Micro and Macroclimate effects on reproductive performance of Common Eiders

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Declaration

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

Summary

The physical environment has a strong influence on the lives or organisms by limiting the way energy is gained and expended determining the capacity of organisms to invest in activities like reproduction. The avian nest site and structure, through its effects on the thermal conditions of the proximal environment of the incubating parent can affect several aspects of an individual’s reproductive success. On a larger scale, characteristics of the oviposition site can impact the spatial distribution of a species and consequently several aspects of population dynamics. In this thesis I investigate the importance of the thermal environment and nesting habitat on the reproductive performance of a sea duck, the Common Eider (*Somateria mollissima*) breeding in a cold environment.

First I described the spatial variation in nest distribution in relation to female’s and nest attributes. Females of similar quality formed aggregations of nests and clusters of high productivity were occupied earlier in the season and at higher densities. Eiders seemed to choose to nest sites based on biotic (conspecifics) rather than abiotic (microclimate) cues. By providing females with artificial shelters I tested some of the effects of microclimate on individual physiology and use of energy during incubation. Females experienced improved microclimatic conditions provided by well-sheltered nest-sites. Nest shelter conferred advantages both to incubating females by allowing energy savings and to their clutches by providing more stable incubation conditions. Shelter did not have an appreciable effect on the female’s stress response. However, in exposed areas, females with high levels of corticosterone hatched a lower proportion of eggs than females with low corticosterone.

Behavioural and functional aspects nest construction were tested first, by removing down from nests on repeated occasions throughout incubation and then by testing the effects of different amounts of down on the microclimate of incubation. Females did not replace the removed down suggesting the existence of constrains on the allocation of down to the nest. Large amounts of down in the nest contributed to more stable incubation conditions but females were able to counterbalance poor nest insulation and keep incubation temperature constant but the costs of doing this are unclear.

Finally, I assessed the influence of environmental variability on the onset of incubation and short-term fluctuations in population size for the study colony with data from 1977 to 2006. I found that after mild winters female Eiders lay earlier in the season perhaps because milder conditions allow them to attain the necessary body condition for reproduction sooner. Summer temperature had a lagged effect (2 yr) on colony size that could be related to the delayed maturity (age at first reproduction) presented by Common Eiders and the influence of climate on influence recruitment rate to the population.

The evidence presented here shows that Common Eiders are strongly influenced by their thermal environment on reproduction but by choosing a good nest they can ameliorate those effects. However nest site selection seems to be strongly linked to female quality rather than to nest properties.

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Chapter 1

General introduction

The physical environment has a strong influence on animals' lives by constraining the way energy is gained and expended. Climate, through its influence on the organism's physiology, regulates the balance between energy acquisition and expenditure and therefore is of most importance in determining the capacity of organisms to invest in activities like reproduction, growth or in resistance to stress. By having the potential to shape the variability in life history traits, the interaction between environment and organisms is a fundamental point in the study of evolutionary biology.

Reproductive output of individuals is highly determined by various environmental factors. While many elements can act as limiting factors on the life of an organism, food availability is often considered the principal. However, limitation in habitat availability can have important effects on breeding densities of animals and consequently on availability of mates. By constraining breeding density for example, shortage of suitable breeding sites can prevent some individuals from reproducing.

Nest-site choice has been regarded as a trait in the life history of oviparous organisms that is comparable to egg size, age at maturity (Resetarits 1996). As such, it should be affected by natural selection and subject to evolution. Decisions that parents make when selecting a nest site should have evolved to optimise parental fitness in specific habitats.

Across taxa, there is plenty of evidence showing that heterogeneity in the quality of oviposition sites can lead to variation in reproductive success and survival of individuals (Martin 1988, Robertson 1995, Munday 2001, Kolbe and Janzen 2002). At the individual level, the nest site can influence parental fitness, for example, by increasing hatching success, offspring development and survival. Hence, there should be strong pressure for parents to distinguish between high and poor-quality sites. On a larger scale, the location of oviposition can impact the spatial distribution of a species and consequently several aspects of population dynamics such as population size and growth rate (Rodenhouse et al. 1997).

The work presented in this thesis investigates the importance of nesting habitat on the reproductive performance of long-lived marine duck, the Common Eider (*Somateria mollissima*). Reproductive success and adult physiological condition are strongly influenced by environmental conditions for the following reasons: first, they are considered capital breeders (see below); secondly, they are uniparental incubators that present fasting throughout incubation. Therefore it is likely that in eiders even small increases in reproductive effort in the present affect the ability to invest in future reproduction. In particular in this study, I focus on the following questions: How does the nest site influence the microclimate of incubation, what is the effect of microclimate on incubation performance? And finally, what role does the macroclimate play in population dynamics?

Within a geographic location, avian species often use a wide variety of nest sites. Both the geographic area and the nest type can cause incubation conditions to vary both for parents and eggs and thus potentially affect the reproductive success of individuals. Nest-site selection is likely to involve many tradeoffs such as choosing between a site with a nest microclimate promoting optimum conditions for the eggs and one providing maximum adult protection from predators or favourable thermal properties from the perspective of the parent. Whenever there is heterogeneity in breeding areas, individuals will preferably choose the best site possible. If some intraspecific competition for access to better quality sites occurs, most probably older or better quality individuals will obtain the best nests resulting in a non-random distribution of parental quality across the available nest sites. In this context, the aim of **Chapter 2** was to identify the factors associated with temporal and spatial variation in nest occupancy by Common Eiders.

Why is avian incubation interesting?

Reproduction is a very demanding event in terms of time and energy in an organism's life, therefore, optimal allocation of energy between reproduction and self-maintenance is very important to maximise fitness. This trade-off constitutes a central point in the study of life histories (Stearns 1992). In species with parental care, fitness consequences of reproduction have been mainly attributed to the costs of offspring provisioning (Lessells 1991, Roff 1992), with egg production and egg care being relatively disregarded. In general, the importance of egg care (the regulation and of physical factors influencing development, Drent 1975) in the context of reproductive strategies has received little attention. In addition, theory predicts that long-lived organisms should limit their investment in offspring to a greater extent when compared to short–lived individuals. This is so, because even a small reduction on adult survival would decrease the prospects of future breeding (Charlesworth 1980). It has been suggested that, in order to maximize their own survival, long-lived organisms present a fixed level of investment independent of offspring need (Ricklefs 1992).

Incubation can be energetically demanding (Williams 1996) can set limits to current and future reproductive success (Heaney and Monaghan 1996, Reid et al. 2000). Recent literature has shown that increased energy expenditure in incubation often does occur, for example, when incubating under temperatures below the thermal neutral zone (temperature at which individuals have to start generating extra heat to maintain body temperature). Under such conditions, energetic demands of incubation can be very similar to those of rearing nestlings (Williams 1996) and have fitness consequences (Monaghan and Nager 1997). Some of these extra costs arise as a result of parental thermoregulatory demands, others may occur as a result of incubating large clutches (Thomson et al. 1998).

Uniparental incubators show high incubation constancy and must balance their own daily energetic demands against energy expenditure on egg production and incubation (Williams 1996). They must meet these demands from body reserves and/or limited foraging opportunities. An increase in nest attentiveness requires a greater use of body reserves and nest abandonment could occur if adult survival prospects and hence future reproduction is decreased (Erikstad et al.1998, Hanssen et al. 2003). Furthermore, some species of birds have developed fasting endurance as a strategy to reduce nest predation and to minimise extra costs associated with leaving the nest to feed (Korschgen 1977). In these species, the rate of energy utilisation during incubation can be an important determinant of breeding success.

Nests can provide parents physical protection from the environment. In cold environments the rates of energy expenditure for incubating birds are among the highest found so far (Piersma et al. 2003). Low temperatures, especially when joined to strong winds and low solar radiation, have a negative impact on heat preservation and this can result in an increase in metabolic rates of individuals (Carey 2002). There is evidence that nest placement in relation to microhabitat can help females reduce their energy demands (Gabrielsen et al. 1991, With and Webb 1993). In this context, **Chapter 3** examines how nest exposure can influence the microenvironment of incubation at two different levels: a) the environment of the eggs and b) the environment of the parent. Attention is paid to the role of nest shelter on the female's energy expenditure during incubation.

For many species of open-nesting birds, exposure to harsh weather represents a great threat to parents and offspring. In particular, extreme temperatures can act as stressful stimuli with potential negative effects on parental condition. Organisms respond to stressors by activating physiological mechanisms that facilitate survival. However, some of these mechanisms can operate in opposition to parental behaviour. Thermal stress can impair reproductive success if adults are unable to attend their nests continuously. The influence of nest exposure on the stress response of incubating females is investigated in **Chapter 4.** Here, I present observational and experimental data on the corticosterone levels of females incubating in nests with different levels of exposure.

Any parental behaviour that increases offspring fitness is considered as parental care (Clutton-Brock 1991). Nest construction and regular maintenance is a common form of parental care since nest structure is essential to provide the protection and insulation needed for embryonic development of eggs and growing young. Nest insulation depends on the materials used in the construction of the nest. Good insulation improves the incubation conditions for the eggs, but also has the potential to affect the incubation effort of the parent by reducing incubation thermal demands (Collias and Collias 1984). The use of feathers in nests has been proposed as a mechanism evolved to improve the insulating, protective properties of the nest under detrimental weather conditions. As such, it would constitute a form of parental care. Throughout incubation the quality of nest insulation can decline as result of weather effects. Parental behaviours, such an increase in nest attentiveness or regular nest maintenance, can be expected to arise in order to keep the microclimate of incubation within an optimal range. Nest maintenance in response to experimental deterioration in nest insulation is studied in **Chapter 5**. **Chapter 6** shows correlational and experimental data on the importance of the amount of down placed in the nest by female eiders for the regulation of temperature and humidity inside the nest.

At the population level, the environment plays a very important role in population numbers. Climate, for example, exerts a strong influence on adult survival, propensity to breed and reproductive performance in most vertebrates leading to changes in the distribution and geographical range of species. In recent years there has been an increasing amount of evidence showing climate effects in phenology of reproduction and migration (Sparks and Mason 2004). In order to understand how animal populations change in response to environmental variability it is necessary to investigate its impact on demographic parameters. Correspondingly, **Chapter 7** describes the influence of climate on phenology of reproduction and fluctuation in colony size of eiders breeding in SW Iceland over the past 30 years.

In **Chapter 8,** I conclude with a consideration of the links between individual energetics to population dynamics from an ecological point of view, I discuss about the significance of my results in the context of the study of evolution of life histories.

The study system.

The Common Eider (*Somateria mollissima)* belongs to the order Anseriformes and to the family Anatidae. This is the largest of the ducks from the northern

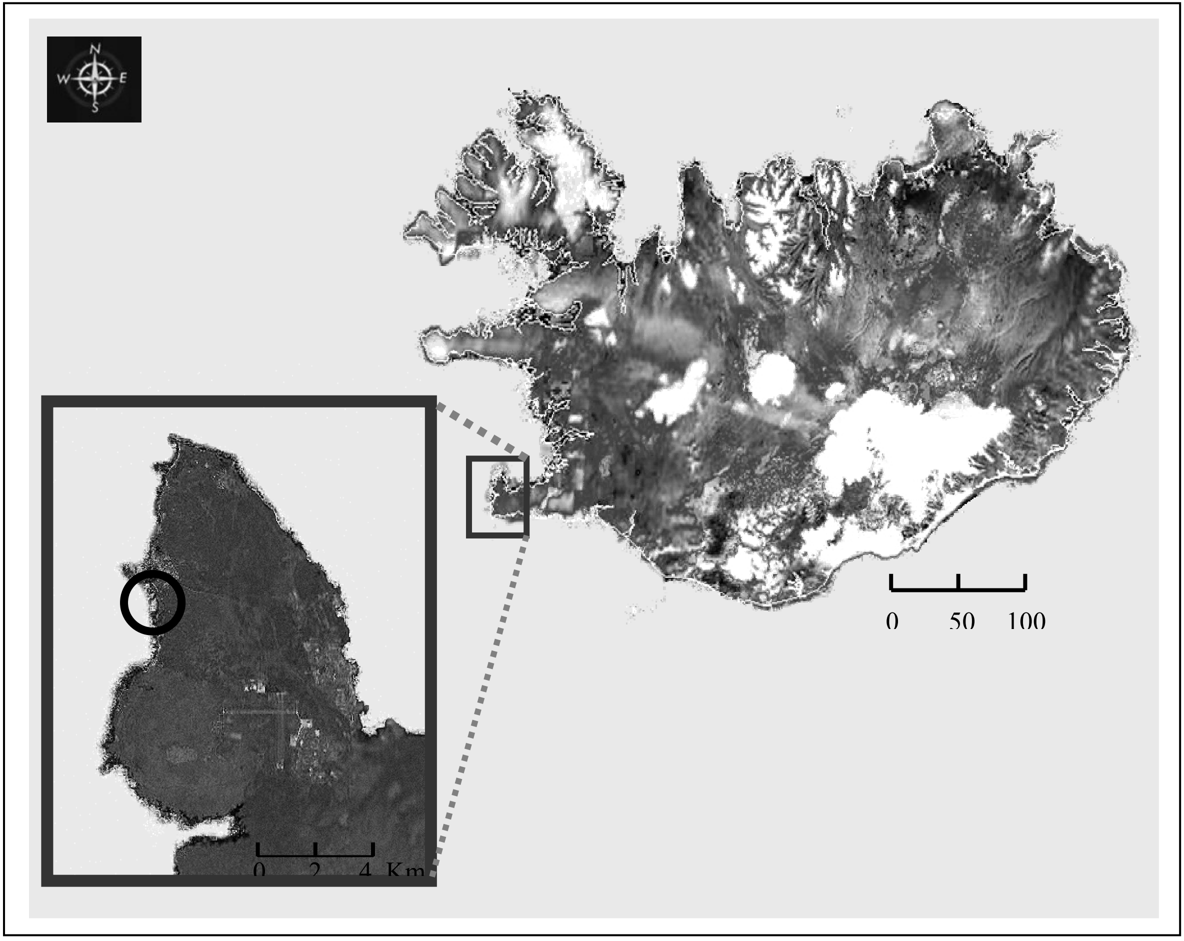
Hemisphere (Ogilvie 2005). It is almost exclusively marine, breeding on offshore islands, islets and coastal shores. This study was performed on the subspecies *S.m.borealis*, which is found from Baffin Island in northeast Canada, Greenland, Iceland, Svalbard (Norway) to Franz Josef Land (Ogilvie 2005). Common Eiders show uniparental incubation and brood care. They are considered capital breeders (Drent and Daan 1980), since they meet their reproductive requirements from stored body reserves, mainly burning fat and metabolised protein from muscle tissue (Parker and Holm 1990). Females are strongly philopatric, they nest on the ground usually on existing nest bowls that are re-used across years (Reed 1975, Bustnes and Erikstad 1993). Hens lay between 3 and 6 eggs, which they incubate for 21 to 26 days (Ogilvie 2005). Because females rarely feed during incubation, they show a mass loss of approximately 35-40% of the initial body weight (Korschgen 1977, Parker and Holm 1990, Gabrielsen et al. 1991). Female and hatchlings leave the nest within 24 hours of hatching to feed at sea. Their diet is based on molluscs, crustaceans and some echinoderms that are obtained from the bottom of the sea in shallow waters (0 -12m) (Guillemette et al. 1992).

The amount of energy needed for incubation depends on the breeding habitat (Kilpi and Lindstrom 1997) and costs of incubation are determined, to a large extent, by the parental thermoregulatory demands (Gabrielsen et al. 1991). Nesting success varies considerably in this species with predation being the main cause of nest failure (Bolduc and Guillemette 2003) but low nest attentiveness (associated with a deterioration in female body condition) can also lead to nest desertion and reproductive failure (Criscuolo et al. 2002a). Chick abandonment may serve as a strategy to increase survival probability when females are in low condition (Bustnes and Erikstad 1991). Eiders are long-lived with a reported annual adult survival of over 85% (Coulson 1984) and variable yearly reproductive output (Yoccoz et al. 2002).

This work was carried out in the municipality of Reykjanesbær, SW Iceland (64°01’3” N, 22° 42’ 27”W). Its location south of the Arctic Circle gives Iceland a cold temperate and oceanic climate (Fig 1.1). The Eider is the most common anatid in Iceland, with an estimated population size around half a million birds. In Iceland, this species is protected all year-round. During the breeding season a large proportion of eiders nest in colonies reaching densities up to 2,000 nests per hectare. Most colonies are on the mainland near farms where, for centuries, Icelandic farmers have profited from the large nesting densities by harvesting the down that each hen lines in its nest during the incubation period. The down is used as insulation in bedclothes and down jackets and its exportation has considerable economical importance. The practice of eiderdown collecting has led to intensive predation management programs run by the farm owners. Farmers hunt eider predators (arctic fox, *Alopex lagopus*; american mink *Mustela vison* and lesser black-backed gull *Larus fuscus*) in and near the eider colonies and take preventive measures like setting up electric fences surrounding their lands, hunting is paid for by the government and local authorities. Habituation of eiders to human contact and low nest predation rate inside the farms facilitate various practical aspects of studies such as the present one. In addition, it allows testing several hypothesis of nest-site selection based, for example, on factors like nest microclimate, which might be of higher relative importance compared to predation pressure when choosing a nest in these colonies.

While a number of studies have documented variation in energetic costs of incubation in birds, there has been very little investigation of the links between energy expenditure, nest design and location and individual condition. The Common Eider experiences a potential conflict between the allocation of energy resources to egg production and to self-maintenance during incubation. This makes Eiders an interesting system to examine the importance of the bird-nest unit in the maintenance of a suitable incubation environment and the energetic costs of incubation associated with environmental conditions.

Fig.1.1 The study area is located in the Reykjanes Peninsula (within rectangle) in SW Iceland



Chapter 2

Spatial distribution of nests and breeding success in the Common Eider.

Abstract

Within a geographic location, birds often use a wide variety of nest sites. Both the location and the nest properties can cause incubation conditions to vary both for parents and eggs and thus potentially affect the reproductive success of individuals. The aims of this study were to evaluate the relative importance of nest and individual quality on a) hatching success and b) the spatial and temporal distribution of eider nests. Variables measured were grouped in two categories: 1) female quality included laying date, clutch mass and female body mass and condition. 2) nest site quality comprised nest shelter, proximity to water, presence and number of conspecifics. Hatching success was positively influenced by clutch mass and negatively influenced by laying date and proximity to water. Nests showed a non-random spatial distribution; this nest aggregation was partly explained by some female quality variables, for example, nests separated by short distances initiated laying in closer synchrony and showed more similar clutch masses than nests separated by longer distances. Female features were also related to breeding density, with early nests with heavy clutches having more and closer neighbours than late nests with light clutches. No relationship of female or nest quality with the temporal distribution of nests was found. Settling patterns of Eiders in this colony seem to be mainly explained by social cues rather than on nest characteristics. By staying close to other birds (potentially being relatives) females can gain reproductive benefits. However, females might be constrained, by remaining close to relatives, when trying to improve individual decisions on nest selection.

