1996). Such low levels of adult predation are unlikely to have a significant negative impact on the puffin population as a whole. In contrast, Harris (1980) found that, in areas where puffins nested at low densities on Dun, 4.2% of breeding adults were predated by great black-backed gulls. This high level of predation is above the total annual mortality rate for adult puffins of 2.5% (measured on the Isle of May during a period when predation of adults was low; Harris et al., 1997). Under such circumstances gulls were almost certainly having a significant impact on the puffin population, although only in a limited part of the colony (Harris, 1980).

The proportion of immature birds predated by great black-backed gulls increased significantly as the season progressed. This change reflects an increase in the number of immatures present in the colony later in the season (Harris, 1984). However, the proportion of immature puffins killed by great black-backed gulls breeding on Dun was greater than the proportion present in the colony, suggesting that gulls may have been targeting the most inexperienced birds (Harris, 1984). In this study, we found no evidence that great black-backed gulls targeted inexperienced birds; 40% of puffins killed in July were immatures, which was in direct proportion to the number expected to be present in the colony at that time (Harris, 1984).

The proportion of gulls specialising on adult puffins varies greatly between colonies (Harris, 1984). All 40 pairs of great black-backed gulls breeding on Dun were puffin-specialists. Puffins made up over 95% of the number and virtually all of the biomass of their prey, with an average of 65 puffins killed per pair (Harris, 1984). On the Isle of May, only three pairs of gulls killed more than 20 puffins during the season and the maximum number of puffin corpses recorded at any one nest was 38. This is well below that recorded for the puffin specialists on Dun (Harris, 1980) and suggests that a substantial proportion of the diet was made up by other prey items. Great black-backed gulls on the Isle of May also feed extensively on rabbits, feral pigeons and both the adults and chicks of other seabird species.

During the 2001 season, 0.1% of adult puffins breeding on the Isle of May were predated by great black-backed gulls. This is low compared to an annual rate of mortality of 2.5%, calculated during a period when there were few great black-backed gulls present on the island (Harris et al, 1997). Therefore, under current conditions, it is unlikely that predation by great black-backed gulls has a significant negative impact on the puffin population as a whole. Thus, from a management perspective, there is no need for any immediate measures to be taken. However, two factors are critical in this conclusion, the great back-backed gull population is currently very small and the proportion of puffin specialists is low.

Following termination of the gull control programme in 1989, the population of great black-backed gulls has increased exponentially, with an annual rate of increase of 17.5%. If this were to continue, predation by great black-backed gulls could potentially become a problem in the future. A simple model was therefore used to estimate the potential impact of predation by great black-backed gulls on breeding puffins over the next 20 years, assuming that the gull population continued to increase at its current rate. The proportion of breeding puffins predated in any given year P_p was calculated using the following equation:

$$P_p = [xgg_s + yg(1-g_s)]/P \qquad \text{[Eq.1]}$$

where g is the number of great black-backed gull pairs, g_s is the proportion of great black-backed gulls specialising on full-grown puffins (puffin-specialists), x and y are the number of breeding puffins killed by puffin-specialists and non-specialists respectively and P is the number of breeding puffins.

The model suggests that, if the puffin population continues to increase at its current rate, predation by great black-backed gulls will not have a significant impact on the puffin population within the next 20 years (Fig. 8.6a). Indeed, if the rate of increase in the size of the puffin population was to decline by half to 5% year^{-1}, predation by great black-backed gulls would still not have a significant impact on puffin population growth, unless there was a dramatic increase in the proportion of puffin-specialists within the gull population (Fig. 8.6b). Finally, if the puffin population remains at its current size, any predation by great black-backed gulls would cause the population to decline (Fig. 8.6c). However, it should be noted that this model focuses only on predation of breeding adult puffins. Great black-backed gulls also predate young puffins, particularly at fledging. The number of both young and immature puffins killed would also need to be taken into account in order to assess the full impact of great black-backed gulls on the Isle of May puffin population.

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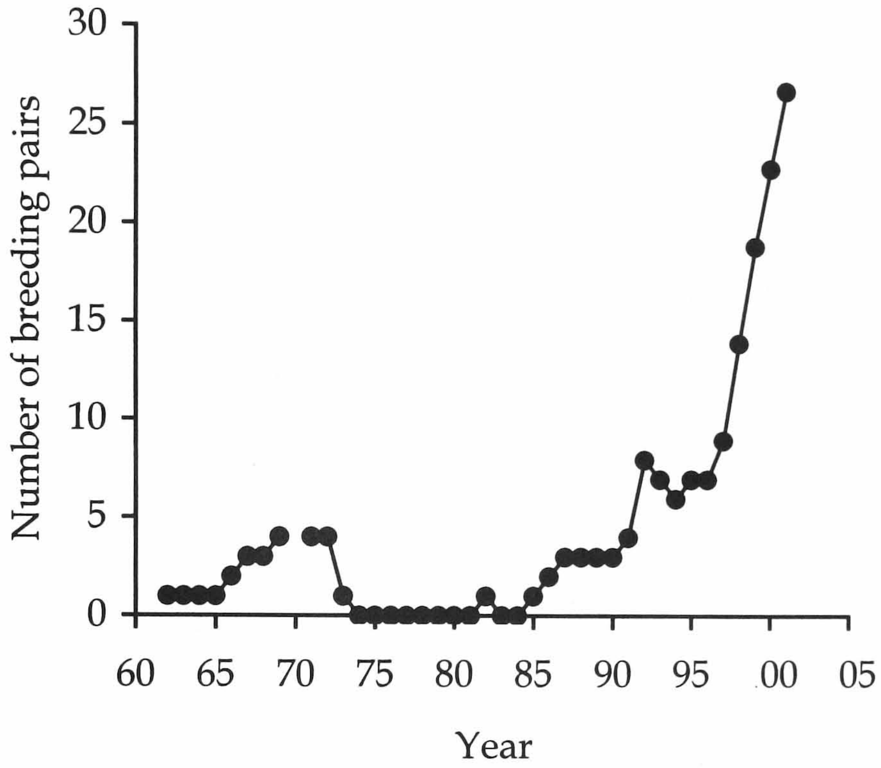

Figure 8.1: Population size of great black-backed gulls breeding on the Isle of May between 1962 and 2001 (Harris et al., 2000).