Introduction

A random distribution of breeding sites is rare in nature and it is often accepted that non-random distribution patterns arise by natural selection (Cody 1985). The location of a nest can have profound effects on reproductive performance (Burger 1985). Both the geographic area and the nest type can cause incubation conditions to vary both for parents and eggs and thus potentially affect the reproductive success of individuals (Badyaev 1995).

Whenever there is heterogeneity of quality in breeding areas, individuals will select the best sites. If some intraspecific competition for access to nest sites occurs, older or better quality individuals are likely to occupy the best patches (Potts et al 1980, Møller 1991, Newton 1991, Pärt 2001) resulting in a non-random spatial aggregation of nests. The classic model of ideal despotic distribution (Fretwell and Lucas 1970) has been applied to studies of distribution of individual birds among habitats (Holmes et al. 1996). The model states that habitat is selected in order to maximize fitness; when individuals differ in competitive abilities, dominant individuals will secure high quality habitats while forcing less competitive individuals into unfavourable habitats resulting in areas of lower reproductive success (Fretwell and Lucas 1970).

Preferences for nest sites are assumed to be adaptive (Collias and Collias 1984) because usually individuals in preferred sites breed more successfully (Harris et al. 1997; Stokes and Boersma 1998, Velando and Freire 2003). The effect of individual quality on breeding performance confers a layer of complexity to studies trying to discriminate the fitness consequences of physical attributes of nests. Among birds, numerous environmental factors can shape nest-site preferences (Lima and Dill 1990; Martin, 2001). Predation is often considered as the primary factor influencing the selection of nest patches (Martin 1988). Other alternatives include nest microclimate, presence of conspecifics or proximity to resources.

Nest-site selection in Common Eiders (*Somateria mollissima*), as in many other birds, is likely to involve trade-offs between these factors such as choosing between a site with a nest microclimate promoting optimum conditions for the eggs and one providing adult security, favourable thermal properties or accessibility to resources.

For example, closeness to fresh water is important since females will take short bouts off the nest to drink (Bottitta et al. 2003 Criscuolo et. al 2000). Time spent away from the nest can increase the risk of egg predation and will result in excessive egg cooling (Kilpi and Lindstrom 1997). It has also been shown that fresh water is needed for optimal post-hatching chick growth and development (DeVink et al. 2005). In addition, Eider females, as other precocial species, bring hatchlings to areas where they can feed. Close proximity from the nest to the sea might decrease the risk of chick predation, therefore, minimising the distance to both, fresh water and sea might be an important trait that females consider when choosing a nesting site.

Protection from weather conditions is important for incubating eiders, by nesting in sheltered areas females can decrease energy expenditure during incubation (Kilpi and Lindström 1997) which in turn could help improving their incubation performance. Selection of a nesting site can also be influenced by the presence of other individuals in the same area. Incubating parents may, for example, gain benefits from nesting in areas of high density since this is often related to increased protection against predators (Anderson and Hodum 1993, Brown and Brown 2001) and in Eiders, it allows females to spend more time sleeping (Criscuolo et al. 2001).

Many studies have succeeded in identifying the factors influencing the selection of nesting sites in birds (Clark and Shutler 1999). However, in order to improve our understanding of the adaptiveness of nest placement, more work is needed to detect temporal and spatial variations in the differences between successful and unsuccessful sites. Accordingly, in the present study I investigate the factors associated with temporal and spatial variation in nest occupancy by Common Eiders. First I examine the habitat characteristics associated with hatching success, then I test whether there is a spatial aggregation of nests of similar productivity, and finally I investigate if the pattern of nest distribution is related to female and/or nest site features.

Methods

Study population.

The breeding colony of Common Eiders used in this study holds ca 2000 pairs nesting on private farmland (Nordurkot, Reykjanesbær, SW Iceland; 64^{o}01’3” N, 22^{o} 42’ 27”W). Eiders at Nordurkot nest along the coast and in close proximity to small freshwater ponds. In 2005 I followed a sample of nests that were located in an area of c.0.08 km^{2} and that is geographically separated from the rest of the colony (Appendix 1) creating a natural sub sample, all the nests with eggs in this area were recorded (n=207). When a new nest was found, I registered its location (GPS, Garmin UK) and I followed it every day until hatching in order record the fate of the eggs. I registered clutch size, fresh egg mass (within 24 hrs of being laid), laying and hatching date of all eggs. I also characterised each nest site recording the following variables: a) minimum walking distance from each nest to the sea (distance that females would have to walk with the chicks), b) minimum walking distance from each nest site to fresh water, c) number of neighbours within a 6 m radius "breeding density", d) distance to the nearest neighbour and e) degree of nest vegetation (exposed, intermediate or sheltered) using a composite measure of the vegetation coverage and height of the surrounding vegetation and/or rocks (details of the procedure described in Chapter 3).

From all the nests in the sample I captured 78 females within 10 days after I found the first egg in the nest. The weight and size (tarsus, head-bill length and wing) of females were recorded using spring balances and callipers respectively. In order to have a single measure of female structural size I ran a PCA analysis on the three body size measurements and the first principal component that explained 68% of variance was taken as a measure of body size. Because I did not trap females at the same time in their incubation period I extrapolated body mass of females to day 1 of incubation using the linear equation: $M_1 = M_t + (M_L \times T)$, where $M1$ is the initial female mass, Mt is the mass when the female was trapped, ML is the daily mass loss which was calculated for females of this colony (24.35 ± 2.29 g/day, n = 44 females; D'Alba unpublished data), and T is the elapsed time from the start of incubation to the day the female was trapped. Female condition was then estimated using the residuals of a regression between female initial mass and size.

Statistical analysis

Variables influencing hatching success. Because I was interested in analysing the spatial aggregation of nests in relation to female and nest site characteristics I distinguished between variables related to female quality (laying date, clutch mass, female mass and condition), and to nest site quality (shelter, proximity to water). I tested the effects of nest site and female variables on hatching success (proportion of hatched eggs from the original clutch size) fitting generalized linear models (GLM) with a binomial error distribution and a logit link function (Crawley 2002). A full model was built using the female quality and the nest site variables as predictors. I chose the variables describing the female quality first (since these should have the most direct effects) followed by those describing the quality of the nest site. The significance of these factors was tested by means of stepwise backward elimination, starting with the full model and testing biologically interesting two-way interactions first. I based the decision to remove terms on the basis of likelihood-ratio tests. To investigate the spatial aggregation of nests in relation to female features I obtained a composite measure of female quality based on a Principal Component Analysis including the variables related to female quality held in the final model (that significantly influenced hatching success).

Spatial aggregation of nests.

In order to test for spatial correlation among nests I applied techniques of geostatistical analyses. The semi-variance is widely used to detect spatial patterns within data sets (Bailey and Gatrell 1995), and to model dependence among observations. In this study the semi-variance function describes how female characteristics spatially covaries among nests.

It is defined as

$$y(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[z(x_i) - z(x_i + h) \right]^2$$

where *h* is a vector of distances between nests, *N* is the number of inter-nest distances and *y* is the observed values of the variable (female quality index) on two points separated by the distance *h*.

The semi-variance is a measure of dissimilarity. A plot of semi-variance against distance (termed "variogram") was used to explore how dissimilarity in female quality changes with distance between nests (i.e. spatial scale). Eider nests in this sample (N=207) showed an average ± SE distance of 5.7 ± 1.3 m to the nearest neighbour. Therefore I chose 5 m-wide distance classes in constructing the variogram. If there is spatial independence among the data, values of the female quality index (PC1) should be distributed at random among nest sites. I tested the hypothesis of spatial independence with a random labelling test (Ribeiro et al. 2003): the function *y(h)* computed on the observed quality index was compared with 1,000 random reallocations of the values of the female quality index. After ordering the 1,000 simulated values of *y(h)*, a bilateral *P* value was computed following Manly (1991), as twice the proportion of simulated values more extreme or equal to the observed value of *y(h)*. A 95% confidence envelope was derived from the 25th and 975th values of *γ(h)*. The hypothesis of spatial independence between quality index was rejected at the 5% significance level when the observed variogram was outside this envelope. All spatial statistical analyses were performed using the program R v2.3.1 following Crawley (2002).

Results

Effects of nest and female characteristics on hatching success.

Hatching success was associated with female characteristics including laying date and clutch mass (Table 2.1). For example, females that laid clutches with average fresh egg mass higher than 100g and that laid before the 23rd of May hatched a high proportion of their eggs (hatching success > 75 %) than clutches laid after the 1st of June and with smaller eggs (<90 g per egg) (hatching success < 30%). A Principal Components Analysis including laying date and clutch mass was performed to obtain the index of female quality. The first principal component (PC1) explained 69.3% of the variance analysis was considered to calculate the experimental variogram.

Hatching success was also higher for nests that were located close to the sea or the edge of freshwater (Table 2.1). Hatching success was not associated with the degree of nest shelter or female condition, neither with the site density (number of neighbours) nor the proximity to the nearest neighbour (Table 2.1). The main causes of hatching failure included female nest abandonment (occurring in 3.7% of total number of nests), predation by gulls (7.9%) and, egg rotting (10.7%).

Spatial distribution of nests.

Nests were not distributed randomly in space: female quality index showed a significant spatial aggregation so that nests that were separated by short distances (< 25 m) were initiated in closer synchrony (laying date) and showed more similar clutch masses than nests separated by longer distances (Fig 2.1). Females tended to occupy the nests that were closer to the entrance to the sea earlier in the season but the relationship was not significant ($r = 0.12$, $p = 0.07$, $n = 207$). There was no relationship between the laying date and the proximity of nests to fresh water (r = 0.08 p, = 0.30, n = 207). Mass of the clutch showed no association with proximity to water (distance to sea r = 0.02 p, = 0.74; distance to fresh water r = -0.01 p, = 0.80). Interestingly, female quality index was related to breeding density: early nests with heavy clutches had more and closer neighbours within a radius of 6 m than late nests with light clutches which tended to be more scattered and separated from neighbours (minimum neighbour distance $r_s = -0.14$, $p = 0.04$; number of neighbours $r_s = 0.195$, $p = 0.005$, $n = 207$; Fig 2.2).

Table 2.1. Results of the GLM testing the effects of female and nest site variables on hatching success (proportion of eggs hatched) for Eider nests in Nordurkot, Iceland 2005.

Proportion of hatched eggs	F	df	p	Estimate	se
Female attributes					
Laying date	18.53	1,206	<0.001	-0.103	0.02
Clutch mass	10.40	1,205	0.001	0.005	0.002
Female condition	0.03	1,202	0.85	0.141	0.410
Nest attributes					
Distance to sea	5.97	1,204	0.01	-0.017	0.008
Distance to fresh water	4.04	1,203	0.04	-0.014	0.007
Nest shelter	0.03	1,201	0.84	-0.055	0.324
Distance to nearest neighbour	0.06	1,200	0.79	-0.015	0.053
Number of neighbours within 6 m	0.04	1,199	0.83	-0.009	0.042

1 Generalised linear model with a binomial error distribution and a logit link. The significance reported is the F value when the explanatory variable of interest is dropped from the model.

2 The following two-way interactions between variables were tested but not significant (p>0.05; results not shown in table): laying date*distance to sea, laying date* distance to fresh water, laying date*number of neighbours, clutch mass*distance to sea, clutch mass*distance to fresh water, clutch mass*number of neighbours, female condition* nest shelter.

Fig. 2.1. Variogram of the observed female quality index (laying date and clutch mass PC1; solid line) with the bilateral random labelling test (α = 5%) of spatial independence among nests. Dotted line: mean of the simulated values; dashed lines: 95% confidence envelope. The PC1 scores were randomized conditional on the similarity between nests.

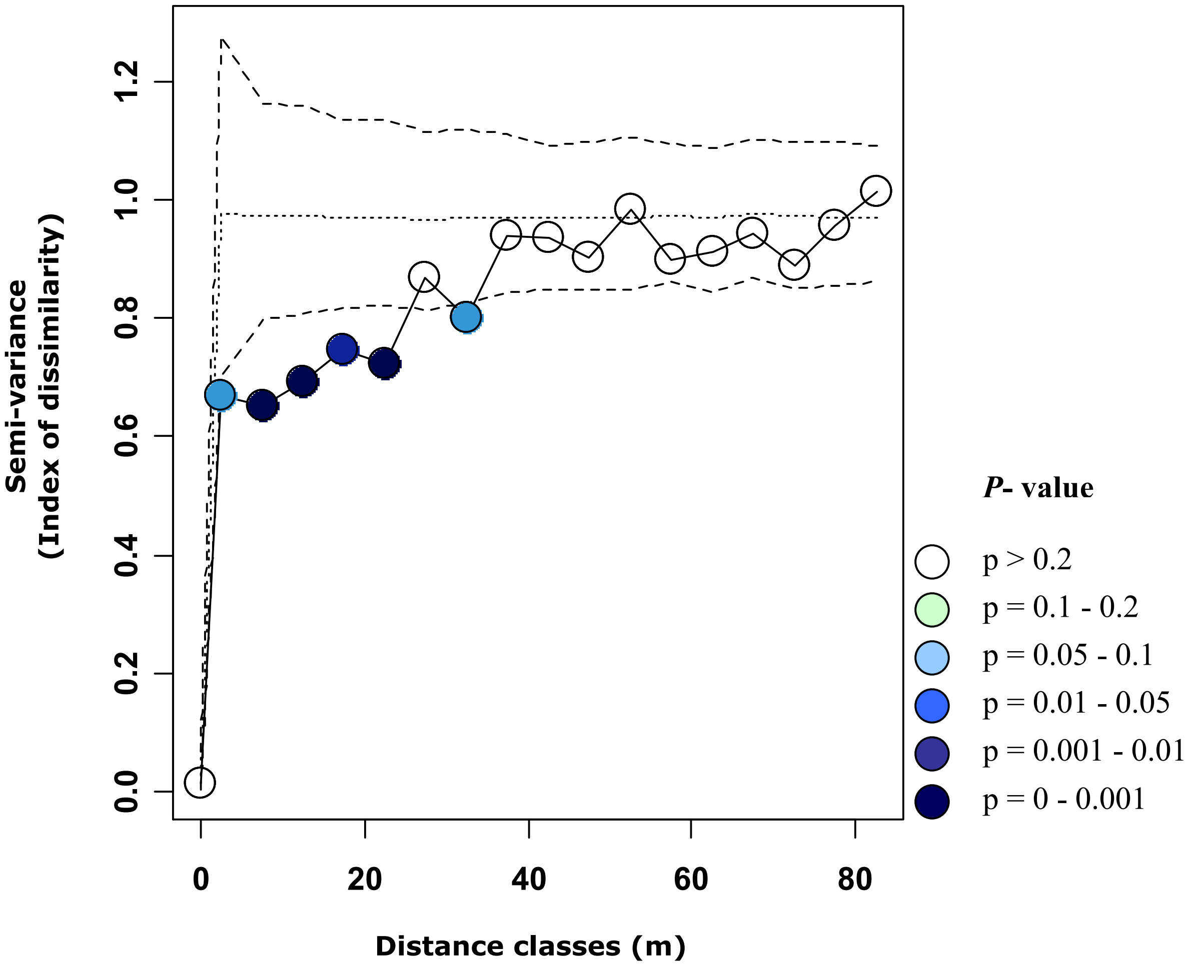
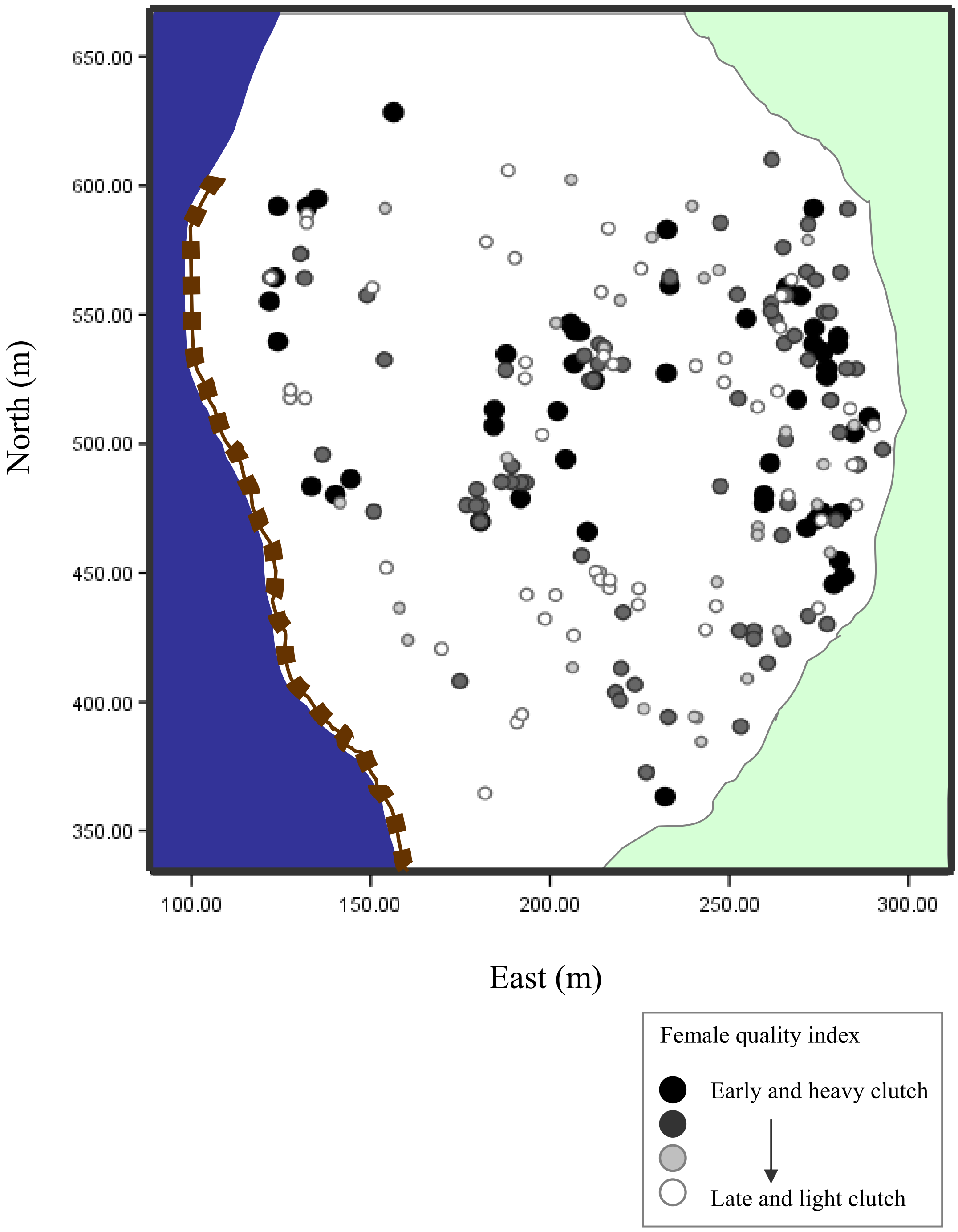


Fig 2.2. Spatial pattern of nest distribution in relation to female quality (PC1 of laying date and clutch mass). Data were grouped according to the 25th, 50th, 75th, percentiles of the distribution of female quality index (in the analysis, the PC1 was used as a continuous variable). The area in green represents fresh water. The line of continuous squares represents a wall of rocks (ca. 150 cm) that can not be crossed by females with chicks. Access to the sea (area in blue) is possible only by walking across the area free from rocks.



Discussion

I found that hatching success was influenced by female and nest features. The data also showed that areas of high productivity were occupied earlier in the season and in higher densities. Eiders showed a non-random pattern of nest distribution that offers evidence of nest site selection in this species. Female features explained the spatial variation of nests: birds with similar clutch masses and laying date nested in proximity to each other.

That better quality individuals perform better during reproduction in not surprising. However, often defining the quality of organisms is subject to misrepresentations and can lead to misleading results. The index of quality I used was based on clutch mass and laying date, and it was strongly related to hatching success. In Eiders, it has been shown that females that invest in big clutches have a higher capacity to increase reproductive effort (Hanssen et al. 2003), have a higher nest success (Erikstad and Tveraa 1995), have a lower rate of abandonment of ducklings (Erikstad et al. 1993) and higher return rates and survival (Yoccoz et al. 2002). In addition, for many birds it has been shown that even small differences in laying date can signal variation in parental quality (Sydeman et al. 1991; Brouwer et al. 1995), with better individuals laying earlier in the season. This would support the finding that female Eiders that laid heavy clutches earlier in the season hatched a higher proportion of eggs.

Distance to water was important for hatching success suggesting some ongoing selective process is shaping the nest-settling pattern in this species. However, there was also a strong influence of female attributes (clutch mass and laying date) on hatchability. Correlations between nest site and female characteristics are often present in nature; this makes it difficult to tease apart the effect of nest quality from attributes of the individuals on reproductive success (Harris et al. 1997; Stokes and Boersma 1998, Kim and Monaghan 2005). Because this study relied simply on correlational data, at present I cannot disentangle these two interactive effects. Although experimentation might prove to be difficult, in future studies it would be interesting to test whether changes in nest distance to water influence the reproductive performance of females of similar quality.

One hypothesis to explain the settling patterns observed in this study is that nest selection is a result of a priori decisions based on nest quality. This would require that females rely on certain biotic and abiotic cues to assess the suitability of a patch. For example, Common Guillemots (*Uria aalge*) preferably occupy nests that offer physical protection for the eggs and preferred sites tend to be more successful (Kokko et al. 2004). Past experience can also indicate an individual about the prospects of success in particular nests (Switzer 1997). Individuals normally should not choose nests in which they have been unsuccessful ('win-stay, lose-switch' theory, Switzer 1993). More often the decision on nesting in a specific patch is influenced both by the quality of the site and the individual's past experience (Kokko et al. 2004). Breeding experience in long-lived birds like the Common Eider could be of great relevance when selecting a nest. If in Eiders like in other species oldest or more experienced individuals are able obtain good sites (e.g. Shags, *Phalacrocorax aristotelis*; Potts et al. 1980) then the higher success in these patches may simply be a result of the positive correlations between bird quality and site.

It has been reported Eiders generally are highly philopatric to breeding areas but show less fidelity to nest sites (Swennen 1990, Goudie et al. 2000), indicating that nest site selection is a dynamic process and decisions can be changed over time.

That good quality females settled in dense nest clusters suggests that some social cues can have important effects on nest site selection. As McKinnon et al. (2006) showed, Eider females prefer to nest close to kin and remain in family groups during incubation and brood rearing. Kin coalitions might have fitness benefits by reducing predation during chick rearing (where chicks are adopted by "aunties" when mothers are in poor condition; Ost et al. 2003). Thus, this social structure presented during reproduction can act as a selective pressure for nest-site choice (McKinnon et al. 2006). On the other hand individual females might be constrained, by remaining close to relatives, when trying to improve individual decisions on nest selection.

Chapter 3

Nest shelter, incubation temperature and female performance during incubation in the Common Eider

D'Alba

Abstract

In species with parental care, the quality of the environment that the parents provide for developing eggs plays an important role in determining reproductive success. In birds, the degree of exposure of the nest is likely to play an important role in determining reproductive costs via its effects on the thermal conditions for the incubating parent and the clutch. In the absence of experiments, it is difficult to separate effects of nest site quality from those of parental quality, since the two are usually correlated. I used two approaches (correlative and experimental) to evaluate the effects of nest shelter on the microclimate and breeding performance of the Common Eider *Somateria mollissima*. Females that lay larger clutches choose to nest in well-sheltered nests, where they experienced milder nest-site temperatures (on average 1.4°C higher than exposed nests). These birds provided higher (on average 0.3 °C) and less variable (25%) incubation temperatures for their developing eggs and incubation periods were shorter. Hatching success was not related to nest shelter, but the costs associated with nesting in exposed sites appears to be greater as evidenced by mass loss of the incubating females. The body mass at hatching of females at sheltered sites, and important determinant of post hatching parental care levels in this species, was 11% higher than that of females nesting at exposed sites. When I experimentally enhanced the shelter at exposed nests, nest temperature was higher and more constant than in equivalent unmanipulated sites. While hatching success and incubation duration were not affected, females at these enhanced sites experienced a lower body mass loss. This study shows that apparently very small changes in the climatic conditions at the nest site can have substantial consequences for reproductive costs.

Introduction

The optimal allocation of resources between reproduction and self-maintenance is a very important life history trade-off. In iteroparous breeders, it is generally assumed that selection will have favoured reproductive decisions that maintain adult body condition above some threshold level that does not compromise future reproduction and survival (Lessells 1991, Roff 1992, Stearns 1992). In species, where the parents actively maintain optimal conditions for offspring development, the choice of the breeding site may have a substantial effect on the level of investment required.

Avian incubation is particularly interesting in this context; since parents usually regulate the temperature of their developing eggs using heat generated from their own bodies, and must supply this at least until the eggs hatch (Deeming 2002). It has become increasingly evident that incubation can be a relatively demanding phase of avian reproduction (e. g. Tatner and Bryant 1993, Williams 1996, Thomson *et al*. 1998). This is particularly so when birds incubate in cold and exposed environments and when only one partner incubates (Tinbergen and Williams 2002, Cresswell *et al*. 2004). In many species, the energy demands during the incubation period are determined principally by the parent’s requirements for thermoregulation, which can account for up to 40% of the daily energy expenditure (Rauter and Reyer 2000).

Nesting in a relatively sheltered site can reduce exposure to winds that rapidly dissipate body heat. For example, birds incubating in circumpolar environments show daily energy expenditures 50% higher than the same species in lower latitudes possibly as a result of the climatic conditions (Piersma *et al*. 2003). By constructing or choosing a suitable nest site, incubating birds can reduce the energetic costs of incubation (Rauter and Reyer 2000, Hilton *et al*. 2004) and/or improve their incubation performance (Kim and Monaghan 2005).

The degree of exposure of the nest site will therefore have a potentially large effect on the amount of energy that the parents must expend in maintaining their own body temperature and thus the resources that they have available for investment in reproduction. Hence, nest site preference will be under strong selection and it is expected that parents occupying preferred nest-sites will show better breeding performance than parents occupying less preferred nest sites (Martin 1998, Clark and Shutler 1999, Lloyd and Martin 2004).

When available nesting sites vary in quality, individuals will generally prefer the higher quality sites (Newton 1998). If intra-specific competition for access to better quality sites occurs, usually older or better quality individuals will have access to the better breeding sites (Matthysen 1990, Porter 1990). This can therefore confound studies of the association between the suitability of the nest site for incubation and breeding performance (Lloyd and Martin 2004, Kim and Monaghan 2005).

The Common Eider *Somateria mollissima* is a species of sea duck in which females incubate without male help and rely upon accumulated body reserves during laying and incubation (Drent and Daan 1980, Erikstad *et al*. 1993, Hanssen *et al*. 2003). Because female Eiders rarely feed during incubation, they lose approximately 35-40% of their initial body weight during incubation (Gabrielsen *et al*. 1991). Kilpi and Lindström (1997) found that female Eiders nesting on a windswept island lost body weight faster than those in more sheltered colonies. Such an effect could arise because poorer quality birds nest in these areas, or because the exposure to weather at the nest site directly influences mass loss. Experimental studies are required to disentangle these two confounding, but not mutually exclusive, effects.

In this study of incubating Common Eiders at a colony in Iceland, I investigated the relationship between the ambient temperature that females experience at their nest site, the incubation conditions experienced by their eggs in the nest, and female incubation effort. To measure conditions for the offspring, I recorded incubation temperature within the nest. To estimate incubation effort, I measured female body mass loss during incubation and incubation duration. To take into account the possible effects of female quality on nest-site preference, I manipulated the degree of exposure of the nest-site by providing artificial shelters. I applied artificial shelters to (a) a random sample of females whose clutch size was standardised to reduce different demands due to clutch size differences, and (b) a sample of females laying the same clutch size and nesting in similarly exposed sites, and presumably therefore of similar quality, where I expected the benefits of additional shelter to be greatest.

Methods

General protocol

Fieldwork was carried out from May to July 2004 and 2005 in a breeding colony of the Common Eider in Sandgerdi, SW-Iceland. The area is covered by a mixture of salt marsh grasses dominated by *Agrostis stolonifera* and *Puccinellia maritima*; there are also patches lined exclusively with the brown algae *Pelvetia canaliculata* (Appendix 2). In both years, ca. 2,000 pairs nested in a fenced area where local people harvest the down lining the nests at the end of the incubation period for commercial purposes. Nesting birds in the area are accustomed to close and regular presence of the farmers. Hence, any extra disturbance caused by our visits is likely to have been minimal.

The study area was searched for nests and fresh nests were marked with numbered sticks. Nests were visited daily during laying until clutch completion and fresh eggs were individually labelled in the order they were laid. For each nest, I recorded laying date and fresh egg mass (weighed on the day of laying to the nearest 0.1 g). Incubation in eiders generally starts after the third egg is laid (Mehlum 1991, Hanssen *et al*. 2002). I considered the start of incubation as the day on which the fourth egg was laid. Nests were again checked daily for hatching from 24 days after the first egg has been laid onwards (Mehlum 1991) and hatching date and success was recorded for each egg. Incubation duration was calculated as the time elapsed from the start of incubation until the first egg hatched. In 2005, females from each study nest were caught, measured and weighed early in incubation (1-8 days after the first egg was laid) and again at day 26 of incubation (on average two days before the eggs hatched). Nest desertion occurred at three of the 48 nests where females were caught, and, in all three cases abandonment occurred at the end of incubation when eggs were due to hatch.

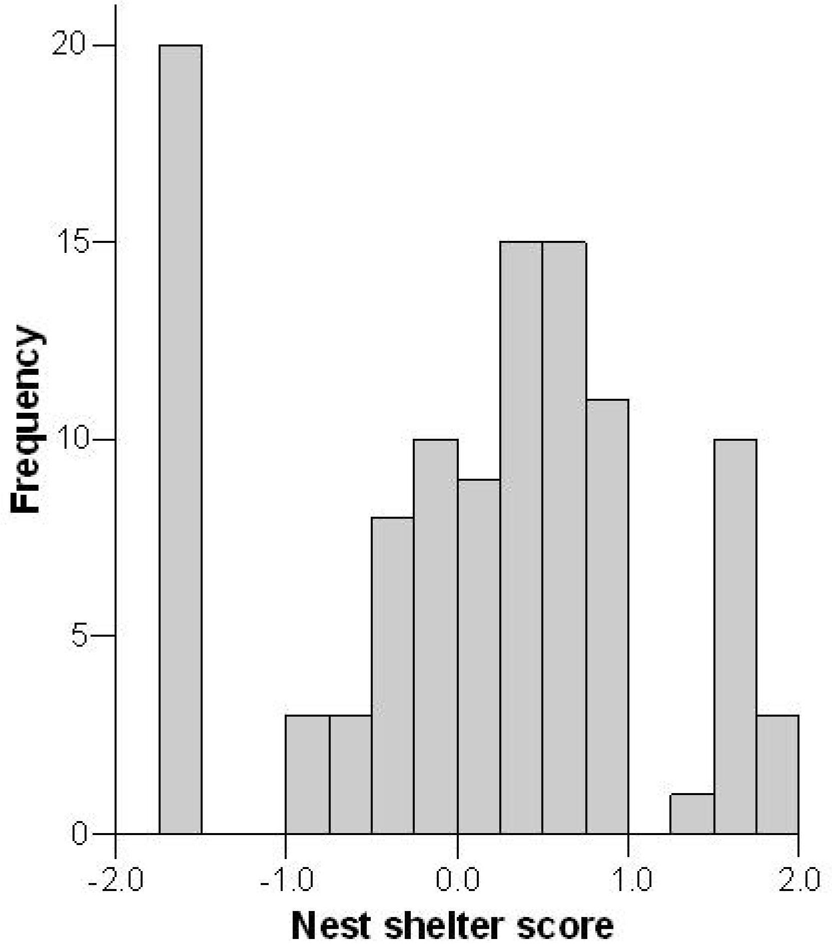
For each nest, I recorded measures for microclimate and nest shelter. Continuous measures of temperature using TinyTag data loggers (Gemini Data Loggers LTD, Chichester, UK) were taken to the nearest 0.01 °C, over 22 hr periods. Nest-site temperature was taken outside the nest by attaching the thermistor to a small pole at 5 cm distance from the edge of the nest and at the approximate level of the female's head when incubating (ca. 10 cm). To estimate the developmental conditions experienced by the offspring, I placed a second thermistor among the eggs in the centre of the nest, to record incubation temperature. The thermistor was secured to the ground so it could not be moved. For each nest a total of three measurements of nest-site and incubation temperature were taken in early (within day 4 to 9), mid (day 10 to 18) and late incubation (day 19-26; day 1 is the day the first had been laid). For each 22-hour measurement period, I calculated an average temperature and temperature variability (mean and coefficient of variation, respectively). In addition, continuous ambient temperature and wind speed were obtained from the weather station at Keflavik airport, 3 km from the study area. The average daily air temperature from April to the end of June was 8.3 ± 2.8 °C (mean ± sd; min-max: 1 to 12 °C) in 2004 and 7.5 ± 2.7 °C (min-max: –2 to 13 °C) in 2005. Wind speed averaged 21 km/h (max. speed: 57 km/h; annual variation: 19.2 km/h) in 2004 and 18km/h (max. speed: 62km/h; annual variation: 17.5 km/h) in 2005.

At the beginning of incubation, I assessed the degree of natural nest shelter for all nests by measuring the percentage of the nest circumference covered by surrounding vegetation and/or rocks within a 0.5 m radius of the nest cup and the average height of the surrounding vegetation and/or rocks. The level of shelter remained constant throughout the breeding season because no vegetation ever grew within a 0.5 m radius of completely exposed nests and, although the vegetation turned green in vegetated areas, the height of vegetation clumps did not change (pers. obs.). A Principal Component Analysis including average height of plants and/or rocks and percentage of the nest circumference that was surrounded by them produced a first principal component (PC1) that explained 86.6% of the variance. PC1 was used as a composite measure of nest shelter and showed a trimodal distribution (Fig. 3.1). Therefore nest shelter is considered as a categorical factor with three levels.

The sample for the correlative component of the study comprised 43 nests in 2004 and 35 nests in 2005 that were randomly selected from throughout the colony and in which no experimental manipulations were performed. A further 21 nests in 2004 and 15 in 2005 were used in the experimental manipulations of nest shelter described below. Since the birds were not ringed in 2004, I cannot discount the possibility that some females were sampled in both years. However, Common Eiders show high nest-site fidelity (Bustnes and Erikstad 1993, Tiedemann *et al*. 1999) and nests were sampled at different locations between years to decrease the chances of using the same females in both years.

Figure 3.1. Frequency distribution of nest shelter as the first principal component based on vegetation height and percentage of cover of nest circumference (see text). Data shown includes all nests from 2004 and 2005. The higher the score the more sheltered the nest. Nest shelter was allocated to the following categories: 1) completely exposed nests (nest shelter score < -1.0), 2)

partially sheltered (40% covered with vegetation height < 17cm; shelter score between –1.0 and 1.0), and 3) well-sheltered nests (with 80% surrounding vegetation and > 20cm height; shelter score > 1.0).



Experimental nest shelters

Artificial nest shelters are commonly used in several breeding colonies of Common Eiders (e.g. Divoky and Suydam 1995, Woolaver 1997, Jonsson 2001). Plastic screens (garden lawn edging) of 15 cm height and 50 cm of diameter were used to make artificial nest shelters in experimental nests. The plastic shelter was placed encircling the nests after the third egg was laid (or as close as possible to the start of incubation) to diminish possible abandonment. The addition of plastic shelters in experimental nests was equivalent to the well-shelter category in unmanipulated nests (shelter score > 1.0; Fig. 3.1). After placing the shelter the females were observed from a distance to ensure that they resumed normal incubation. In all cases females returned to the nest within 10 minutes and sat on the eggs almost immediately. Females did not appear to have any difficulties with access to the nest after the shelters were in place. The percentage of nests that were abandoned in both years by females in control (7 %, n = 78) and experimental nests (8.3 %, n = 36) was not significantly different (χ^2 = 0.67, df = 1, P = 0.79). The shelters were opened when the first pipping egg of the clutch was detected to ensure that the chicks could leave the site easily.

In 2004, when a new nest was found, it was randomly assigned to either the unmanipulated (n = 43) or artificial shelter (n = 21) group. In order to reduce a potential effect of clutch size on incubation temperature, the clutch was standardised to the median clutch size of 4 eggs (Erikstad *et al*. 1993; the mean clutch size in the two study years was 3.9 ± 1.08 eggs; mean ± sd, n = 64), by adding or removing the appropriate number of eggs two days after the third egg of the original clutch was laid. Contiguous nests (not included in the study) with similar laying dates as the study nests were used as a source of extra eggs or as host nests for removed eggs.