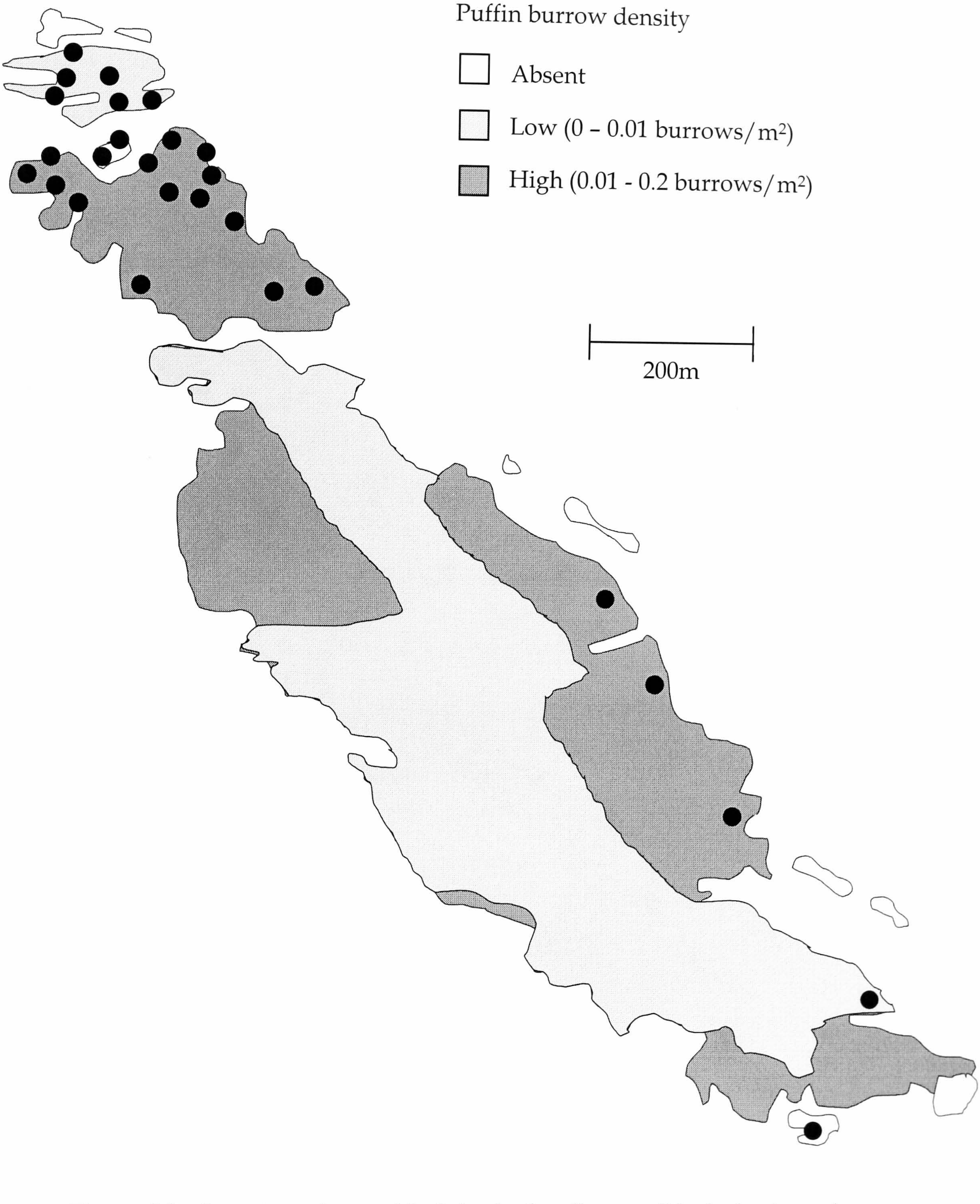

Figure 8.2: Location of great black-backed gull nests (black dots) on the Isle of May during the 2001 breeding season. Puffin burrow density is calculated from data collected during an all island count made in 1998.

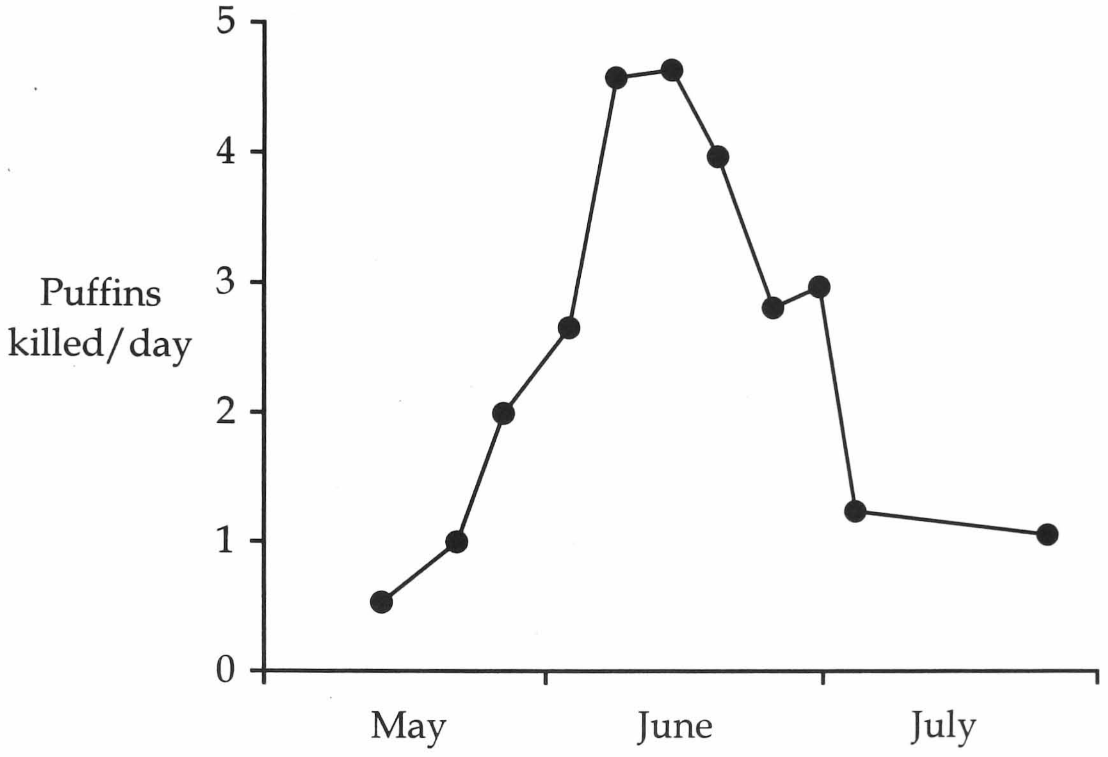

Figure 8.3: Predation rate of adult puffins by great black-backed gulls. Based on averages over 5-6 day intervals (includes one 30 day interval at the end of July).

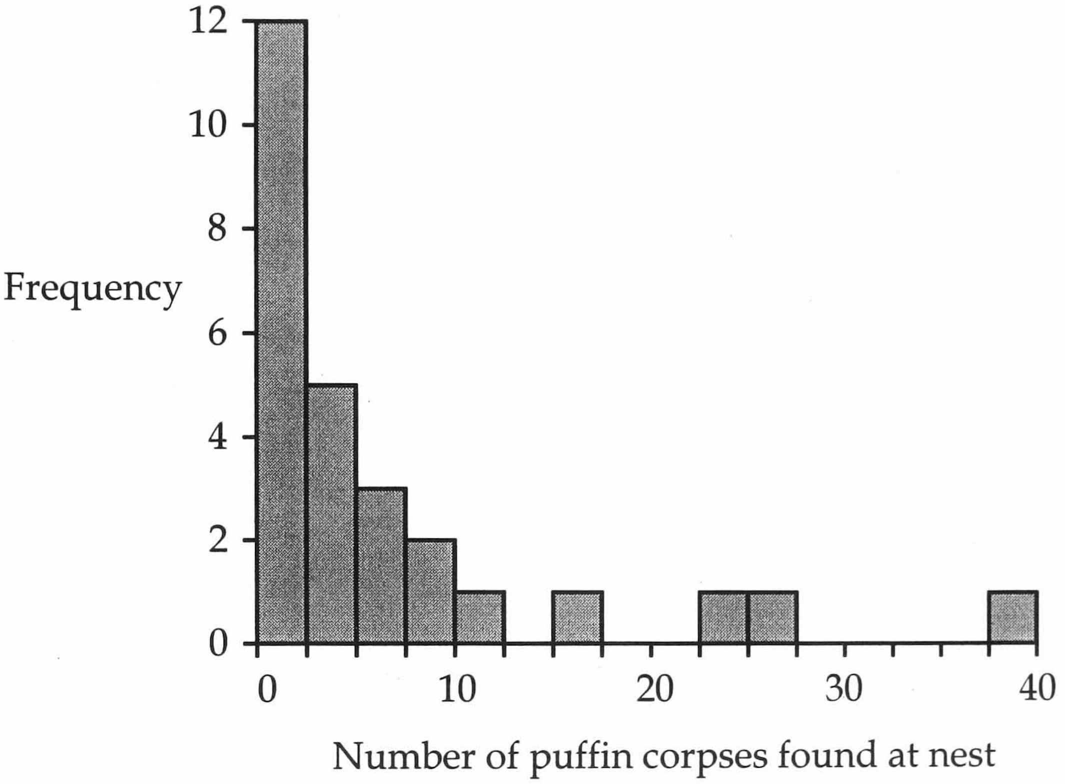

Figure 8.4: Frequency distribution showing the number of puffin corpses found at great black-backed gull nests.

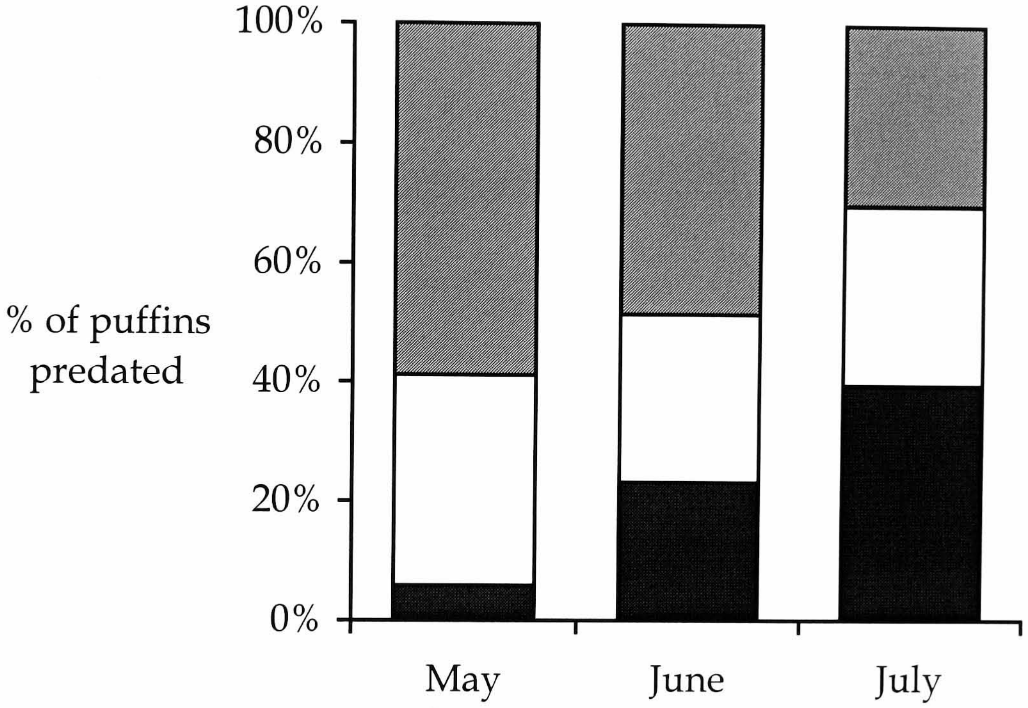

Figure 8.5: Status of puffins killed by great black-backed gulls on the Isle of May; breeding birds (grey bars), immatures (black bars) and unknown breeding status (white bars). Difference between months, χ^2=10.40, df=4, P=0.034.

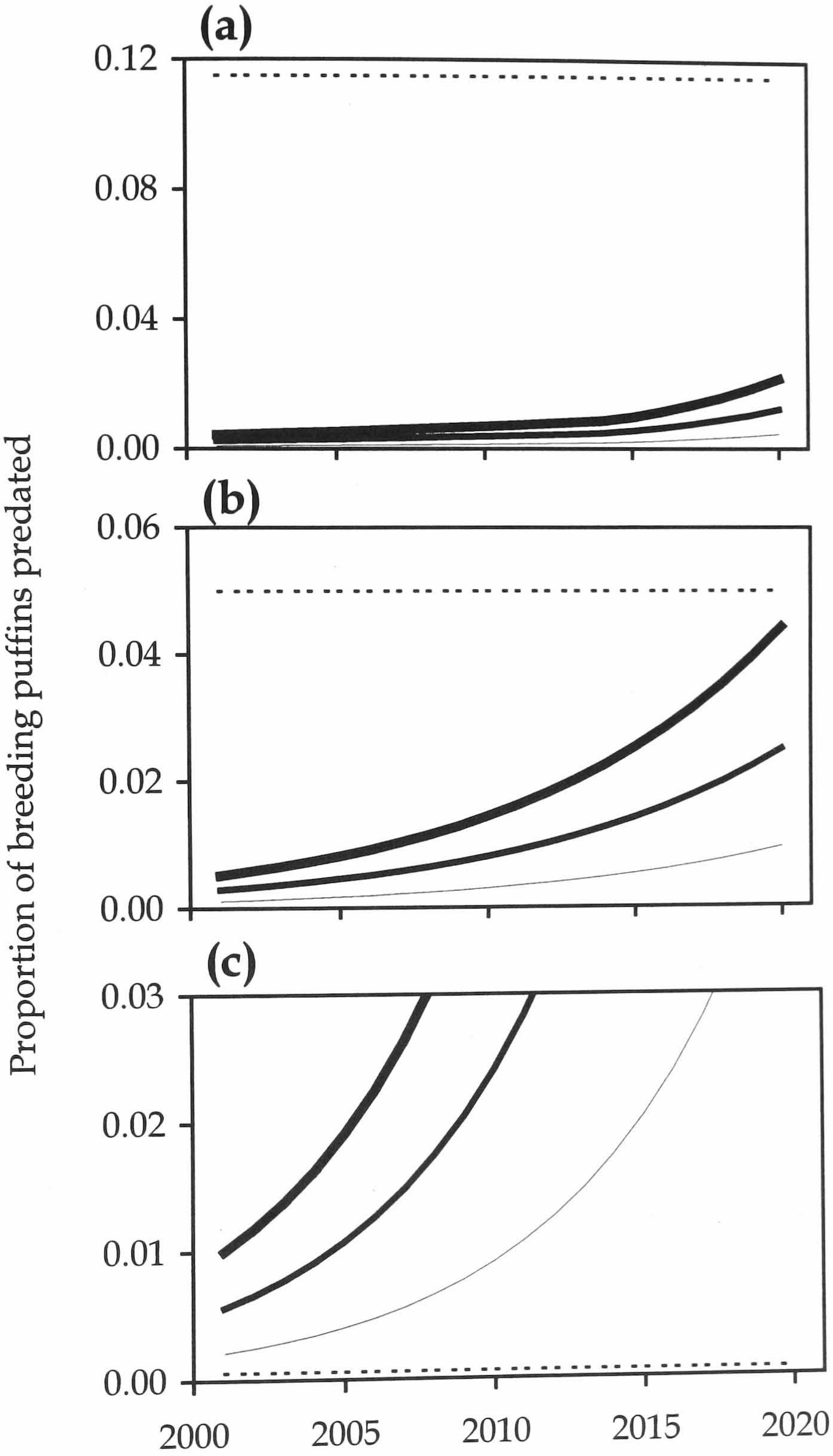

Figure 8.6: Proportion of breeding puffins predated by great black-backed gulls over time, assuming that the puffin population growth rate (a) remains at its current level of 11.5% year^{-1}, (b) is reduced by half to 5% year^{-1} and (c) is zero. Solid lines represent the proportion of puffin-specialists within the gull population: 0.1 (thin line), 0.5 (medium line), 1.0 (thick line). Dashed line indicates the level at which gull predation would cause the puffin population to decline, assuming no immigration.