The correlative results (see below) from 2004 suggested a positive association between female quality, as indicated by the clutch size she laid, and the degree of shelter at her nest-site. Accordingly, I repeated the shelter manipulation in 2005 using only females nesting in exposed sites, since in these females I expect to find the greatest benefits of nest shelter. These nests were compared with unmanipulated nests with the same natural shelter. Nests were randomly assigned to the unmanipulated (n = 15) and artificial shelter group (n = 15). Original clutch size was not manipulated, and did not differ between treatment groups (t_{28} = 0.28, P = 0.78).

Statistical analyses

For each nest, nest-site and incubation temperature data included estimates for the average temperature and temperature variability from three 22-hour periods. I therefore analysed the data using generalised linear mixed models with a repeated measures statement (first, second or third temperature record from each nest), autoregressive covariance structure and Satterthwaite approximation (PROC MIXED, SAS version 9.1). The significance of the variance component of the repeated measures from the same nest was tested using a Z-test. Hatching success was considered a binary measure with two levels; nests where at least one egg failed to hatch vs. nests where all eggs hatched. Data on hatching success were analysed using generalised linear models with binomial error structure and logit link function (MACRO GLIMMIX, SAS version 9.1).

To measure early incubation body mass, not all females were trapped for the first time on the same day of incubation, but all females were trapped within the first third of the incubation period. When I analysed data on early incubation body mass or the percentage of body mass lost throughout incubation, I therefore included in the analysis the number of days elapsed between the start of incubation and the day the female was first trapped as a covariate. Female mass loss between early incubation and day 26 of incubation was expressed as the percentage of the body mass in early incubation. When analysing the relationship between early incubation mass and original nest shelter, I included all 48 females trapped in 2005 (manipulated and unmanipulated nests), including clutch size and the number of days of incubation until they were trapped as covariates, since this analysis refers to nest-site preference expressed prior to the experimental manipulation.

Wind speed was not normally distributed and therefore it was log-transformed prior to statistical analysis. Values are given as means ± se unless otherwise stated. All statistical tests are two tailed and the criterion of significance is $P < 0.05$.

Results

Nest shelter, microclimate and incubation performance in unmanipulated nests.

Nest-site temperatures differed between years and between natural nest shelter categories, the effect of natural nest shelter depended on wind speed (Table 3.1). Average nest-site temperature did not differ between natural nest shelter categories at low wind speeds, but at higher wind speeds, exposed and partially sheltered nests had lower average nest site temperatures than well-sheltered nests (Fig. 3.2). The effect of year on nest-site temperature reflects differences in ambient temperatures between the two years: the nesting period in 2005 was on average 4.1 ± 0.11 °C cooler than in 2004. The variability in nest-site temperature (indicated by the Coefficient of Variation) was higher in exposed (45.69% ± 3.58, $n = 13$) and intermediate (42.50 ± 3.19, $n = 18$) than in well-sheltered nests (32.19% ± 3.39, $n = 12$) and nest-site temperature was more variable in 2005 than in 2004 (Table 3.1). Incubation temperature was independent of natural nest shelter and higher and less variable with increasing average nest-site temperature (Table 3.1). Incubation temperature was more variable in 2005 than in 2004 (Table 3.1). Repeatability of incubation temperature within females across the incubation period was low in both years (2004: $r = 0.10$, $P = 0.52$, $n = 43$; 2005: $r = 0.09$, $P = 0.60$, $n = 35$).

Table 3.1 Results of Generalised Linear Mixed Model analysis to test the effects of natural nest shelter and wind speed on nest-site and incubation temperature (model of incubation temperature also considered nest-site temperature as a covariate). I considered both the average and the coefficient of variance (CV, as a measure for variability) of nest-site and incubation temperature. Data for 2004 and 2005 were combined and the effect of year was included in the model as a fixed factor. Nest shelter was included as a main factor with three levels (see Fig. 1). Day of incubation when temperature was measured was entered as a repeated measures factor within the same nest (nest-site temperature, average: $Z = 1.50$, $P = 0.13$; CV: $Z = 0.86$, $P = 0.38$; incubation temperature, average: $Z = 1.82$, $P = 0.07$; CV: $Z = 1.30$, $P = 0.18$). Only statistically significant interactions are shown.

	Average		Variability	
	df	*F*	*df*	*F*
Nest-site temperature				
Nest shelter	2,126.7	2.42	2,66.1	3.45*
Year	1,75.7	11.1**	1,72	61.9**
Wind speed	1,126.7	1.47	1,131	1.63
Nest shelter * wind speed	1,126.7	3.54*	-	-
Incubation temperature				
Nest shelter	2,60.5	0.74	2,60.4	0.29
Year	1,69.4	0.001	1,69.2	5.69*
Nest-site temperature	1,103.4	4.92*	1,106.6	4.36*
Wind speed	1,103.4	0.12	1,106.6	1.13

* $P < 0.05$

** $P < 0.001$

In both years, females that laid larger clutches nested in more sheltered nests (Fig. 3.3). Clutches in 2004 (3.6 ± 0.18 eggs, $n = 64$) tended to be larger than in 2005 (4.0 ± 1.11 eggs, $n = 50$), but the difference was not statistically significant ($t_{112}= 1.81$, $P = 0.07$). Female mass during early incubation was not related to structural size (tarsus and head-bill length; $r = 0.20$, $P = 0.15$, $n = 48$); presumably therefore heavier females had more body resources. In 2005, early body mass was not associated with clutch size, natural nest shelter or laying date (laying date: $F_{1,42} = 0.12$, $P = 0.73$; shelter: $F_{2,43} = 0.41$, $P = 0.67$; clutch size: $F_{1,45} = 1.22$, $P = 0.27$; number of days incubating: $F_{1,45} = 9.42$, $P < 0.01$).

Figure 3.2 Nest-site temperature (mean ± se) in relation to wind speed of well-sheltered (circles), intermediate (triangles) and exposed (squares) nests. See Figure 1 for classification of natural nest shelter. The analysis included average nest-site temperature as dependent variable, nest shelter as factor and wind speed as covariate (see Table 1 for results). Data plotted include the two study years.

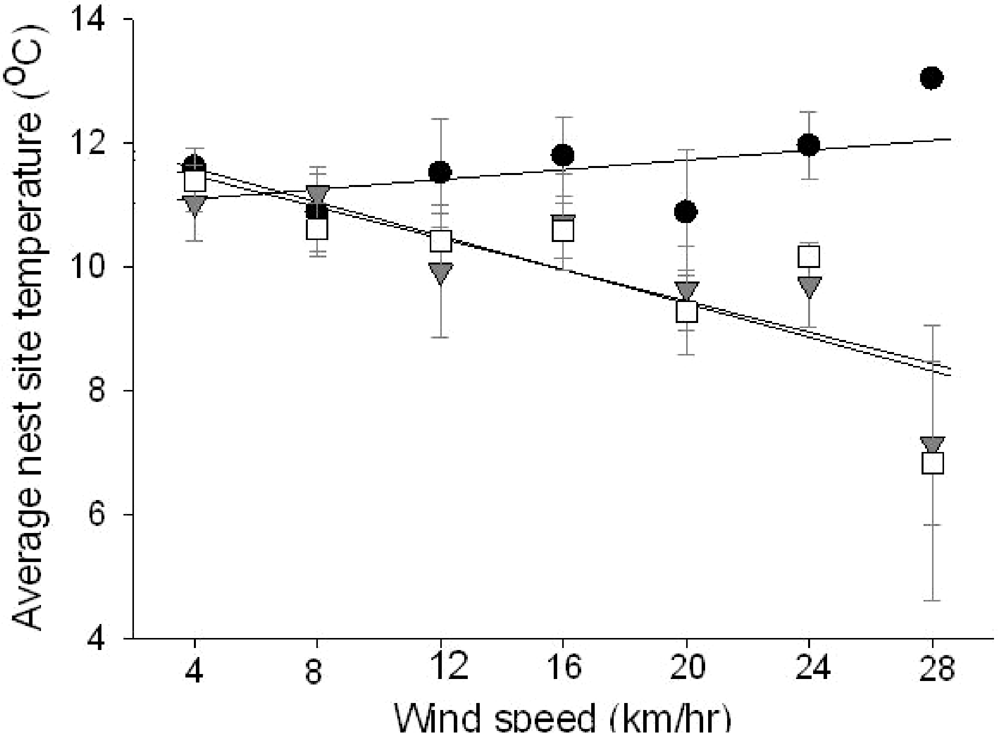
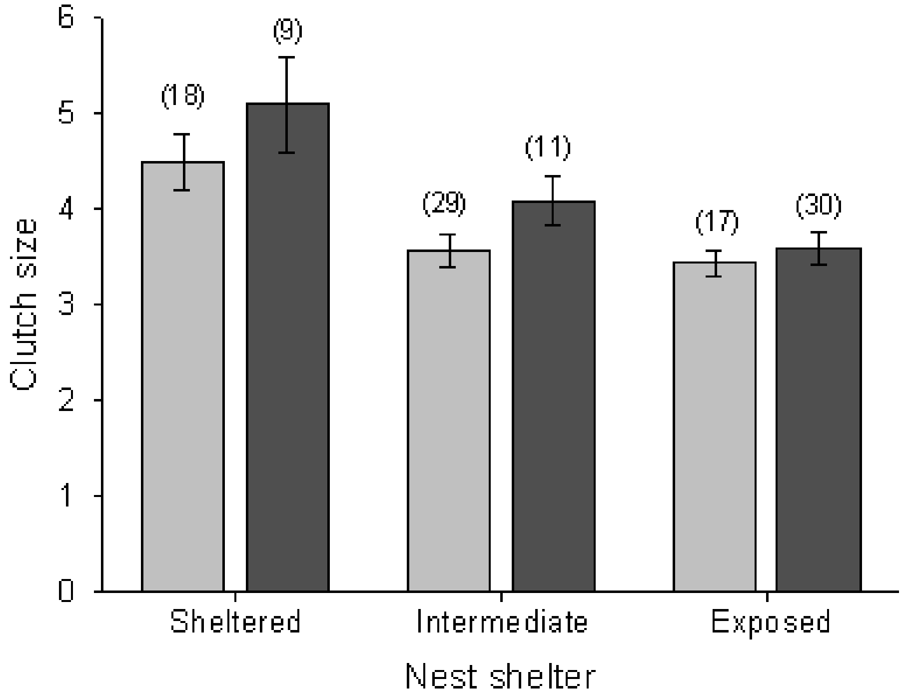


Figure 3.3 Clutch size (mean ± se) and average natural nest shelter score (see Fig. 3.1) in unmanipulated nests. Data shown include nests in 2004 (light bars) and 2005 (dark bars). Females at sheltered nests laid larger clutches than females at exposed nest sites (ANOVA, effect of shelter: $F_{2,101}$ = 4.30, P = 0.01, effect of year: $F_{1,101}$ = 3.79, P = 0.054; no significant interaction.



Manipulation of nest shelter

In 2004, the proportion of control and experimentally sheltered nests in the three natural shelter categories did not differ from each other before the manipulations ($\chi^2 = 1.99$, $df = 2$, $P = 0.15$). The provision of nest shelters (in a random selection of nests with clutch size adjusted to 4 eggs) increased the average nest-site temperature compared to unmanipulated nests (Table 3.2). The nest-site temperature of experimental nests was also less variable than in control nests (Table 3.2). Adding the artificial shelter to the nests also affected incubation temperature with artificially sheltered nests having a higher incubation temperature than unmanipulated nests, regardless of the original clutch size (Table 3.2, effect of original clutch size: $F_{1,\ 65.3} = 0.45$, $P = 0.50$). Incubation temperature was also less variable in artificially sheltered nests than in unmanipulated control nests (Table 3.2; effect of original clutch size $F_{1,\ 71.9} = 2.05$, $P = 0.15$).

Table 3.2 Comparison of nest site and incubation temperature of nests with artificial plastic shelters and unmanipulated nests. Values presented are mean ± se. The *F* values correspond to the GLM analysis where the shelter treatment was entered as a factor (with two levels) and either the average or the variability of nest / incubation temperatures were considered response variables. The coefficient of variance (CV) was used as a measure for variability temperature. The *Z* values correspond to the nest identity term entered as a repeated measure.

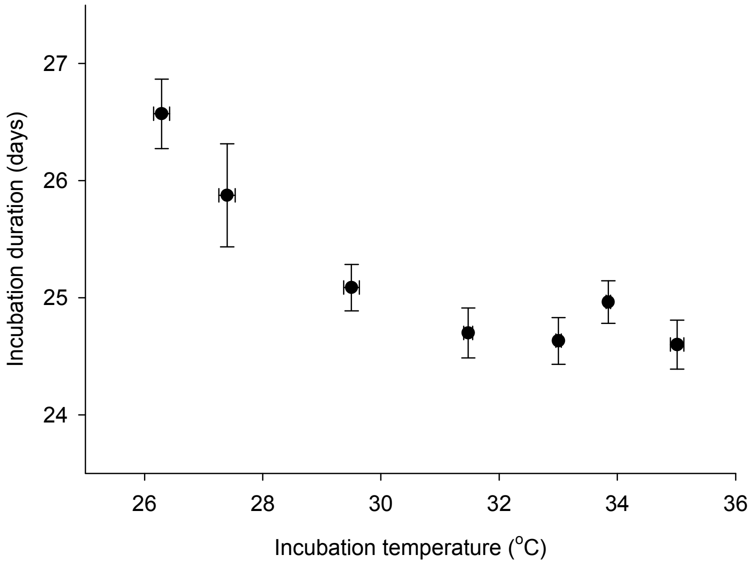
	Artificial shelter	Control	*df*	*F*	*Z*
Nest site temperature					
2004					
Average (°C)	11.71 ± 0.25	11.03 ± 0.18	1, 60.2	4.62*	0.31
Variability (%)	25.25 ± 2.13	30.49 ± 1.49	1, 61.6	4.04*	1.74
2005					
Average (°C)	11.70 ± 0.44	9.9 ± 0.44	1, 35.5	8.10**	-1.20
Variability (%)	51.93 ± 2.14	64.27 ± 4.1	1, 35.7	4.22*	3.09**
Incubation temperature					
2004					
Average (°C)	32.43 ± 0.40	31.37 ± 0.28	1, 62.65	4.73*	0.74
Variability (%)	6.71 ± 0.59	8.28 ± 0.43	1, 69.53	4.19*	-0.21
2005					
Average (°C)	32.35 ± 0.31	31.35 ± 0.32	1, 34.1	6.91*	0.51
Variability (%)	9.35 ± 0.70	11.38 ± 0.70	1, 32.2	3.76	0.16

In 2005 the manipulation was carried out only in exposed nests that laid a similar number of eggs (see Methods). Nests with artificial shelters had higher average and less variable nest-site temperature (Table 3.2) compared with unmanipulated control nests with the same degree of original nest shelter. The artificial shelter also increased the average incubation temperature ($P < 0.05$), and tended to decrease, although not quite statistically significant ($P = 0.06$), the variability of incubation temperature (Table 3.2).

Consequences of nest shelter for incubation performance

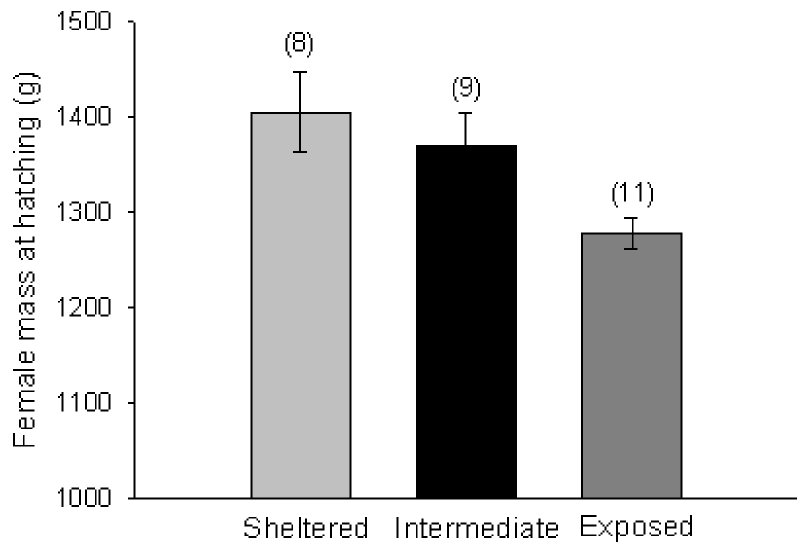
Hatching success was not affected by the natural nest shelter in control nests (effect of shelter: $F_{2,52} = 0.89$, $P = 0.41$; effect of year: $F_{1,52} = 0.50$, $P = 0.48$; no significant interaction). Similarly, hatching success was not affected by the artificial shelter, but in 2005, 53% of the nests successfully hatched their entire clutch compared to only 28% in 2004 (effect of shelter treatment: $F_{1,109} = 0.83$, $P = 0.37$; effect of year: $F_{1,110} = 8.14$, $P < 0.01$, no significant interaction). Among unmanipulated females, incubation duration was shorter when the incubation temperature was high and had little variability (Fig. 3.4). Despite the observed difference in incubation temperature between nests with and without artificial shelter, there was no difference in incubation duration between the artificially sheltered (25.8 ± 0.22 days, $n = 48$) and control nests (25.4 ± 0.32 days, $n = 45$; effect of shelter treatment: $F_{1,90} = 0.53$, $P = 0.46$; effect of year: $F_{1,90} = 0.33$, $P = 0.57$; 21 clutches were abandoned, predated or failed to hatch).

Figure 3.4. Relationship between incubation duration and incubation temperature. Data include the average incubation temperature of 43 (2004) and 32 (2005) control nests. For presentation purposes only, data were grouped according to the 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles of the distribution of average incubation temperatures (in the analysis, incubation temperature was used as a continuous variable). The horizontal error bars represent ± 1 se of incubation temperature within each group; vertical error bars represent ± 1 se of incubation duration within each group. Incubation duration was affected by the average incubation temperature (shown in the figure, $F_{1,58} = 13.6$, $P < 0.01$) and the coefficient of variation in incubation temperature (not shown, $F_{1,58} = 19.7$, $P < 0.001$; effects of clutch size, laying date and year: all $P > 0.1$; repeated measures estimate = 1.37 ± 0.14; $Z = 9.22$, $P < 0.001$). The quadratic term of average incubation temperature was tested, but it was not significant ($F_{1,57} = 1.32$, $P = 0.25$).