Chapter 9

Behavioural responses of Atlantic puffins *Fratercula arctica* to visitor disturbance

Abstract

The recent increase in the number of people involved in recreational activities geared towards viewing wildlife has lead to concern about the possible detrimental impact of human activity on many animal species. The Atlantic puffin *Fratercula arctica* has a physical appearance and animated behaviour that frequently attracts large numbers of visitors and may therefore be particularly at risk. In this study we quantified the impact of visitors on breeding puffins by comparing both colony attendance and chick provisioning rates on days with and without visitors present. The presence of visitors significantly reduced colony attendance by repeatedly flushing puffins from the nesting area. Furthermore, the rate at which puffins delivered food to their chicks was significantly lower on days when visitors were present compared to visitor-free days. However, although breeding puffins showed measurable behavioural responses to human activity, it is unlikely that reproductive performance or adult survival were significantly affected.

Introduction

The recent increase in the number of people involved in recreational activities geared towards viewing wildlife has lead to concern about the possible detrimental impact of human activity on many animal species (Kenchington, 1989; Reynolds and Braithwaite, 2001). During the breeding season, colonial waterbirds are particularly susceptible to human disturbance because of their high-density nesting habits. When approached, birds often flush from nests leaving eggs and chicks exposed to thermal stress or predation and imposing an energetic cost on the adults, which could potentially reduce reproductive output.

Several studies have indeed found evidence of a significant negative impact of visitor disturbance on a wide range of waterbird species. For example, least terns *Sterna antilliarum* breeding in areas frequently visited by humans had a significantly lower nesting-rate and reproductive success compared to individuals breeding in areas with little human disturbance (Burger et al., 1995). Similarly, Anderson (1988) found that the clutch size and fledging success of brown pelicans *Pelecanus occidentalis californicus* was lowered as a result of human activity; disturbance caused either temporary or permanent abandonment of nests, which were then predated by gulls (*Larus* spp.) or crows *Corvus brachyrhynchos* (Anderson, 1988). Due to the increased risk of thermal stress and predation, it is generally perceived that species nesting on the ground surface are more at risk from disturbance than species nesting in burrows. As such, little work has been undertaken to quantify the effect of visitor disturbance on burrow-nesting birds (but see Hill and Rosier, 1989; Fowler, 1999).

One species that may be particularly vulnerable is the Atlantic puffin *Fratercula arctica,* which has a physical appearance and animated behaviour that frequently attracts large numbers of visitors to colonies both in Europe and North America. Puffins are highly colonial burrow-nesting auks that lay a single egg clutch (Cramp, 1977). The chick remains in the burrow for 38-44 days and is brooded and fed by both members of the pair (Harris, 1984). During the chick-rearing period, the adults spend much of their time away from the colony, presumably feeding or resting on the water but may remain near their burrows for several hours after delivering food to the chick. Previous studies of the impact of disturbance on breeding puffins have focused on that caused by researcher activity (Pierce and Simons, 1986; Rodway et al., 1996). Frequent disturbance at the burrow in order to obtain laying and hatching dates and to monitor chick growth has been shown, in some cases, to reduce breeding success and delay fledging (Pierce and Simons, 1986; Rodway et al., 1998). However, the response of puffins to less intrusive human activity, such as tourists visiting the colony, has received relatively little attention.

At many colonies, ecotourism is actively encouraged, both for educational purposes and to help with fundraising activities. However, in areas where visitor pressure is high, a conflict arises between the benefits from people visiting the colony and the possible detrimental impact of human disturbance on the birds themselves. When approached by humans, most puffins take flight, returning again once the danger has passed (Nettleship, 1972; Pierce and Simons, 1986). Large numbers of visitors to accessible colonies could potentially have a negative impact on puffins through repeated flushing of birds from the breeding grounds. The aim of this study was to quantify the impact of visitors on breeding puffins on the Isle of May National Nature Reserve by comparing both colony attendance and chick provisioning rates on days with and without visitors present.

Methods

The study was carried out on the Isle of May, Firth of Forth, Scotland (56°11′N, 2°33′W) during the 2001 breeding season. The island is 57 hectares in size with 50 m high cliffs along its west and south west sides. Elsewhere on the island the ground slopes gently down to the sea. The island supports over 42000 breeding pairs of Atlantic puffins and is the largest colony on the east coast of Scotland (Harris, 2000). The Isle of May was designated as a National Nature Reserve in

1956 due to its large populations of breeding seabirds (Ratcliffe, 1977). The island is officially open to visitors from May until September and, apart from the occasional private boat that lands, all visitors to the reserve arrive on one boat that carries a maximum of 100 people. The boat stays for three hours, usually sometime between 1000 and 1800 BST depending on tides. The boat is licensed to bring visitors to the island six days per week but usually comes less frequently as sea conditions often prevent a safe landing. Visitors to the reserve must remain on the designated footpaths that run the length of the island. There is a total footpath length of approximately 4 kilometres on the island, of which approximately 1 kilometre passes through areas of high puffin burrow density.

A study plot (approximately 20m by 40m) was set up at a point where the footpath passes through the main puffin breeding colony. There were no breeding gulls within the study plot. The plot consisted of two sections; the first section bordered the footpath (0-10 m) and the second section was 10-25 m from the path (Fig. 9.1). Observations were made from a temporary hide and were carried out between 7 June and 7 July, during the main chick rearing period. A total of 26 watches were carried out, each lasting two hours. Watches were divided into two groups, 13 were on days when visitors were present on the island and 13 were on days with no visitors. Watches in the two groups were balanced for time of day and state of the tide. Weather conditions were also similar; there was no significant difference between the two groups in temperature (t-test: df=23, t=0.71, n.s.), wind speed (t-test: df=22, t=0.01, n.s.) or the number of days with easterly or westerly winds (chi-square: df=1, χ^2=1.39, n.s.).

The observer arrived in the hide 15 minutes before observations began to allow time for the birds to return following the disturbance caused by entering the hide. A count of the number of puffins present in both sections of the study plot was made at the beginning of each observation period. Further counts were made every five minutes and the mean of these measurements was used as an index of puffin attendance. The total number of puffins landing and going down a burrow with fish within Section 1 of the study plot was also recorded. Marker posts were placed on the footpath at the points where people approaching first became visible to puffins in the study plot, this was approximately 30 m either side of the plot. The time of arrival and departure of all people to the section of path between these two posts (referred to as the study area) was recorded. Although some puffins went down burrows in response to human disturbance, the majority of individuals took flight. The term "flushed" is therefore used to describe all birds no longer visible in the study plot after a disturbance event. The proportion of puffins flushed was calculated using the data from the counts of adult puffins made immediately before and after a person entered the study area. Data on the proportion of birds flushed were only used in the analyses in cases where at least 15 minutes had elapsed since the previous disturbance event. Proportion values were arcsine transformed before being used in the analysis. Means are presented ± one standard error.

Results

There were 2414 visitors to the Isle of May in June and July 2001 (Scottish Natural Heritage unpublished records). This value was similar to the long-term average of 2340, based on visitor numbers over the previous five years. During the 2 hour observation period, people were present within the study area for a mean of 32.4 ± 5.3 minutes on days when the visitor boat was present compared to 3.6 ± 1.6 minutes on days when there was no boat, this difference was statistically significant (t-test: df=14, t=4.62, P<0.001). Regression analyses showed that there was no significant seasonal change in the number of visitors to the island ($F_{1,11}$=0.01, n.s.) or the amount of time that visitors were present within the study area ($F_{1,11}$=0.72, n.s.).

There was no significant difference between days with and without visitors in the number of puffins present at the beginning of the observation period, i.e.

before the first people arrived in the study area (Fig. 9.2a). However, when a person entered the study area, the birds took flight and circled above the colony before landing again once the person had left, a response to disturbance that is typical in puffins (Nettleship, 1972; Pierce and Simons, 1986). The presence of visitors on the island therefore reduced the number of puffins standing at the colony. Mean attendance over the two hour observation period was significantly lower on days when visitors were present compared to visitor-free days (Fig. 9.2b). The similarity in the attendance counts made at the beginning of the observation period between days with and without visitors confirm that this difference was due to an increase in the number of people on the island, rather than the presence of visitors simply coinciding with days of low puffin attendance.

There was no evidence that puffins became habituated to the presence of people on the footpath as the season progressed. The proportion of birds flushed in response to a person entering the study area did not vary significantly with date (Fig. 9.3). Moreover, in the section closest to the footpath, almost all birds were flushed each time a person entered the study area (mean 0.97 ± 0.01, Fig. 9.3a). However, in the section further from the footpath, the birds were more tolerant of people on the path and a significantly smaller proportion of birds were flushed in response to people entering the study area (mean 0.74 ± 0.04; $n=49$, $W=3059$, $P<0.0001$).

The presence of visitors on the island therefore reduced puffin attendance in areas of the colony adjacent to the footpath by repeatedly flushing birds. Furthermore, we found no evidence that puffins became habituated to the presence of people on the footpath as the season progressed. In line with these results, the frequency with which puffins delivered food to their chicks was significantly lower on days when there were visitors on the island compared to visitor-free days (Fig. 9.4). Adult puffins did not deliver food to their chicks while there were people present in the study area.

Discussion

Almost all puffins standing within 10 m of the footpath flew away when a person walked past. However, the proportion of birds flushed decreased significantly within a further 15 m of the path. The distance within which human activity begins to induce a measurable response in birds is known as the "approach distance" and can vary greatly among different species (Nisbet, 2000). An approach distance of 100-200 m is likely for terns (Rodgers and Smith, 1995) whereas a buffer of only 30 m between visitors and nesting penguins has been recommended in a number of studies (Hockey and Hallinan, 1981; Culik et al., 1990). The results from our study show that human activity at a distance of 25 m is sufficient to cause a significant behavioural response in breeding puffins, the actual approach distance is therefore likely to be far greater.

We found no evidence that puffins habituated to the presence of visitors as the season progressed. However, the study plot was along a section of path that has been used by people for many years. It is therefore possible that the puffins in this area already have a high level of tolerance compared to individuals breeding in areas of the colony where human intrusions are less frequent. Habituation to repeated human intrusions has been found in several species including terns (Nisbet, 2000) and penguins. Fowler (1999) found that Magellanic penguins *Spheniscus magellanicus* that had been exposed to very high levels of human visitation via tourism did not respond to human presence as a stressor, whereas those exposed to moderate levels of disturbance showed no evidence of habituation. Habituation has thus been recommended as a form of management in areas where visitor pressure is likely to be great, the idea being that the more the birds become habituated to human intrusions, the less likely they are to be adversely affected by the next intrusion (Robert and Ralph, 1975; Nisbet, 2000). It has been recommended that visitors should be concentrated in a small part of the breeding colony, allowing birds in the area to habituate, and leaving the remainder of the colony free from disturbance (Fowler, 1999).

The presence of visitors on the Isle of May reduced colony attendance by repeatedly flushing puffins from the nesting area. However, this in itself should not be interpreted as adverse unless the chicks are exposed to thermal stress, predation or show a reduced growth rate, or unless the metabolic cost to adults is sufficient to cause desertion or reduced survival (Nisbet, 2000). Puffins are burrow nesters and the chicks are therefore protected from predation. Furthermore, the chick is regularly left unattended in the burrow soon after hatching under normal conditions. The impact on adult birds is more difficult to quantify but is unlikely to be severe enough to reduce survival. Adults do not need to remain close to the nest to protect the chick and can therefore temporarily move to a less disturbed location.

The rate at which puffins delivered food to their chicks was however significantly reduced when visitors were on the island. Puffins returning to the colony with fish did not land when there were people in close proximity to their burrows. However, there is a strong diurnal pattern in puffin feeding behaviour with a peak of food deliveries in the early morning and a second smaller peak in the evening, feeding rates during the middle of the day are generally low (Harris, 1984). Visitors are present on the island for only three hours between 1000 and 1800 BST and it is therefore unlikely that the reduced feeding rate observed in this study would have a significant negative impact on chick growth or survival. The results from this study therefore support the current visitor management policy of controlled access to the island (Scottish Natural Heritage unpublished records), specifically (a) keeping visitors on designated footpaths and (b) avoiding large numbers of visitors in the early morning and the evening.

From a conservation perspective, human disturbance is only important if it causes a significant reduction in the survival or fecundity of the species concerned and hence causes the population to decline (Gill et al., 2001). Although adult puffins breeding on the Isle of May showed measurable behavioural responses to human activity, it is unlikely that reproductive performance or adult survival were significantly affected. However, it must be stressed that the conclusions drawn from this preliminary study are based only on data collected from one area of the puffin colony. Repetition of the work in more areas, particularly in the less intensively visited parts of the colony, would be needed to determine if the results from this site are more widely applicable. Furthermore, monitoring chick growth rates at varying distances from the footpath would allow the importance of the reduced feeding rate observed in this study to be assessed.