In 2005, female body mass at hatching was associated with natural nest shelter; females nesting in exposed nests ended incubation with a lower body mass than females in naturally sheltered nests (Fig. 5). Mass loss during incubation was not related to incubation duration (r_{26}= -0.07, P = 0.71). Early incubation body mass of females of control (naturally exposed) and artificially sheltered nests did not differ (effect of shelter treatment: $F_{1,45}$ = 1.02, P = 0.31, number of days incubated: $F_{1,45}$ = 11.38, P < 0.01). However, control females nesting in exposed nest sites lost a higher percentage of their body mass (33 ± 1.01 %, n = 14) during incubation than did females whose exposed nest had received an artificial shelter (30 ± 1.0 %; n = 14; effect of shelter treatment: $F_{1,26}$ = 6.38, P = 0.02, inter-measurement interval: $F_{1,26}$ = 0.01, P = 0.95).

Figure 3.5. Female body mass at the end of incubation in nests with different shelters (shelter: $F_{2,29}$ = 4.2, P = 0.03; clutch size: $F_{1,28}$ = 0.5, P = 0.5; no significant interaction). The values shown are mean ± 1 se.



Discussion

This study provides evidence that nest-sites with little shelter represent less favourable micro-thermal environments for incubating Common Eiders. Females incubating in less sheltered nest-sites put more effort into incubation, as indicated by their having to incubate for longer and experiencing a higher body mass loss. Despite this increased incubation effort the female cannot entirely buffer their offspring from the less favourable environmental conditions. In less sheltered nest-sites developing embryos experienced lower and more variable incubation temperatures. It is thus apparent from this study that the improved microclimatic conditions provided by well-sheltered nest-sites conferred advantages both to incubating females by allowing energy savings and to their clutches by providing more stable incubation conditions and potentially promoting offspring early development.

Our results showed that well-sheltered nest-sites provided females with higher and steadier temperatures in the immediate surrounding of the nest, but the effect differed between years. Whereas in 2005 nest-site temperature of sheltered nests was always higher than in exposed nests, in 2004 natural shelter had a thermal advantage only in windy conditions. Weather conditions differed in the study area between the two years, with lower ambient temperatures and stronger winds in 2005; these differences were probably responsible for the observed between-year difference in nest-site temperatures. These results suggest a thermal advantage of sheltered over exposed nest-sites, in particular protecting the incubating female against wind chill.

The relationship between ambient temperature and nest attentiveness (or the amount of time in which adult and eggs are in contact, Carey 1980) has been studied in many species (reviewed in Conway and Martin 2000) focussing mainly on the effects of temperature on duration and frequency of incubation recesses. However, to what extent variation in the female's proximate environment can influence her capacity to maintain optimal incubation temperature is still poorly understood. In control nests in our study, irrespective of nest shelter, increased nest site temperature was associated with higher and more constant incubation temperatures. Furthermore, in nests that were provided with artificial shelters, incubation temperature was higher than in control nests.

The large variability and low repeatability of incubation temperature within nests shown by the data could have been caused by methodological problems with the steadiness of the thermistor inside the nest. In this case, it would be inaccurate to say that my measure of incubation temperature would reliably represent incubation conditions experienced by embryos. However, incubation temperature represented a good measure of nest attendance because any changes in temperature would be caused by females moving, standing or leaving the nest. This is supported by the fact that incubation temperature (nest attendance) differed between years, with lower and more variable incubation temperatures in 2005, the year with the more severe weather during incubation. On the other hand, female eiders in exposed nest-sites had a higher incubation effort as reflected by increased body mass loss compared to females in sheltered nest-sites. Hence despite an increased incubation effort, female eiders incubating under less favourable microclimatic conditions were unable or unwilling to completely buffer the embryo against external conditions. This is likely to have consequences for the fitness of both offspring and mother.

Large fluctuations in incubation temperature can retard embryo development, result in extended incubation periods and reduced embryo growth efficiency (Deeming and Ferguson 1991, Wilson and Verbeek 1995, Zicus *et al*. 1995, Hepp *et al.* 2005, Kim and Monaghan 2006, Olson *et al*. 2006). Our data give further support to this idea. I observed that, irrespective of clutch size, at exposed nest sites where the incubation temperature was lower and more variable, incubation period was longer than at sheltered nest sites. The experimentally induced differences in incubation temperature between control and experimental nests were small relative to the natural variation and our test did not have enough power to detect any significant difference in incubation duration between artificially sheltered and control nests. I did, however, not find any effect of incubation conditions on embryo mortality as I did not find differences in hatching success between experimental and control nests or between the two study years. Sub-optimal conditions during incubation can also have long-term consequences on offspring fitness, such as poorer fledgling condition or reduced fecundity (Larsen *et al*. 2003, Gorman and Nager 2004). In contrast, Hanssen *et al.* (2002) proposed that eider females in good condition increase incubation periods to ensure optimal embryo development and more synchronously hatching clutches. Long-term data on post-hatching performance of offspring will be required to evaluate the effects of duration of incubation period and incubation temperature on offspring fitness.

In addition, increased incubation effort (i.e. incubating large clutches or for extended periods) can have consequences for current reproduction (lower hatching success, Thomson *et al*.1998) and for adult survival or future reproduction (Visser and Lessells 2001, Hanssen *et al*. 2005). Females incubating in less favourable climatic conditions generally have to work harder to keep a constant body and incubation temperature, which in turn gives rise to higher energy expenditure (Wiersma and Piersma 1994, Tinbergen and Williams 2002). Female eiders that incubated at low ambient temperatures indeed spent more energy when incubating (Gabrielsen *et al*. 1991) and I found a smaller mass loss in females that incubated in artificially sheltered nests compared to control females. This resulted in females nesting in exposed nest-sites having a lower body mass at hatching than females nesting in sheltered nest-sites and they have less resources to allocate to subsequent offspring care (Erikstad and Tveraa 1995).

The breeding area presented female eiders with a great variety of nest-sites differing in their degree of shelter from weather conditions (Appendix 2). Weather conditions affect nest-site selection in many seabird species (Buckley and Buckley 1980) and our results indicate that protection from the weather has important consequences for nesting Common Eiders. Interestingly, in our study females that laid the largest clutches also nested in the thermally more favourable nest-sites. Several studies have reported that females of better quality chose more favourable nest-sites (e.g. Goodburn 1991, Espie *et al*. 2004, Kim and Monaghan 2005), presumably because these individuals are better in gaining access to them in the first place. Hence, better quality individuals may occupy the more favourable nest-sites leading to a positive association between nest-site quality and reproductive performance. Our data showed that natural nest shelter is associated with clutch size, which has often been linked to female quality in Common Eiders. Females that laid larger clutches have a higher capacity to increase reproductive effort (Hanssen *et al*. 2003), have a higher nest success (Erikstad and Tveraa 1995), have a lower rate of abandonment of ducklings (Erikstad *et al*. 1993) and higher return rates and survival (Yoccoz *et al*. 2002).

In order to properly disentangle the effects of female and nest-site quality on incubation performance, I carried out two slightly different experimental designs. In 2004, females were randomly allocated the artificial shelter or control treatment irrespective of their clutch size. In order to avoid effects of the actual number of eggs being incubated on incubation performance (e.g. Biebach 1984, Jones 1987, Smith 1989, Wiebe and Martin 2000), I experimentally standardised clutch size to four eggs in all nests. The results showed clearly that incubation period and incubation temperature was determined by the nest shelter; I did not find any additional influence of original clutch size as an indicator for female quality on incubation performance. In 2005, I included only exposed nest-sites and so females nesting in control and artificially sheltered nest-sites were of similar quality and had chosen similar nest sites. This allowed the effect of nest-site quality to be tested in a homogenous group of birds. The result of this experiment confirmed the conclusions from the experiment in 2004. Hence, nest-site microclimate has a measurable influence on parental incubation effort and incubation conditions the offspring experience, and I found no evidence that females of presumably better quality can compensate for differences in nest-site quality during incubation (but this can occur when selecting for nest sites).

Sheltered nest sites provided a more favourable microclimate for incubating eider females and therefore natural selection could act on preference for sheltered nest-sites. Better-sheltered nests, however, were not occupied earlier in the season as one could expect if nest shelter was an attribute for which a strong competition exists. To find conclusive evidence for adaptive nest-site preference is often difficult due to the complexity and variety of factors influencing selection for nest-site preference such as parental quality, predation and climate (Lloyd and Martin 2004). Nest predation is the principal cause of nesting failure in most open-nesting species (Martin 1995) and is often regarded as one of the main factors influencing selection on nest-site preference (Cody 1985, Forstmeier and Weiss 2004, Naiwanga et al. 2004). Although only three out of 114 nests predation caused breeding failure due to the active protection of the breeding eiders by the farmers, nest predation may still be a strong selective force on nest-site preference in the areas adjacent to the study farm. Females may trade-off favourable microclimate and protection of the eggs in sheltered nest-sites with her own survival in exposed nest-sites that may provide better visibility of approaching predators (Götmark *et al.* 1995, Wiebe & Martin 1998). Although at the moment our data do not provide conclusive evidence that nest-site microclimate is a determinant of nest-site preference, based on our observations, I propose that variability in microclimate and the low predation risk may favour nest-site preference based on thermal properties of the nest site in this population of Common Eiders. This is in contrast with other studies that concluded that microclimatic selection is unlikely to be an important factor in nest-site preference in ducks (Gloutney and Clark 1997). In future, it will also be necessary to look at additional factors determining nesting success including spatial considerations such as distance to the nearest water (e.g. Clark and Shutler 1999) to understand better the trade-offs that female eiders face when selecting a nest site.

Chapter 4

Plasma corticosterone of birds incubating in nests under different degrees of exposure.

Abstract

During incubation, birds are exposed to various stressful stimuli such as unpredictable climate events. This stressors jeopardise the stability within the organism. A hormonal response forms part of the physiological systems that ensure that homeostasis in attained. In open nesters, one way to ameliorate the stress caused by environmental conditions is to incubate in a sheltered site. Previously it was found that in eiders, sheltered nests provide more favourable thermal conditions for females and lead to lower body mass loss throughout incubation (Chapter 3). In consequence, the aim of this study was to examine whether differences in reproductive effort arising from nest exposure result in differences in plasma corticosterone concentrations of females. Baseline levels of corticosterone were measured for females incubating under different natural conditions of exposure. In addition, an experiment was designed to improve the thermal environment of females nesting in exposed sites, by supplying them with artificial shelters. Nest shelter did not influence CORT levels in either unmanipulated or experimental nests. Hatching success in unmanipulated nests was not affected by hormonal levels. However, in experimental nests, which were located in exposed sites (being occupied by females of lower quality, Chapter 3) higher corticosterone levels were related with lower hatching success. This suggests on one hand, that good quality females can afford high levels of corticosterone without risking reproduction and secondly, that moderated elevations in corticosterone can have positive effects on individual performance by perhaps, increasing aggression and vigilance during a stressful period. Plasma corticosterone seems to be an indicator of physiological condition rather than resulting from differences in habitat quality in this system.

Introduction

Reproduction represents a phase where individuals are most vulnerable and often exposed to various stressful stimuli that can exert a great influence on performance and survival. In order to cope with the stressor that threatens homeostasis in the organism (Wingfield et al. 1997), some physiological systems are activated, this is preceded by a release of glucocorticosteroids into the blood, of which corticosterone is the most common in birds (Wingfield and Farner 1993, Silverin 1989). There is plenty of evidence showing that individuals living in extreme environments or exposed to stressful stimuli present higher levels of circulating corticosterone. This hormonal response ensures an adequate regulation of energy balance in suboptimal conditions (Dallman et al. 1993) and in most cases can be considered adaptive because it promotes survival of individuals but this often is related with ceasing activities that demand high amounts of energy such as reproductive behaviour (Silverin 1986, Wingfield et al. 1998).

Ambient temperature can trigger endocrine events as part of the stress response of organisms; it has been reported that elevations in plasma corticosterone can arise after short or long-term exposure to low temperatures in turkey, pigeon and some passerines (El-Halawani et al 1973, Jeronen et al. 1976, Romero et al. 2000). Birds are physiologically adapted to predictable environmental conditions encountered in any particular stage of their life cycle and certainly it is inappropriate to refer to the stress induced by long-term climate conditions (Wingfield et al. 1997) even when they are extreme. However, in subarctic regions, weather can be harsh and unpredictable, characterized by strong winds, storms and is often below thermal neutrality during the reproductive season, imposing important energetic constraints, increasing reproductive effort (Piersma et al. 2003) and inducing potential stress responses on individuals.

For open-nesters, one way to ameliorate the effect of weather conditions for them is to locate their nests in more insulated areas or places with potential wind breaks or where temperatures are higher and/or less variable (With and Webb 1993; Gloutney and Clark 1997).

The idea that birds select the nest site based on its microclimate in order to diminish potential temperature-induced stress seems apparent but it represents an oversimplified assumption. This is supported by observations made on many birds breeding in cold environments that nest in sites with little or no cover. Apart from providing a good microclimate for incubation, nests must also provide protection against predators for parents and offspring. Predation pressure can influence various reproductive parameters as well as survival in birds (Martin 1995, Martin et al. 2000) accounting for 50% of nest failure in ground nesting birds (Ricklefs 1969).

Certainly, in species with uniparental incubation, physical condition (fat reserves) determines the parental ability to meet the energetic demands of incubation. The physiological condition of individuals is often related with hormonal levels. Birds in poor condition (for example after fasting) generally show increased levels of corticosterone (Kitaysky et al. 1999). In addition, energetic constrains can be size dependent (Shutler et al. 1998), consequently, light individuals can be more susceptible to thermal stress (Gloutney and Clark 1991) and therefore could potentially show a higher endocrine response as a result of deterioration in body condition.

From the literature, it seems evident that not only the exposure to the physical environment and predators, but also the perception of predation risk can lead to chronic stress (Scheuerlein et al. 2001). Despite this knowledge, so far no studies have tested whether variation in nest shelter can induce a stress-response in birds. Therefore, I studied the variation in basal levels of corticosterone of incubating Common Eiders (*Somateria mollissima*) in relation to the level of exposure of the nest. In this capital breeder, females incubate without the help of the males and fast during the incubation period (Korschgen 1977, Parker and Holm 1990), they loose approximately 40% of their initial body mass (Gabrielsen et al. 1991) and show large variation in the quality of their nest sites (Robertson 1995, Kilpi and Lindstrom 1997).

Sheltered nests provide more favourable thermal conditions for females and lead to lower body mass loss throughout incubation (see Chapter 3). I first present correlative data on the concentration of plasma corticosterone of mothers nesting at sites with different degrees of natural shelter. In addition I performed an experiment to test the effect of nest shelter on plasma corticosterone of incubating females. I expect that, as a result of exposure to weather, if the provision of artificial shelters significantly affects the reproductive effort of incubating females then differences in corticosterone levels between females incubating in sheltered and exposed nests will be observed.

Methods

The study was performed during the summer of 2005 at the Reykjanes Peninsula in SW-Iceland. The 45 nests used in this study belong to the same sample reported in Chapter 3. Nests were selected at random from throughout the colony, followed from the building stage and visited every day until the entire clutch hatched (on average after 26 days of first egg laid; Ogilvie 2005). Nest shelter was measured and classified in three categories following the procedure described in Chapter 3 Incubating females were randomly assigned to the unmanipulated (n = 30) and artificial shelter group (n = 15).

Experimental nest shelters

Following the same experimental protocol described in Chapter 3, I provided plastic shelters to nests that were found only in exposed areas of the colony. The reason for not including nests from sheltered zones in the experiment is because nest shelter is associated to female quality (see Chapter 3) and I was interested in testing the effect of nest shelter on the stress-response in an homogeneous sample of females (reducing the potential influence of female condition).

Corticosterone and female measures

Females were caught using a landing net, measured (tarsus, head-bill length and wing) and weighed early in incubation (day 5 ± 2.2 s.d. after the first egg was laid) and again on average at day 23 (± 2.3 days). When females were trapped towards the end of incubation, one blood sample (100 μl) was obtained (within 3 min of trapping which should represent baseline levels of corticosterone) from the brachial vein with a 25 gauge needle, blood was collected in heparinized capillary tubes then centrifuged and the plasma stored at -20°C for subsequent hormone assay. I only obtained one blood sample (at end of incubation) for each incubating female. However, Criscuolo et al. (2005) showed that in Eiders, baseline plasma corticosterone do not change during incubation, therefore a single sample should be representative of the baseline circulating corticosterone throughout incubation. Because it was not possible to catch all the females exactly at the same stage of incubation the number of days elapsed from the start of incubation (day when the fourth egg was laid) to the moment of capture were considered as covariates in the analysis. Female mass loss between early incubation and day 26 of incubation was expressed as the percentage of the body mass in early incubation

Hormone analysis

Corticosterone (CORT) concentrations were measured after extraction of 20μl aliquots of plasma in diethyl ether, by radioimmunoassay (Wingfield, 1994; Maddocks, Goldsmith, and Cuthill, 2001; Spencer et al., 2003) using anticorticosterone antiserum code B3-163 (Esoterix, USA) and [1,2,6,7-3H]-corticosterone label (Amersham, U.K.). Two birds, out of a total of 45, showed corticosterone levels below the detection limit for this assay, in another case the female was bled after 3 min of being caught and the results were excluded from the analyses. Final sample sizes are 28 females in the unmanipulated and 14 in the artificial shelter group. The extraction efficiency was 75-90%. The assay was run with 50% binding at 1.42ng/ml, and the detection limit for 7.3ul aliquots of extracted plasma was 0.16ng/ml. All samples were run in duplicate in a single assay.

Statistical analysis

Since values of plasma corticosterone were not normally distributed (Kolmogorov–Smirnov test, $P<0.05$) data were log-transformed ($P=0.20$) prior to using parametric tests. Figures show non-transformed data unless otherwise stated. To test the effect of nest shelter on CORT levels I performed analyses of covariance (ANCOVA) including female body mass and the number of days elapsed since the start of incubation (incubation day) as covariates. Because avian endocrine response can be influenced by circadian rhythms (Joseph and Meier 1973), I included time of day when blood sampling was performed, as a factor with two levels (1=AM, 2=PM). I performed stepwise modelling based on F-test using type III sum of squares for model determination and factor elimination. The significance of these terms was tested by means of stepwise backward elimination, starting with a full model and sequentially dropping the least significant term.

Incubation duration was calculated as the time elapsed from the start of incubation until the first egg hatched. In order to have a single measure of female structural size I ran a PCA analysis on the three body size measurements and the first principal component that explained 63% of variance was taken as a measure of body size. Female condition was then estimated using the residuals of a regression between female initial mass and size.

Hatching success was considered as the proportion of eggs hatched in a clutch and analysed using generalised linear models with binomial error structure and logit link function (R V.3.2.1) following Crawley (2002). The significance of terms is assessed on the basis of changes in deviance (which approximates a chi-squared distribution). Values are means ± standard deviation.