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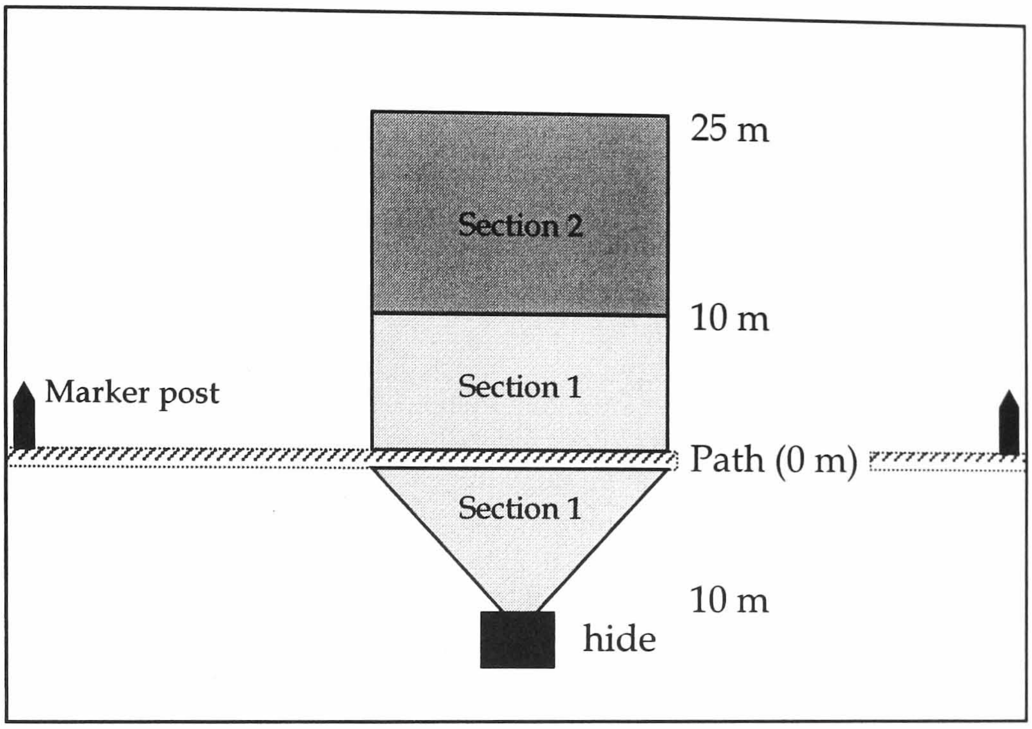

Figure 9.1: Diagram of study plot (shaded areas) showing the section of path where visitor numbers were monitored.

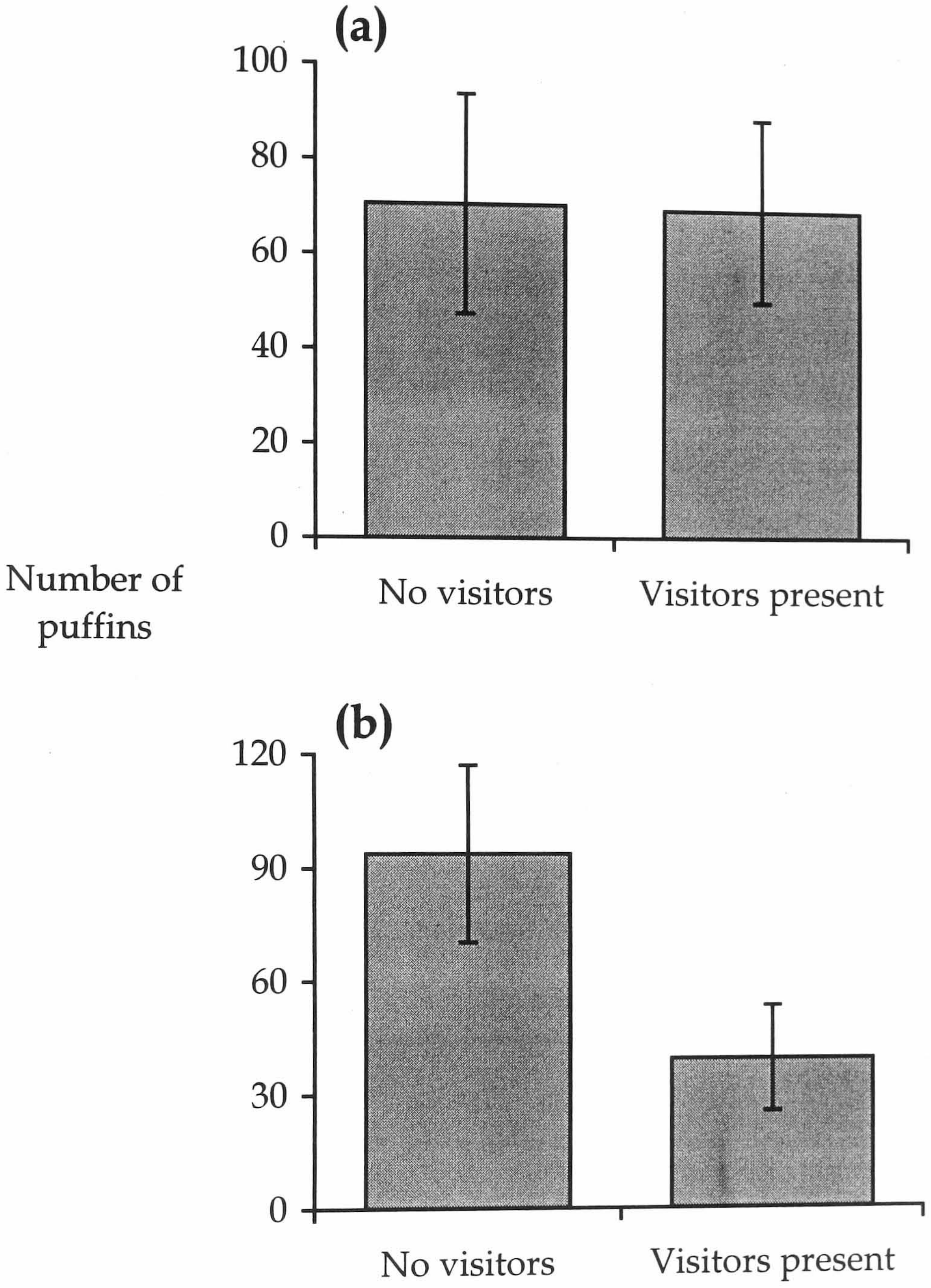

Figure 9.2: Mean (+/- one standard error) puffin colony attendance on days when there was visitors present on the island and on visitor-free days. (a) puffin attendance at the beginning of the observation period (i.e. before any visitors arrived on the island) and (b) mean attendance over the two hour observation period. Difference between days with and without visitors, t-test: (a) df=24, *t* =0.03, n.s., (b) df=24, *t* =1.99, *P* =0.058.