Results

Mass loss at the time of trapping explained 47% of the variability of corticosterone levels with females that lost more weight showing lower concentrations of corticosterone (Table 4.1; Fig 4.1). Similarly, CORT levels were influenced positively by the number of days elapsed in the incubation period (Table 4.1). The time of day in which females were trapped, body condition, clutch size, incubation length, and time from blood sampling until hatching did not contribute significantly to variation in plasma concentrations of CORT and were dropped from the final model (Table 4.1).

Females incubating in nests with different levels of exposure did not show differences in levels of plasma CORT (Table 4.1). Variation in CORT levels of females in exposed (Coefficient of variation CV = 83%) and well-sheltered nests (CV = 118%) was larger than that of females in intermediate-shelter nests (CV = 34%) but differences were not significant (Levene's test $F_{2,25} = 1.5$, p = 0.24) (Fig 4.2). Similarly, hatching success was not related to CORT concentrations or degree of nest exposure (total scaled deviance = 23.79, df = 27; change in deviance: CORT = 1.11, df = 1, p = 0.29; shelter = 0.26, df = 1, p = 0.61).

Table 4.1 The effect of mass loss and incubation progression on corticosterone levels of females incubating in unmanipulated nests.

Source	**Type III**	**df**	***F***	**Sig.**	β
Intercept	1.528	1	16.41	<0.001	2.434
Days incubating	0.413	1	4.46	0.045	0.065
Mass loss	2.765	1	29.69	<0.001	-11.307
Error	2.327	25			
Corrected total	5.241	27			
Adjusted R^2=0.52					
removed from model					
Shelter	0.351	2,23	2.04	0.15	
Body condition	0.084	1,22	0.98	0.33	
Shelter*mass loss	0.162	2,20	0.93	0.40	
Clutch size	0.044	1,19	0.49	0.49	
Days until hatching	0.012	1,18	0.13	0.72	
Time trapped	0.014	1,17	0.14	0.70	

Experimental shelters

The original clutch size and initial body mass did not differ significantly among females of the unmanipulated exposed and experimental shelter groups (clutch size: t_{23} = -1.49, p = 0.15; body mass: t_{23} = 1.02, p = 0.31). As with unmanipulated nests, the effect mass loss during incubation on CORT levels was significant (final model: $F_{1,23}$ = 6.28, p = 0.02). The addition of artificial shelters did not result in significant differences in average plasma CORT between unmanipulated and artificially sheltered females ($F_{1,19}$ = 1.45, p = 0.24;interaction between treatment and mass loss $F_{1,20}$ = 0.18, p = 0.67; terms dropped from the model). Similarly, time of day, clutch size, days until hatching and incubation day did not affect plasma concentrations significantly (time of day: $F_{1,22}$ = 2.60, p = 0.11; clutch size $F_{1,21}$ = 1.02, p= 0.32; days until hatching $F_{1,18}$ = 0.11, p = 0.74; incubation day: $F_{1,17}$ = 0.17, p = 0.68; terms dropped from the model).

Interestingly and in contrast with what was found in unmanipulated nests, hatching success was influenced by the baseline levels of CORT levels regardless of the shelter treatment; so that females that showed higher levels of corticosterone hatched a smaller proportion of eggs (total scaled deviance = 22.11, df = 24; change in deviance: CORT = 6.06, df = 1, p = 0.01; treatment = 0.05, df = 1, p = 0.82; Fig 4.4).

Figure 4.1. Baseline corticosterone levels in relation to female body mass loss during incubation in unmanipulated nests. Estimates of the linear regression are: r = 0.69, p < 0.001; corticosterone = 3.242+ -0.088 (mass loss).

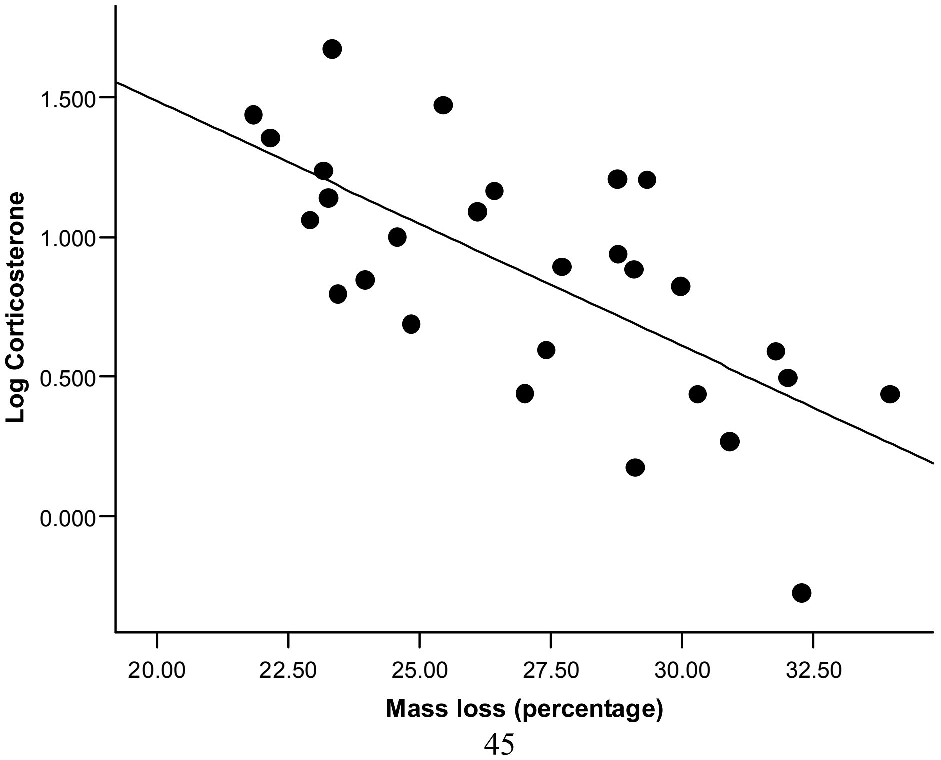


Figure 4.2 Concentration of baseline corticosterone of female incubating in unmanipulated nests with different degrees of shelter. Mean values ± 1SD of CORT for the three nest shelter groups are: exposed nests (11) = 13.87 ± 11.56 ng/ml, intermediate (n=9) = 10.99 ± 3.78ng/ml; and well-sheltered (8) = 5.59 ± 6.62 ng/ml.

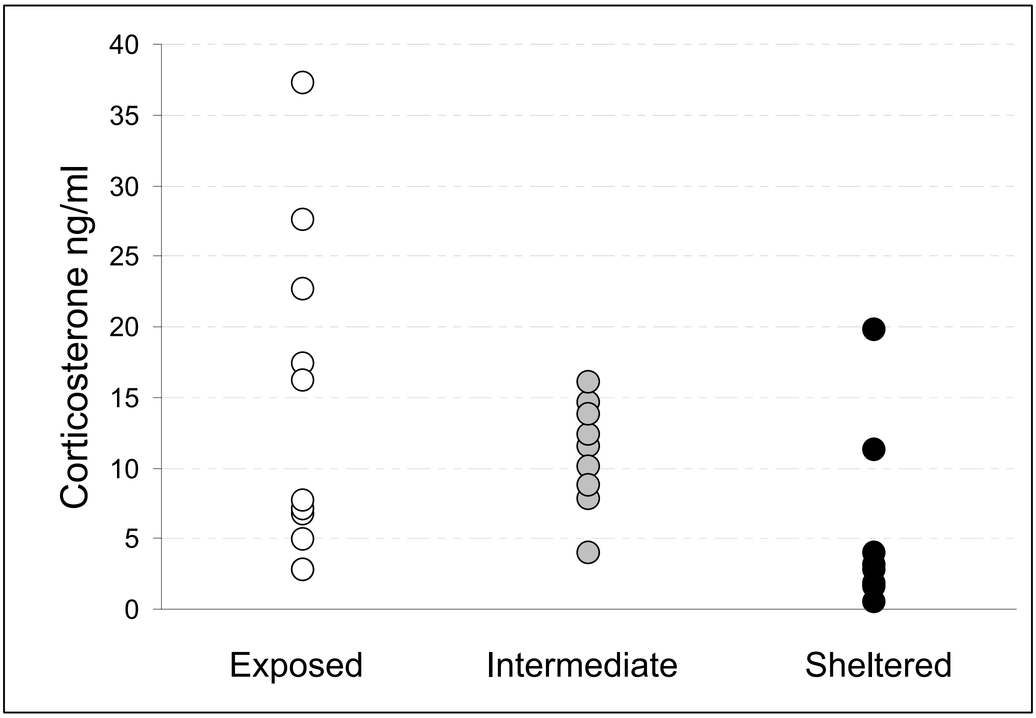


Figure 4.3 Average corticosterone levels of females incubating in unmanipulated exposed nests (n=11) and exposed nests provided with plastic shelters (n=14).

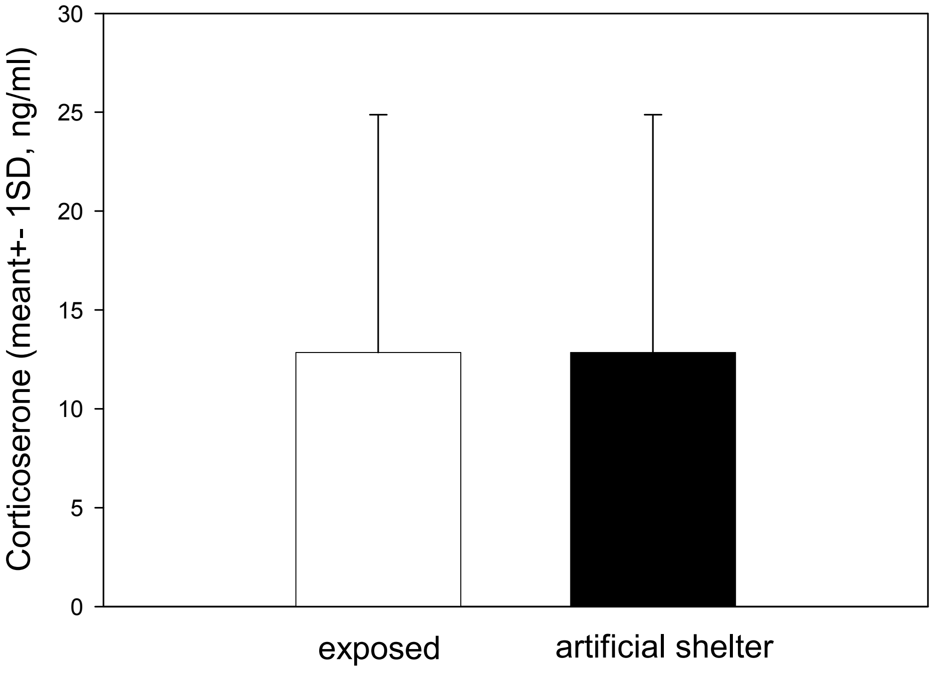
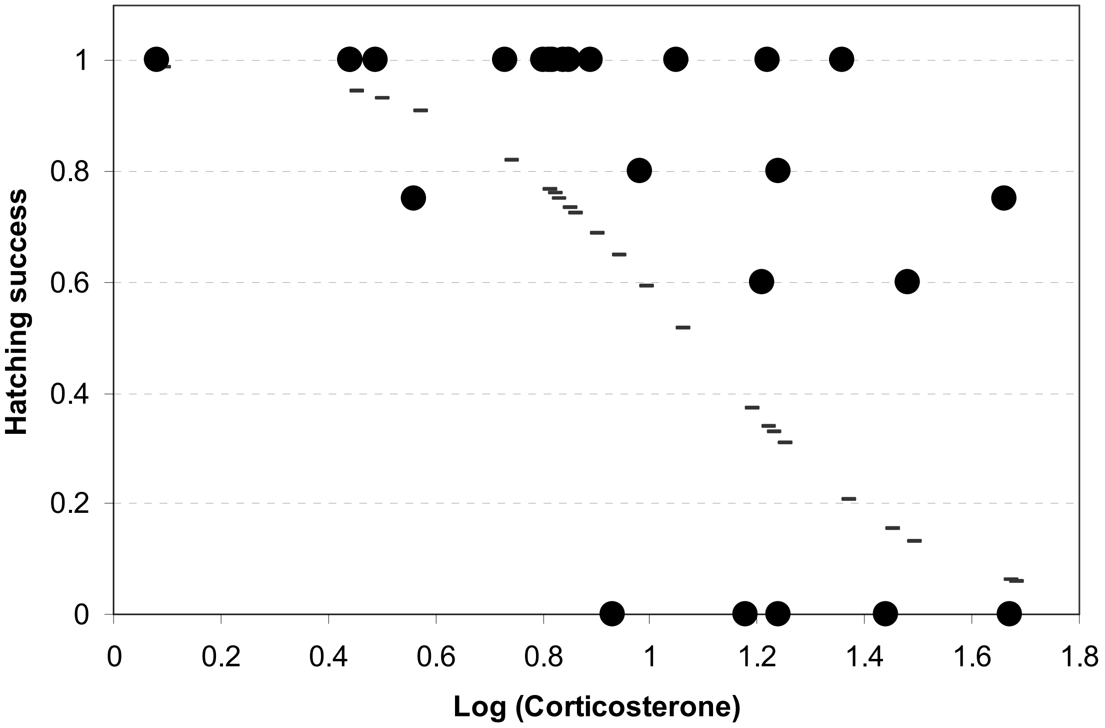


Figure 4.4 Hatching success (proportion of eggs hatched in a clutch) in relation to (Log)CORT levels of experimental nests. The black circles show observed data points, the small squares show predicted values obtained from the logistic regression.



Discussion.

This is the first study of variation in corticosterone levels in relation to nest microclimate in a fasting bird. Previously it was shown (Chapter 3) that nest shelter can influence reproductive effort, with females that nest in exposed nests undergoing a higher body mass loss as a result of experiencing lower and less constant temperatures. In this study I expected that differences in reproductive effort arising from nest exposure would result in differences in plasma corticosterone concentrations of incubating females. Indeed, these differences in female mass loss were reflected in the baseline levels of plasma corticosterone. These results contrast with findings from another study on the Common Eider (Criscuolo et al. 2005) where it was shown that corticosterone was not related with the decrease in body mass during incubation. Cherel et al. (1988) showed that plasma corticosterone rises only after birds reach an extreme deterioration of body condition. It has been shown that the relationship between physiological condition, fitness costs and baseline corticosterone does not follow a linear trend (Cherel et al. 1988), For example, recently Brown et al. (2005) showed that there are survival costs associated with both high and low levels of corticosterone so that intermediate levels are favoured. Elevated levels of corticosterone in general have been associated with deterioration in body condition (Kitaysky et al. 1999, Walker et al. 2004) and deleterious physiological effects that affect survival (p.e. immunosuppression; Saino et al. 2003). However, moderated elevations in corticosterone can have short-term positive effects on survival by increasing aggression and food intake during a stressful period (Kitaysky et al. 2003).

On the other hand, Hanssen et al. (2003) proposed that only good quality females (laying larger clutches) are able to compensate for changes in reproductive effort by reducing or increasing body mass loss during incubation. It is possible that in my study, only females in good condition invest more during incubation (higher mass loss) and can afford having elevated corticosterone, while being more able to deal with environmental stress or more capable to cope with predation pressure without incurring in reproductive costs.

Nest shelter did not influence CORT levels in either unmanipulated or experimental nests. It is possible, on one hand, that the increased exposure to weather conditions in unsheltered nests was not sufficient to lead birds to result in a marked stress response. On the other hand, in my study, females did not reach a deteriorated state such as that described by Criscuolo et al. (2002), where a marked hormonal response was seen. Because in fasting birds corticosterone is associated with reproductive failure when lipid reserves are depleted (Pereyra and Wingfield 2003), it seems logical to think that in order to increase their chances of reproductive success, female eiders downregulate their adrenocortical response to stressful stimuli (Love et al. 2004) to avoid high levels of corticosterone and the associated enhanced protein catabolism (Cherel et al. 1988).

I found that hatching success in unmanipulated nests was not influenced by hormonal levels, However, in experimental nests, which were located in exposed sites (being occupied by females of lower quality, Chapter 3), females with higher CORT levels were less successful at hatching eggs. It is possible that failure was caused by lower attentiveness in stressed females. This contrasting result could reflect differences in strategies to cope with stress among individuals. Individuals differ in physiology these differences can be associated with behavioural responses to stressful situations (Korte et al. 2005). Whereas good quality females can afford high levels of corticosterone without risking reproduction, lower quality individuals can be more susceptible to stress and incapable to counterbalance the negative fitness consequences of elevated corticosterone by increasing reproductive effort.

In conclusion, plasma corticosterone seems to be an indicator of physiological condition rather than resulting from differences in habitat quality. Female eiders seem to be well protected from the impact of physiological extremes but individual condition plays an important role in determining the outcome of stress.

Chapter 5

Nest maintenance by female Common Eiders in response to experimental reduction of the nest lining.

Abstract

It has been shown that by building and maintaining a nest in optimal thermal condition, birds can reduce the energetic demands of incubation and regulate the nest microclimate more effectively. Common Eider females rely on body reserves for egg production and incubation. Conserving energy during this phase is important for reproduction, in this context, a well-insulated nest is potentially of great significance for reproduction and survival. However, at the moment, it is unknown whether nest maintenance occurs in this species and if females are able or willing to replenish down lost during incubation. By experimentally removing the nest lining during incubation I examined if when nest insulation deteriorates, female eiders supplement the amount of down they put in the nest. Females in nests where down was removed did not replace it. However, in nests with deteriorated insulation, a proportionally larger amount of various non-feather materials were added by females in comparison with control nests. The fact that missing down was not replaced by females suggests the existence of functional and physiological constrains in eiders on plucking body feathers to line the nest with. On the other hand, the addition some non-feather materials to the nest lining when the down was removed could help preserve the thermal properties of the nest. Because females used only non-feather materials available in the near proximity of the nest, collecting nest materials could represent an inexpensive way to cope with deterioration in nest insulation.

Introduction

In breeding birds, the location and structure of the nest can have important fitness consequences, potentially providing shelter from both the physical environment and from biotic factors such as predators (Dow and Fredga 1985, Yerkes 1998, Hansell and Deeming 2002). The amount of energy that incubating parents need to expend in order to maintain incubation temperature varies with the magnitude of heat loss from the eggs, nest and body of the incubating parent. Accordingly, by choosing and/or building a nest with good thermal properties and maintaining it in optimal condition, birds can reduce the energetic demands of incubation (Rauter and Reyer 2000, Hilton et al. 2004) and regulate the nest microclimate more effectively (Drent 1975; Reid, Monaghan and Ruxton 2000). Thus, from an energetic viewpoint, nest building and maintenance are likely to be particularly important for species breeding in cold and/or exposed environments due to the high energetic requirements of incubation under such conditions (Piersma et al. 2003).

Amongst the nest materials commonly used by birds, down feathers have been shown to have particularly good insulating properties (Hilton et al. 2004). When present as a nest lining, they improve the efficiency of incubation (White and Kinney 1974a, Drent 1975) and offspring survival (Winkler 1993). In this context, studies in geese and ducks of the use and importance of feathers as nest lining are particularly interesting because, in order to insulate their nests, down feathers are plucked by the female from her breast area to line the nest cup (Lea and Klandorf 2002). To maintain the thermal properties of the nest, parents may also need to replenish feathers lost from the lining during incubation. For example, Canada geese (*Branta canadiensis*) continuously pluck feathers from their bellies to replace the down that has been blown off by the wind (Cooper 1978). Since these feathers are important for retention of body heat, there is a potential trade-off between maternal and nest insulation; the need to invest constantly in nest insulation might represent a conflict for the parent, especially if plucking feathers results in naked skin areas that are energetically costly to maintain (Haftorn and Reinerstein 1985), which is particularly the case for smaller individuals (Jónsson et al. 2006).

In the common eider (*Somateria mollissima*) incubation is known to be energetically demanding (Gabrielsen et al. 1991, Erikstad and Tveraa 1995). In this species, conserving energy during incubation is especially important because females do not feed for approximately 26 days and thus they rely on body reserves to meet the requirements of incubation (Erikstad et al. 1993, Hanssen et al. 2003). A well-insulated nest is therefore likely to be very important. Like most ducks, eider females line their nest with down feathers plucked from the breast and abdomen (Palmer 1976). Little is still known about whether nest maintenance occurs in this species and whether females are able or willing to replenish down lost during incubation. By experimentally reducing the nest lining after its construction at various points during incubation I examined if when nest insulation deteriorates, female eiders supplement the amount of down they put in the nest.

Methods

This study was performed from May to July 2004 in the Reykjanes Peninsula in SW-Iceland. Every year ca. 2000 pairs nests of the common eider nest in an area that is fenced as a farm; local people harvest the eider down at the end of the incubation period for commercial purposes. Nesting birds in the colony are accustomed to close and regular presence of the farmers. Hence, any extra disturbance caused by our visits is likely to be minimal. Cold winters with snow cover and summers with cool air temperatures and strong winds characterize the study area. In 2004 the average daily air temperature from May to end of June was 8.3 ^{o}C (±2.8 ^{o}C SD; min-max 1^{o} to 12^{o}C). Wind speed averaged 21 km/hr (max. speed 57 km/hr; annual variation 19.2 km/hr).

The study area was monitored every day in search of new nests. A total of 60 nests were randomly selected from throughout the colony. Nests were included in the sample when the first laid egg in a fresh nest was found and then the nest was randomly assigned to the control or experimental group.

For each nest in the sample, I recorded the laying and hatching date of all eggs. In control nests the entire lining of the nests was collected at the end of incubation to quantify its composition, and for experimental nests also to see whether it had been restored following partial removal (see below). The lining was separated into down and other non-feather components (hereafter "NF-materials"). NF-materials were identified and weighed to the nearest 0.01g with a digital balance. The down was allowed to dry completely in the laboratory before being weighed.

Experimental procedure

The experimental manipulations involved the removal of half of the nest lining three times throughout incubation in a group of 20 nests. The removals took place during early- (day 5-6; day 1 is the day the first egg was laid), mid- (day 12-13) and late (day 19-20) incubation. To ensure that a homogeneous sample was removed, the whole nest lining was first taken out of the nest, mixed and separated into two equal parts; one part was immediately returned to the nest and the other processed in the laboratory. In control nests (n=35), no lining was removed during incubation, but the nest material was mixed in the same way and with the same frequency as in experimental nests.

All of the remaining lining material in both experimental and control nests was collected at the end of incubation. In order to reduce the potential effect of clutch size on the amount of down put into the nest by the female, the incubated clutch was standardized to the median clutch size of 4 eggs (mean clutch size in our study was 3.9 ± 1.0 eggs; mean ± 1SD), by adding or removing extra eggs no later than two days after the third egg of the original clutch was laid. Contiguous nests (not included in the study) with similar laying dates as the study nests were used as a source of extra eggs or as host nests for removed eggs. Eggs were added to 14 and 6 nests and removed from 4 and 1 nest in the control and experimental groups respectively. The original clutch size and laying date did not differ between control and experimental nests (clutch size $t = 0.36$, $p = 0.72$; laying date $t = 0.60$, $p = 0.54$).

For the removal group, a repeated measures ANOVA was used to analyse the changes in mass of the components of the nest lining throughout incubation. I analysed the proportion of eggs hatching per clutch with a GLM with binomial errors and logit link. The number of eggs hatching was used as the response variable, with clutch size as the binomial denominator (Crawley 2002). All statistical tests are two tailed and the criterion of significance is $P < 0.05$.

Five out of the 60 nests were omitted from the analyses because it was not possible to obtain and/or weigh all the down when the nest was predated or when the nest was abandoned; in both cases the down was lost to the wind.

Results

In terms of volume, the unmanipulated nest lining typically comprised over 90% down. In 92% of the control nests, only a single type of non-feather material was recorded. The principal non-feather materials present were moss (13% of nests in the control group), grass (50%), brown algae (20%) and pieces of wood (8%). However, because these non-feather materials are much heavier than down feathers, they represented on average 60% (± 12% SD) of the total mass of the nest lining. Females put on average 28g (± 2.07 g, n=35) of down in the nests.

We expected females to replace the missing down feathers in nests where I repeatedly removed half of the lining throughout incubation, and hence larger total masses of down to have been put into these nests compared to control nests. However, this was not the case. The experimental females did not replace the removed down and hence the total amount of feathers put into the nest did not differ between control and experimental nests (including the mass taken in the removals; $F_{1,53}$= 2.46, p = 0.12; Fig 5.1). However in the experimental nests, the amount of non-feather materials per gram of down increased throughout the incubation (repeated measures ANOVA $F_{3,17}$ = 33.4, p < 0.001, Fig 5.2). Thus some NF material was added. Therefore, the overall composition of lining material collected differed between control and experimental nests: in nests where the down was removed repeatedly a higher percentage (69.66 ± 7.34% vs. 60.72 ± 12.2% in control nests) of the material was non-feather ($F_{1,53}$= 5.13, p = 0.025).

A higher proportion of eggs hatched in the unmanipulated nests (0.82± 0.31 SD) compared with the down removal group (0.66± 0.41 SD), but this difference was not significant (ΔD = 6.95, df = 1 adjustment for over dispersion F= 2.69 p = 0.10). No significant differences in incubation length between control and removed down were found (t= 0.29, p = 0.76, n = 46).

Discussion

Given the harshness of the local conditions and thus the likely importance of nest insulation, our prediction was that when nest insulation deteriorated due to down loss during incubation, female eiders would compensate by adding further down. However, this was not the case. Additional down was not added to the experimental nests. While, some additional non-feather material was added, the down at the end of incubation in the removal group was generally around 30% of the original lining, compared to approximately 40% in the control group.

Observations made on 145 incubating females from this colony, captured at different times during incubation, (D'Alba, unpublished data) suggest that females should have enough body down throughout incubation to be plucked in order to insulate the nest. Hence, the fact that female eiders did not replenish the nest with extra down after the removals results paradoxical. Adding more down might be energetically demanding because new down would have to be plucked from the belly and this could have negative physiological effects on the female. These costs associated with plucking feathers would increase if the time required for down feathers to re-grow prior to migration was insufficient. This speculation needs experimental testing in future studies. In general, little is known about the costs of nest building for birds (Hansell and Deeming 2002). Fargallo et al. (2001) were able to show, for the Chinstrap Penguin, that high investment in the maintenance of the thermal properties of the nest (which involves gathering nest material) can result in decreased parental health status (indicated by haematological measures). In Eiders, however, nest construction and maintenance depend to a lesser degree on collecting material from the surroundings. There may be functional and physiological constrains in eiders on plucking body feathers. This could vary in relation to age, body condition and individual susceptibility to the severity of the weather.

The incorporation of some additional non-feather materials to the nest lining when the down was removed could have a functional basis: by concealing the clutch throughout incubation with a dense mass of nest materials mothers could minimize the risk of detection by predators during incubation recesses (Hansell 1996). On the other hand, such materials could help preserve the thermal properties of the nest. Grass and moss, for example, can help avoid heat loss in the nest; given that nest insulation can help enhance offspring survival (Collias and Collias 1984), in the absence of down, provisioning nests with non-feather materials could represent different solutions to the same problem of regulating the microclimate of incubation (Hilton et al. 2004) and potentially increasing offspring survival over what it would have been, had no additional material been added. This is supported by the fact that no effect of down removal on hatching success was found. It is possible is that when females are present in the nest, the down does not confer any advantage for the clutch in terms of the maintenance of optimal incubation conditions. This would be possible if when any deterioration of nest insulation occurs females are capable to compensate for any thermal deficiency by regulating heat production (See Chapter 6).

The type of materials added to the nest by females in our study was determined by the kind of substrate in the area where the nest was located, suggesting that females use what is available in the close proximity rather than spending time looking for specific components in other areas. Hence, in terms of time, collecting nest materials could represent an inexpensive way to cope with deterioration in nest insulation.

Fig. 5.1 Total amount of down contained in (excluding non-feather materials) in control (n=35) and experimental nests (n = 20). Values presented are mean ± 95%CI. The different colours represented in the repeated removal group refer to the mass of down obtained at different times throughout incubation.

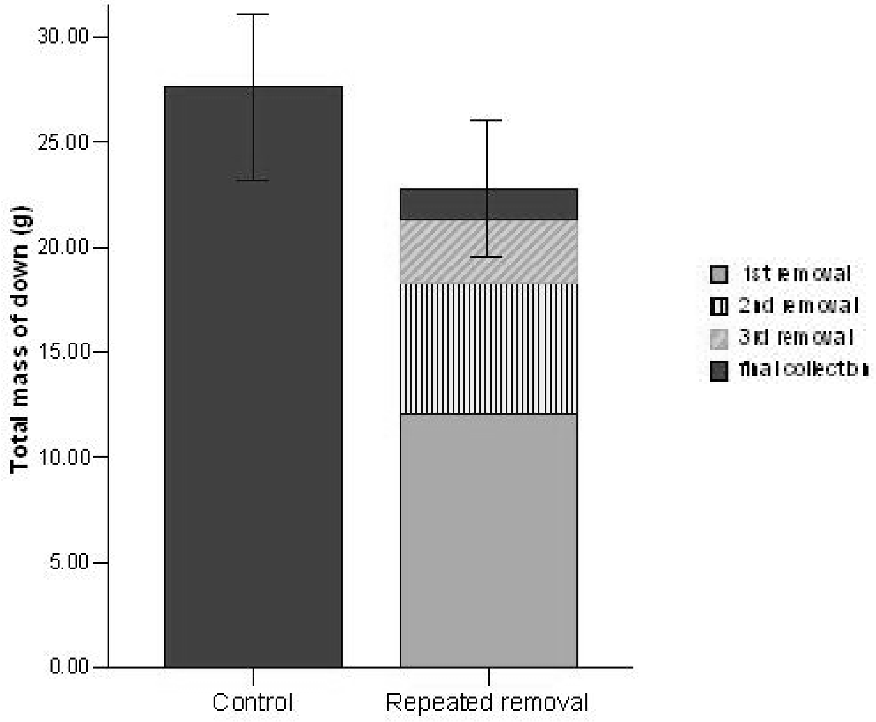
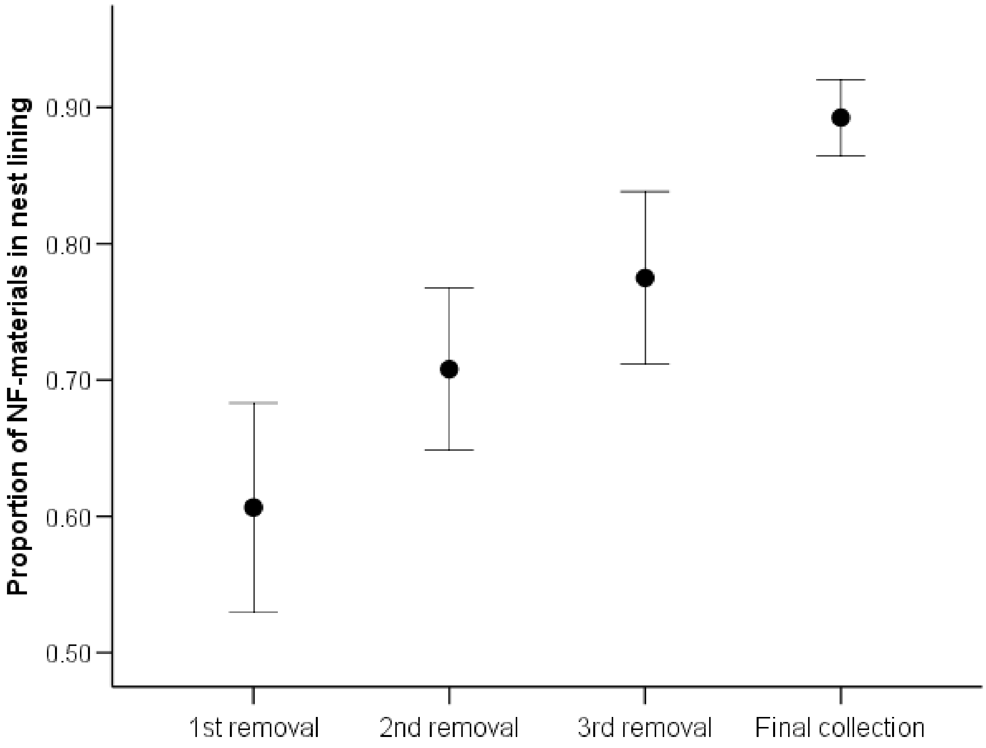


Fig. 5.2 Change in composition of the nest lining during incubation in nests where lining was repeatedly removed (n = 20). Values presented are mean ± 1SE



Chapter 6

The function of Down in Common Eider nests

Abstract

The avian nest must provide the basic needs of eggs and chicks for security and microclimate conditions, its site and structure have an important role in maintaining a suitable incubation environment. In open-nester birds, the maintenance of nest temperature within optimal ranges for development can be energetically demanding since heat is rapidly lost from the nest and its contents, especially for species inhabiting harsh environments. The Common Eider, as other ducks and geese species, line their nests with down feathers, which are among the best insulating materials used by birds in nest construction. Nevertheless, the influence of the amount of down on the microclimate conditions of incubation and reproductive performance has not been investigated so far. In a combination of experimental and correlational methods I examined 1) if variation in the amount of down in nests is related to breeding circumstances (female condition, timing of breeding, degree of exposure of the nest site) and 2) the effect of nest insulation on nest temperature and humidity. Manipulations of the amount of down consisted in the year 2004 on the removal to half the nest material, in 2005: a) the reduction of the amount of down "poor insulation group", b) the addition of down "good insulation group". The results showed that females that nest in well-sheltered nests insulate the nest better (put more down). The deterioration of nest insulation (removal of nest lining or artificial poor insulation) did not result in lower average incubation temperature although it resulted in more variable temperature. From the removal experiments in both years it was evident that, despite the unchanging incubation temperature, decreases in the amount of down in the nest resulted in increased nest humidity. No evident effects of nest insulation on hatching success were found. It was clear that down in the nest contributed to more stable incubation conditions, however, females were able to counterbalance poor nest insulation and keep incubation temperature constant but the costs of doing this are still unclear.

Introduction

Avian nest structure is an elaborate trait that has evolved to meet some of the needs arising during incubation, such as protection from the physical environment and from predators (Hansell and Deeming 2002). Successful embryo growth and development require a relatively narrow range of incubation conditions (Drent 1975, Webb 1987). Since it is energetically costly for parents to keep these conditions within acceptable limits (Williams 1996, Bryan and Bryant 1999), constructing a well-insulated nest can help meet these demands more effectively. Nest insulation is therefore a component of nest structure likely to be of considerable importance, especially for species inhabiting harsh environments where rapid heat loss can occur from both the parental body and from the nest and its contents (Collias and Collias 1984, Hansell 2000).

Parents can reduce heat loss from the nest by lining it with an appropriate material. Feathers have excellent insulating properties, in a study comparing the insulating properties of common nest materials, Hilton et al. (2004) found the lowest cooling rates for eggs covered by down feathers. When present as a lining, feathers can reduce the costs of incubation (White and Kinney 1974b; Drent 1975; Hilton et al. 2004). The thermal benefits of the use of feathers in nests of birds breeding in cold environments has been substantially documented (Collias and Collias 1984; Hanssell 1995) and combined with the idea that down lining of avian nests has often been assumed to be beneficial in terms of improved energy budgets of parents requires direct evaluation. However this hypothesis has never been tested experimentally.

A number of experimental studies have found negative consequences of changing the feather content of the nest for offspring development and/or parental behaviour. Removal of feather lining from Barn Swallow nests (*Hirundo rustica*) increased the cooling rate of eggs and prolonged the incubation period (Møller 1991). In the Tree Swallow (*Tachycineta bicolour*), the same treatment resulted in lower chick growth and higher nest infestation by ectoparasites (Winkler 1993). Removal of feathers from the nests of Village Weavers (*Ploceus cucullatus*) resulted in higher nest attendance by the incubating female, and so reduced her time available for foraging (Collias and Collias 1984). In contrast, changing the amount of feathers in Long-Tailed Tit (*Aegithalos caudatus*) nests did not affect the quality of nest insulation (McGowan et al. 2004).

Waterfowl breeding in cold environments line their nests with down feathers that females pluck from their breast and belly areas (Caldwell and Cornwell 1975, McCracken et al. 1997, Carey 2002). In contrast to most birds that develop brood patches by defeathering, female ducks and geese also pluck down feathers from their breasts and ventral regions to line their nests (Hanson 1962). However, plucking feathers may have negative effects on the female's own thermal costs since this may increase loss of body heat, and thus females may be limited in the amount of down that they are able or willing to provide for nest insulation. Hence, it could be hypothesized that females of small size or in poor body condition would be less able to invest in nest insulation, however, the relationship between female condition and nest lining have not yet been investigated at a within-species level.