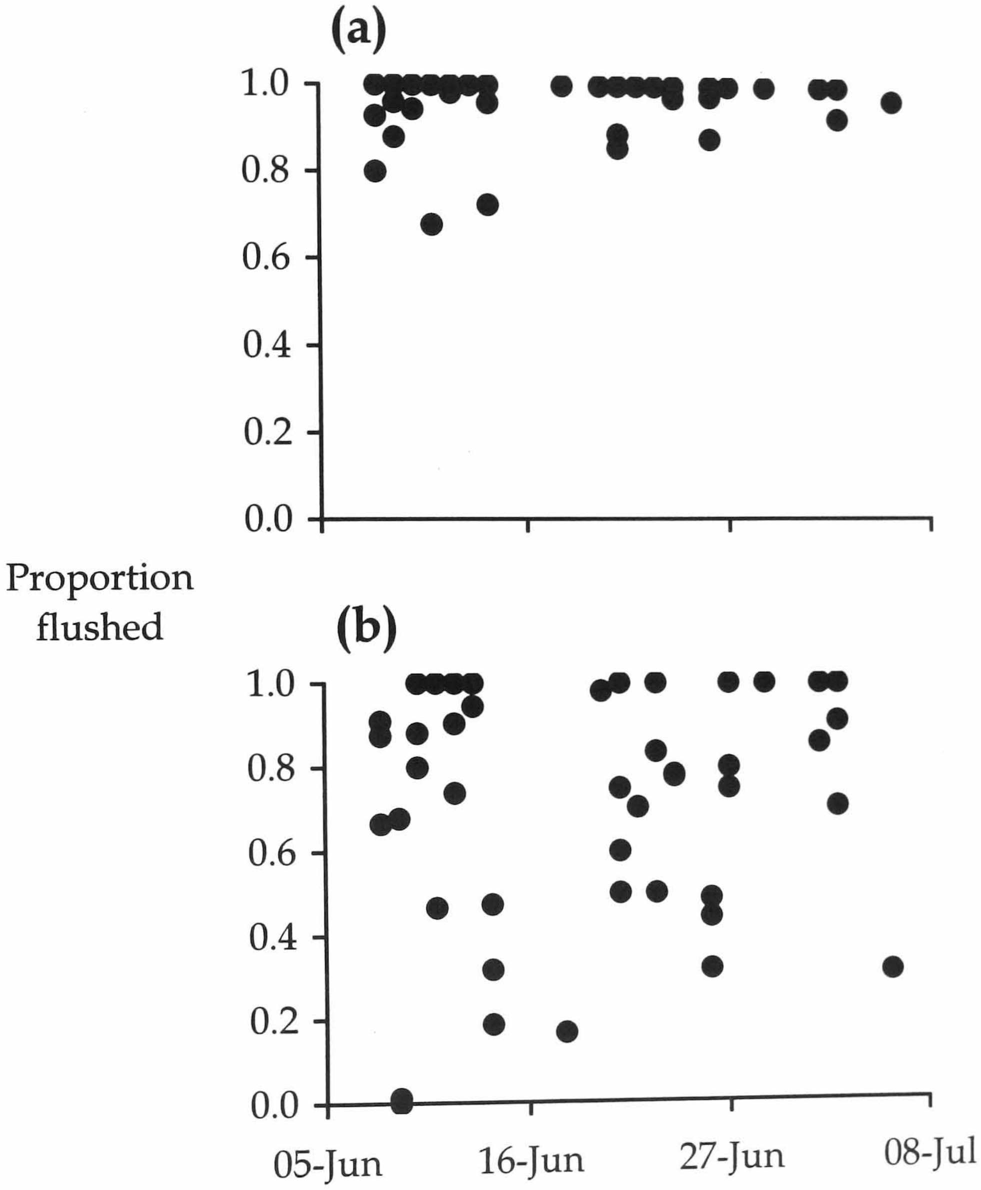

Figure 9.3: Proportion of puffins taking flight from an area (a) 0-10m and (b) 10-25 m from a footpath in response to visitors walking along the path. (Relationship between proportion flushed and date, (a) $F_{1,47}=0.34$, n.s., (b) $F_{1,47}=0.92$, n.s.)

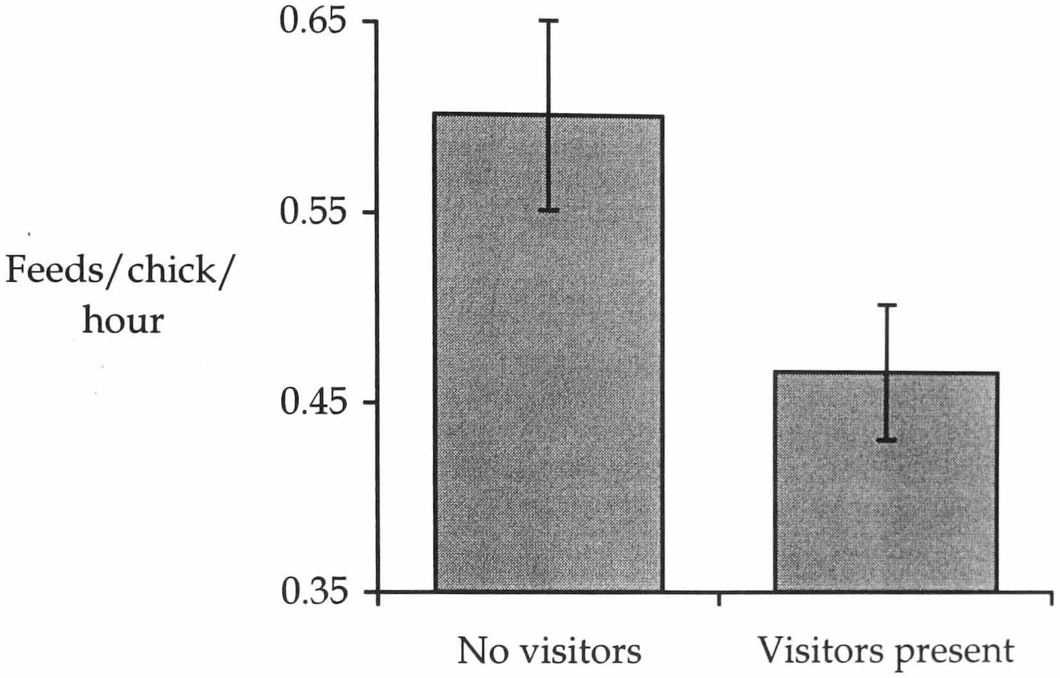

Figure 9.4: Mean (+/- one standard error) feeding frequency of puffins on days when there were visitors present and on visitor-free days (t-test: df=24, t =2.18, P =0.039).

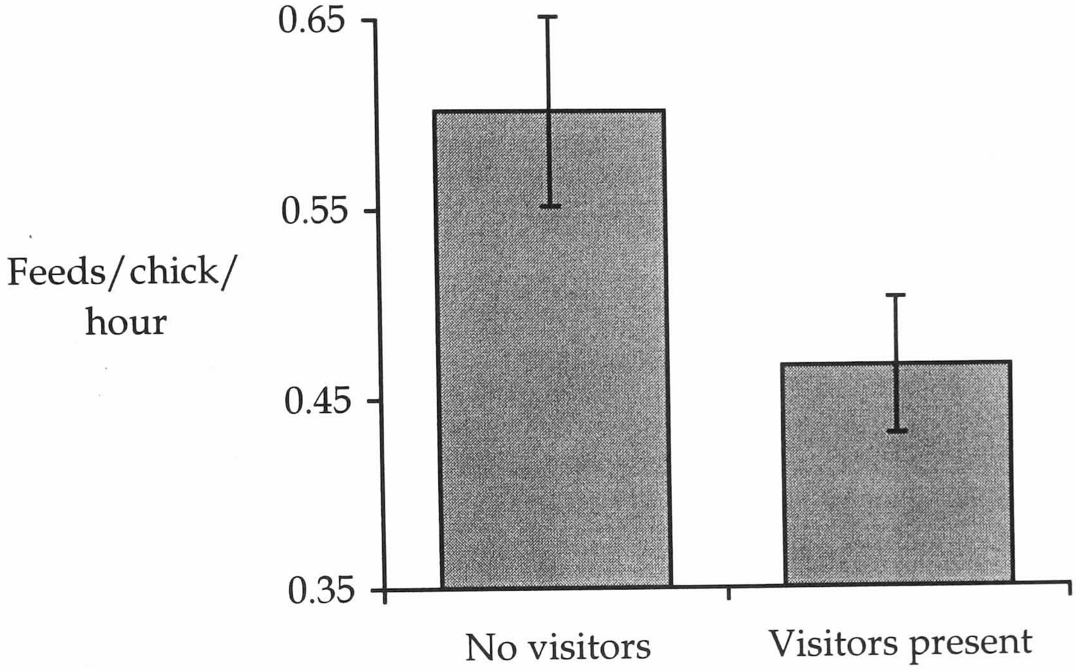

Figure 9.4: Mean (+/- one standard error) feeding frequency of puffins on days when there were visitors present and on visitor-free days (t-test: df=24, t=2.18, P=0.039).

General Discussion

Much conservation concern has focused on the problems associated with habitat loss and environmental degradation (Freidenburg, 1998; Caley et al., 2001). However, an increasingly important factor affecting population dynamics and species conservation is that of interspecific interactions. Species respond differently to human-induced changes in the environment and this has caused major shifts in the balance of interspecific interactions with often important ecological consequences (Jewell and Holt, 1981; Garrott et al., 1993).

Research into species interactions has generally focused on competition and predation, however kleptoparasitism may also be an important factor affecting some animal populations. For example, kleptoparasitism by spotted hyenas *Crocuta crocuta* is thought to have played a significant role in the population decline of the African wild dog *Lycaon pictus* (Carbone et al., 1997; Gorman et al., 1998). Although kleptoparasitic behaviour has been documented in mammals and many invertebrate groups (Vollrath, 1984; Cooper, 1991), it is particularly widespread amongst birds (Brockmann and Barnard, 1979). Food stealing is especially common in seabirds, which often breed in dense colonies and therefore offer a reliable and predictable return of potential hosts to an area (Furness, 1987a). Under such conditions, kleptoparasitism rates can be very high (Watanuki, 1990; Quintana and Yorio, 1999). However, although the occurrence of kleptoparasitism in seabirds has been well documented in the scientific literature (e.g. Furness, 1978; Gilardi, 1994; Oro and Martinez-Vilalta, 1994), few studies have been undertaken to assess the full impact of kleptoparasitism risk on the host species.

Herring and lesser black-backed gulls predominantly kleptoparasitise adult birds as they return to the colony with food for the young. Studies that have investigated the impact of kleptoparasitism by gulls on the host species have thus focused entirely on the direct impact on the growth and survival of chicks, usually finding no significant effect (Fuchs, 1977; Pierotti, 1983; Rice, 1985;

Wilson, 1993; Quintana and Yorio, 1999). Such studies have therefore often concluded that kleptoparasitism does not have a significant negative impact on the host species. However, the negative effects of kleptoparasitism may be very subtle, but still important. For example, previous work on spiders has found that the presence of small kleptoparasitic individuals on the web of a larger species causes the host spider to increase the frequency with which it relocates its web, in an attempt to increase prey capture rate (Rypstra, 1981; Grostal and Walter, 1997). This increase in energy expenditure, coupled with the direct effects of reduced food intake, has been shown to significantly reduce the body mass of the host spider, and thus its future reproductive potential (Higgins, 1992; Grostal and Walter, 1997). In birds, mass loss during the breeding season has been linked to reduced survival and future reproductive success (Monaghan and Metcalfe, 1986; Monaghan et al., 1989, 1992; Golet et al., 1998). The increased stress or energy expended by adult birds in response to kleptoparasitic attacks could therefore have a detrimental impact on the host species if adult mass was negatively affected. Surprisingly however, there have been no published studies of the impact of kleptoparasitism risk on the body condition of adult birds. This is a gap in our current knowledge that merits further attention.

In this study, we found no evidence that puffins increased foraging effort to compensate for lost food loads (*Chapter 4*) and no detectable impact of kleptoparasitism risk on the body condition of adult birds (*Chapter 5*). There was also no significant effect of kleptoparasitism on the growth or survival of chicks (*Chapter 3*). These findings are consistent with previous studies of seabirds, which have suggested that kleptoparasitism does not have a significant negative impact on the reproductive performance of the host species. The additional energetic costs in response to kleptoparasitic attacks by gulls may be insignificant at a time when adults are already working hard to meet the demands of raising young (Nettleship and Birkhead, 1985; Golet et al., 1998). However, analysis of a long-term data set for the Isle of May showed evidence that puffins recruiting to the colony avoided nesting in close proximity to gulls (*Chapter 2*). This suggests that the presence of gulls had a significant influence on the behaviour of puffins, but with consequences that were not detected in this study. However, although an immediate impact on adult condition was not detected, future reproductive performance or survival could still be negatively affected (Wernham and Bryant, 1998). Following individual birds to examine life-time reproductive success would be needed to investigate such long term effects.

The results from this study support the current management practice on the Isle of May of maintaining gull-free areas by the repeated removal of gull nests. Maintaining gull-free areas was effective in reducing kleptoparasitism risk, increasing the frequency of food deliveries to puffin chicks and enhancing the rate of recruitment of first-time breeders. Deterring gulls from breeding in specific areas also reduces the impact of management on the gull population itself, compared to more traditional control methods such as culling, as displaced birds are able to move and establish breeding territories in other areas. Indeed, the average density of breeding gulls in the gull-occupied areas of the island is currently only one quarter of that recorded prior to the cull, indicating that breeding space is not limited at present.

Following a rapid expansion during the middle of the last century, many gull populations have now stabilised and have even shown large declines in some areas (Lloyd et al., 1991; Hagemeijer and Blair, 1997). Both herring and lesser black-backed gulls, until recently regarded as pest species, have now been designated as being of medium conservation concern (Gibbons et al., 1996). Although it has been suggested that this decline results from an increase in the occurrence of botulism due to gulls feeding on rubbish tips (Monaghan et al., 1985), large scale culling has undoubtedly had a major impact on gull populations in some areas. The recent change in both the population size and conservation status of gulls has highlighted the need to take a long-term view when formulating management programmes. However, the populations of many other seabird species are higher now than they have been for most of the previous century (Lloyd et al., 1991). This increase can be attributed in part to reduced human persecution, but may also be a response to wider scale ecosystem changes affecting food availability. Population declines may therefore not always represent a significant conservation concern.

The population expansion of species that have benefited from anthropogenic habitat changes has led to the implementation of control procedures in areas where they threaten economically valuable or rarer species. Although culling has been the most common method used to control vertebrate pests, including gulls (Feare, 1991; Heydon, and Reynolds, 2000), it is rarely the most appropriate management strategy. First, research has shown that culling is often ineffective at reducing the population size of the targeted species. This is due both to a relaxation of density-dependent effects, resulting in increased survival and reproductive success of remaining individuals, and also immigration from surrounding areas (Feare, 1991; Tuyttens et al., 2000). There are often also concerns about humaneness, environmental contamination and scale. Furthermore, culling is inappropriate in situations when the pest species is of conservation interest itself, e.g. great skuas (Jewell and Holt, 1981; Furness, 1987b). The need to assess the effectiveness of alternative control procedures to culling has therefore increased and is an area that is receiving increasing attention in the scientific literature (Barlow, 2000; Redpath et al., 2001; *Chapter* 3).

Given the increasing occurrence of human altered habitats and the restriction of wildlife to limited spaces with artificial boundaries, the need for active management of wild animal populations is likely to increase in the future. This will involve the control of locally overabundant species as discussed above, but could also include measures such as the captive breeding of endangered species (Gibbons et al., 1995), the translocation of individuals between fragmented habitats (VanVuren et al., 1997; Towns and Ferreira, 2001) and even the manipulation of behaviour (Esson, 1991; Gill et al., 2000). Clearly, for these management techniques to be successful, there is a need for sound scientific research on which to base management decisions. Research into subjects such as behavioural ecology, population biology and genetics need to be increasingly directed towards conservation based problems.

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