The nest of the Common Eider is lined by approximately 28g of down but there is large variation among females (Chapter 5). This species, as most Anseriformes, does not form a complete brood patch and down feathers are plucked from the breasts and abdomen by the female in order to insulate the nest (Palmer 1976). So far there is no evidence that female Eiders line their nests with down other than that they pluck from their own body (D'Alba pers. obs.). In this study I address the following questions in a combination of experimental and correlational methods: **1)** Is variation in the amount of down in nests related to breeding circumstances (female condition, timing of breeding or the degree of exposure of the nest site? **2)** Does a nest insulation (amount of down) influence the microclimate conditions?. The prediction being that better insulation (larger amounts of down) provide more stable nest temperature and humidity. **3)** Do Eider females benefit from having well insulated nests by losing less mass during incubation or increasing the hatching success of the clutch?

Methods

Study area and general protocol

This study was performed in a breeding colony of the Common Eider (*Somateria mollissima*) situated in the municipality of Reykjanesbær, SW Iceland (64°01'3" N, 22° 42' 27"W) from May to July 2004 and 2005. The area is characterized by cold winters with snow cover and summers with cool air temperatures and strong winds. In 2004, the average air temperature from May to the end of July was 11.4 °C (±2.3 °C SD.; min-max 1 to 14°C) in 2005 the average temperature was 9.06 °C (±2.7 °C SD.; min-max 2.7 to 14.2°C). Wind speed averaged 20.4 km/h (max. speed 66 km/h; annual variation 19.2 km/h) and 21.9 (max. speed: 62km/h; annual variation: 17.5 km/h) in 2004 and 2005 respectively. The study colony of ca. 2000 breeding pairs is located in a farm where local people harvest the down from the nests at the end of the incubation period for commercial purposes. The colony was monitored every day in search of new nests. A total of 140 nests from both years were randomly selected from throughout the colony. Nests were included in the sample when the first egg was laid and then nests were alternately assigned to the control (n=80) or experimental (n=60) group.

For each study nest, I recorded the laying and hatching date of all eggs in the clutch, the fresh egg mass (eggs weighed within 24 h of being laid) and egg mass at the end of incubation (day 24 of incubation, hereafter "final egg mass"). This was done to obtain the mass loss of eggs during incubation, which can reflects the respiratory gas composition of the nest (and in turn regulates embryo development; Ar and Sidis 2002). The nest was visited everyday, on the day they were found new eggs were marked according to laying sequence with non-toxic markers. All of the down lining from the nests was collected at the end of incubation and thoroughly cleaned (other nest materials removed) and allowed to dry in the laboratory at room temperature. In all nests the nest lining was composed primarily of down feathers; other materials included moss, grass and brown algae. The down was weighed to the nearest 0.01g with a digital balance.

Microclimate of incubation.

During incubation, continuous measures of temperature and humidity were taken inside the nest using one thermistor (-25 to 85°C) and one humidity meter (0-100% relative humidity) per nest connected to TinyTag data loggers (Gemini, UK Ltd, Chichester, UK). The thermistor was placed in the centre of the nest (incubation temperature) and secured to the ground so it could not be moved. The humidity sensor was integral to the TinyTag. In order to record humidity in the nest, the TinyTag was introduced in a small hole dug in the ground underneath the nest in such a way that the sensor protruded 2cm from the floor level within the nest cup. For each nest I recorded the temperature and humidity starting at 1300 h with one-minute intervals during 22 hours after which the loggers were moved to another nest. The mean and variability of (Coefficient of variation) nest temperature and humidity over each 22h period are included in the analyses of microclimate. A total of three measurements of incubation temperature and humidity (RH) for each of the 140 nests were taken in early (within day 4 to 9 of first egg being laid), mid- (day 10 to 18) and late incubation (day 19-26).

Two components of nest structure were measured for all nests: a) nest volume (mm^3), estimated using the formula: volume= $2/3 * \pi * r^2 * h$ where r is the radius of the nest circumference and h is the depth of the nest cup, b) nest shelter, assessed (as described in Chapter 2) by measuring the height of plants or rocks surrounding the nest and the percentage of the nest circumference covered by surrounding vegetation and/or rocks within a 0.5 m radius of the nest cup. The

PCA factor 1 of nest shelter showed a trimodal distribution (Chapter 2). Therefore, the degree of nest exposure was classified as: sheltered nests, intermediate and exposed nests. Previously I showed that female Eiders gain thermal and energetic benefits from incubating in sheltered nests (Chapter 2).

Incubation in the Common Eider starts from day 2 to 4 after the first egg is laid (Hanssen et al. 2002). I considered the start of incubation as the day on which the fourth egg was laid. Incubation duration was calculated as the time elapsed from the start of incubation until the first egg hatched. Mass loss of the clutch was calculated as the average of mass loss of each egg in the clutch. Hatching success of the clutch was estimated as the proportion of incubated eggs that hatched.

Experimental procedure.

The experimental manipulations in both years involved the addition or removal of part of the down lining. Since no additional down is added by the female after the last egg is laid, (Chapter 5) in all cases the down was added or removed within 48h after clutch completion. In unmanipulated nests, no down was removed but the nest material was turned around in the same way and with the same frequency as in experimental nests.

In 2004, I examined the effect of down removal during incubation for the microclimate of incubation and hatching success. In 20 nests, half of the nest down was removed ("reduced" group). Forty additional nests formed the unmanipulated group. In order to reduce the potential effect of clutch size on incubation temperature, the clutch was standardized, in both control and reduced group, to the median clutch size of 4 eggs (Erikstad et al. 1993; the mean clutch size in 2004 was 3.7 ± 1.00 eggs; mean ± sd, n = 60), by adding or removing extra eggs two days after the third egg of the original clutch was laid. Contiguous nests (not included in the study) with similar laying dates as the study nests were used as a source of extra eggs or as host nests for removed eggs. The original clutch size was considered as covariate in all analyses.

In 2005, apart from testing the effect of down removal I examined as well the effect of adding down to the nest. The effect of nest insulation on maternal performance was also investigated. The amounts of down that represented a "poorly" or a "well" insulated nest (and therefore the two levels of down treatment) were determined by performing tests where the cooling rate of eggs, covered by different amounts of down, were measured. To do this, four unfertilised chicken eggs were warmed to approximately 37oC for 30 min in a house oven. One thermistor connected to a Tinytag data logger (10k-NTC, Gemini data loggers, UK) was attached to the upper central part of each egg surface using a small piece of surgical micropore tape. Three eggs were placed in card box dishes and enfolded in 3, 7 and 10 grams of down respectively; the fourth egg was left uncovered. The eggs were left to cool down for 80 min (after which the egg surface reached ambient temperature), egg surface temperature was measured at intervals of 10 seconds. The trials were repeated five times and the average temperature of each treatment was obtained and used as a measure of cooling rate: 10g down = 0.29 oC/min; 7g down =0.30oC/min; 3g down =0.35oC/min; 0g down = 0.5oC/min; ambient temperature = 9.2oC (min-max: 8.3 - 10.4oC). No further insulation benefits were observed when using more than 7 grams of down therefore we decided to use 3 and 7 grams of down for the experimental manipulations (cooling rates 7g down vs. 3g down t1046 = 2.28, p = 0.02).

The original clutch size (mean ± 1SD: 3.93 ± 1.06 eggs) was not manipulated and, as with laying date, did not differ among treatments (clutch size $F_{2,77} = 0.16$, p = 0.85; laying date $F_{2,77} = 0.91$, p = 0.41; unmanipulated down: 3.97 ± 1.26 eggs, laying date = May 19th ± 8.38 days; poor insulation: 3.81 ± 0.95 eggs, laying date = May 22nd ± 9.86 days; good insulation: 3.94 ± 0.62 eggs, laying date = May 23rd ± 9.43 days). In the unmanipulated nests the amount of down ranged from 2.4 to 25g per egg in a clutch (mean=6.11 ± 4.59 g). For the experimental manipulations I used a standardized amount of 7 g per egg in a clutch (i.e. 28 g in a clutch of four eggs) as "good insulation" (n=20) treatment and approximately half that amount (3 g) as "reduced insulation" (n=20). Nests were selected at random from the study area and included in each of the two down treatments, 40 additional nests were included in the unmanipulated down group. To examine the effect of the amount of down on the incubating female, I examined the rate of mass loss in females in the treatment groups. A total of 31 females (12 in the unmanipulated group, 9 females in the poor insulation group and 10 in the good insulation group) were trapped at the nest with a landing net twice during incubation: before day 8 of incubation ("early incubation mass") and on day 25 ("late incubation mass"). Trapped females were weighed to the nearest 1 g with a Pesola spring balance, and the length of the head-bill and tarsus was measured (± 1 mm) to obtain a measure of the structural size. After trapping, the females were observed from a distance to ensure that they resumed normal incubation. In all cases females returned to the nest within 20 minutes and sat on the eggs almost immediately. Measures of incubation temperature and relative humidity for nests of the two experimental and natural level groups were matched so that all three treatments were sampled on the same days.

Statistical analysis

In 12 out of the 140 nests from both years it was not possible to obtain and weigh the down because the nest was predated or abandoned; in both circumstances, all or most of the down was lost to the wind. Final sample sizes for analysis of amount of down for 2004 were: control n = 35 nests, experimental n = 19; for 2005: control n = 35, experimental n = 39. Analysis of effects of down on incubation length and egg mass loss excluded nests where all the eggs of the clutch failed to hatch, therefore sample sizes in those analysis were 47 and 63 nests for 2004 and 2005 respectively.

Data on hatching success were analysed using generalised linear models with binomial error structure and logit link function (GLIM-MIX, SAS version 9.1) the significance of terms is assessed on the basis of changes in deviance (which approximates a chi-squared distribution), resulting from the removal of terms from the model (Crawley 2002). Because not all females caught in 2005 were first trapped on the same day of their respective incubation period (but all were trapped within the first third of the incubation period), the number of days elapsed between the start of incubation and the day the female was first trapped was included as covariate in the analyses of female body mass in early incubation.

Since data on nest microclimate included on average three measures of nest temperature and humidity per nest, generalised linear mixed models (GLMM, SAS version 9.1) with a repeated measure statement (temperature or humidity sample of each nest) and an autoregressive covariance structure were used. The significance of the variance component was tested using a Z-test. This showed variability related to the difference in temperature samples of individual nests. The degrees of freedom of every estimate and test of interest was calculated using the Satterthwaite approximation. Values are given as means ± 1SD unless otherwise stated. All statistical tests are two tailed and the criterion of significance is $P < 0.05$.

Results

1) *Natural variation in nest down*

The mass of down in unmanipulated in both years nests varied from as little as 8.85 g to a maximum of 63.52 g (mean 26.63 ± 9.79 g; 2004 n = 35; 2005 n=35). The degree of nest shelter explained 16.7% of the variability in the amount of down in the nest: in sheltered and intermediate nests, females put on average 8.61 g (± 1.96 g) of down more into their nests than females in exposed nests (Fig. 6.1). No differences in the amount of down between sheltered and intermediate nests were found (Fig. 6.1). The original clutch size, year, laying date of the first egg or nest did not show significant effect on the amount of down (Table 6.1). Using data for females captured on unmanipulated nests in 2005 only, there was no relationship between female mass during early incubation and the amount of down in the nest (early mass $F_{1,9}$ = 1.62, p = 0.23; days of incubation $F_{1,9}$ = 0.54, p = 0.48).

Table 6.1. GLM analysis showing the variability of the amount of down feathers in the nest in relation to physical and biological variables for nests in 2004 and 2005. Non significant terms were stepwise-removed from the model.

Source of variation	Type III	df	*F*	*P*
Intercept	49564.08	1	562.67	<0.001
Nest shelter	1179.17	2	6.69	0.002
Error	5901.78	67		
Corrected total	7080.95	69		
Adjusted R^2 = 0.142				
Rejected terms				
Year * shelter	0.25	2,60	0.01	0.99
Nest volume	6.80	1,62	0.03	0.85
Clutch size	6.07	1,63	0.85	0.77
Laying date	4.46	1,64	0.29	0.59
Clutch volume	112.62	1,65	1.81	0.18
Year	63.27	1,66	1.47	0.22

2.1) *effects of the amount of down in unmanipulated nests*

In unmanipulated nests, incubation temperature increased and in 2005 it also became less variable as the mass of down lining in the nest increased (Table 6.2; Fig 6.2). The relative humidity (average and variability) inside the nest was not affected by the amount of down (Table 6.2). In 2005 nest humidity was more variable (average humidity = 56.45 ± 10.53 % CV=31.04 ± 22.37) than in 2004 (average humidity = 58.83 ± 10.66% CV=14.97 ± 4.53). There was no significant effect of down mass on the average water loss of the clutch (mean = 0.52 ± 0.14g/day, n = 63) or the proportion of eggs hatched in the clutch (Table 6.2). The incubation period was extended on average 0.5 days with approximate increases of 10 g of down (Table 6.2). Clutch size also affected incubation duration: incubation decreased from an average of 26.6 days in one-egg clutches to 22.5 days in clutches of 6 eggs ($F_{1,56}$ = 11.8, p = 0.001). Clutch size was slightly larger in 2005 (3.96 ± 1.35 eggs, n = 40 nests) than in 2004 (3.75 ±

0.67 eggs, n = 40 nests) but the difference was not significant ($F_{1,78}$ = 0.78, p = 0.38).

Table 6.2. Effect of the amount of down in the nest on nest microclimate and incubation performance of unmanipulated nests in both years. The F statistic corresponds to the mix model or GLM analyses; χ^2 correspond to the Generalised linear model between amount of down and hatching success.

	Explaining variable: amount of down	df	F/χ^2	Repeated sample *Z*
Nest microclimate	Temperature average	1,61.9	**12.9**†	
	year	1,65.4	2.22	-0.91
	Temperature variation (CV)	1,65.9	11.6†	
	year	1,64.1	**12.5**†	
	Year*down	1,65.9	**6.2***	-0.34
	Humidity average	1,41.7	0.01	
	year	1,38.9	0.41	0.56
	Humidity variation (CV)	1,38.1	0.08	
	year	1,35.8	**10.6**†	1.85
Incubation performance	Water loss	1,56	0.28	
	Incubation period	1,56	**6.7***	
	Hatching success	1	0.77	deviance = 23.16

*= *P*<0.05

†= *P*<0.001

2.2) *Effects of the amount of down in experimental nests*

Taking into account the amount of down removed from nests, there were no significant differences between unmanipulated and experimental nests in the absolute amount of down placed in the nests by females (t_{52}= 0.31, p = 0.75). Incubation temperature increased with date of measurement (r=0.45, p<0.01,n= 54) but interestingly, the incubation temperature (average or CV) was not significantly influenced by removal of down or original clutch size (Table 6.3). The average (but not variability in) relative humidity in the nest was influenced by down removal: in nests where half of the down mass was removed the average humidity was higher (RH: 59.6% ± 5.3) compared to nests where no down (RH: 53.7% ± 5.6) was removed (Table 6.3). The effect of original clutch size and date of measurement on nest humidity were not significant (Table 6.3).

Down removal did not affect incubation performance: egg mass loss (t_{45} = 1.17, p = 0.24), incubation length (t_{45} = 0.64, p = 0.52), hatching success of the clutch (total scaled deviance = 18.22, df = 53, change in deviance: treatment = 0.89, df = 1, p = 0·34).

In 2005, where the experimental groups comprised nests with "poor insulation" or "good insulation", I found similar results to those in the previous year. There were no differences in the average incubation temperature among natural level and experimental nests (Table 6.4) but nests of the good insulation group showed lower variability in incubation temperature compared to nests in the unmanipulated and poor insulation groups (Table 6.4, Fig 6.3a). As found in 2004, the effect of date of the temperature reading was highly significant: incubation temperature was lower earlier in the season; there was no effect of clutch size on incubation temperature (Table 6.4). The amount of down in the nest had a negative effect on relative humidity: average RH was lower in nests with large amounts of down than in nests in the poor insulation group (Table 6.4, Fig 6.3b), the effect of clutch size and date of measurement were not significant (Table 6.3). There was no significant effect of treatment on incubation length ($F_{2,60}$ = 0.75, p = 0.47), average egg mass loss ($F_{2,60}$ = 0.67, p = 0.51) or hatching success of the clutch (total scaled deviance = 20.99, df = 73, change in deviance: treatment = 0.60, df = 2, p = 0·74; clutch size = 1.02, df = 1, p = 0·31; laying date = 0.10, df = 1, p = 0·75).

3) *Effect of amount of down on parental performance in 2005*

Although females in experimental nests with poor insulation showed a tendency to loose more body mass through incubation (mean = 36.27 ± 2.68% n = 9) than females in nests with good insulation (mean = 33.4 ± 1.58% n = 10) or in unmanipulated nests (mean = 32.09 ± 4.79% n=12) I found no significant differences in the total percentage of mass loss among females of the experimental groups ($F_{2,28}$ = 2.67 p = 0.08; days elapsed between first and second catch $F_{1,27}$ = 1.39, p = 0.24).

Table 6.3. Microclimate of incubation (average and variability of incubation temperature and relative humidity) in relation to down removal in the 2004 experiment.

	Average		Coefficient of variation	
Temperature	d.f.	F	df	F
Down treatment	1,58.57	0.77	1,66.39	0.58
Original clutch size	1,62.30	0.03	1,70.28	3.51
Time of season	1,100.60	**29.82****	1,98.15	3.44
Repeated	*Z* = 2.47 p = 0.01		*Z* =1.32, p = 0.18	
Humidity				
Down treatment	1,37.22	**6.90***	1,36.53	0.67
Original clutch size	1,43.36	1.41	1,42.73	1.80
Time of season	1,39.57	0.32	1,38.78	0.95
Repeated	*Z* = -0.28, p =0.77		*Z* =-0.31,p =0.75	

*= *P*<0.05

**= *P*<0.001

Table 6.4. Microclimate of incubation (incubation temperature and relative humidity) in relation to the amount of down in the nest. Data shown is from the experiment in 2005.

	Average		Coefficient of variation	
Temperature	d.f.	F	df	F
Down treatment	2,59.46	0.57	2,51.19	**4.18***
Original clutch size	1,72.90	1.29	1,59.57	0.40
Time of season	1,103.40	**20.41****	1,85.4	3.2
Repeated	*Z* = 0.92 p = 0.35		*Z* = -0.45, p = 0.65	
Humidity				
Down treatment	2,54.13	**4.65***	1,39.81	1.19
Original clutch size	1,72.81	2.68	1,58.97	1.09
Time of season	1,97.36	2.46	1,88.45	0.03
Repeated	*Z* = 1.00, p =0.31		*Z* =0.97, p =0.32	

*= *P*<0.05

**= *P*<0.001

Figure 6.1. Total mass of down in nests with different shelter level. One-way ANOVA $F_{2,67} = 6.69$, p = 0.002. Difference between the sheltered and intermediate groups is not significant (Tukey test, $P>0.1$. Values presented are mean ± SE.

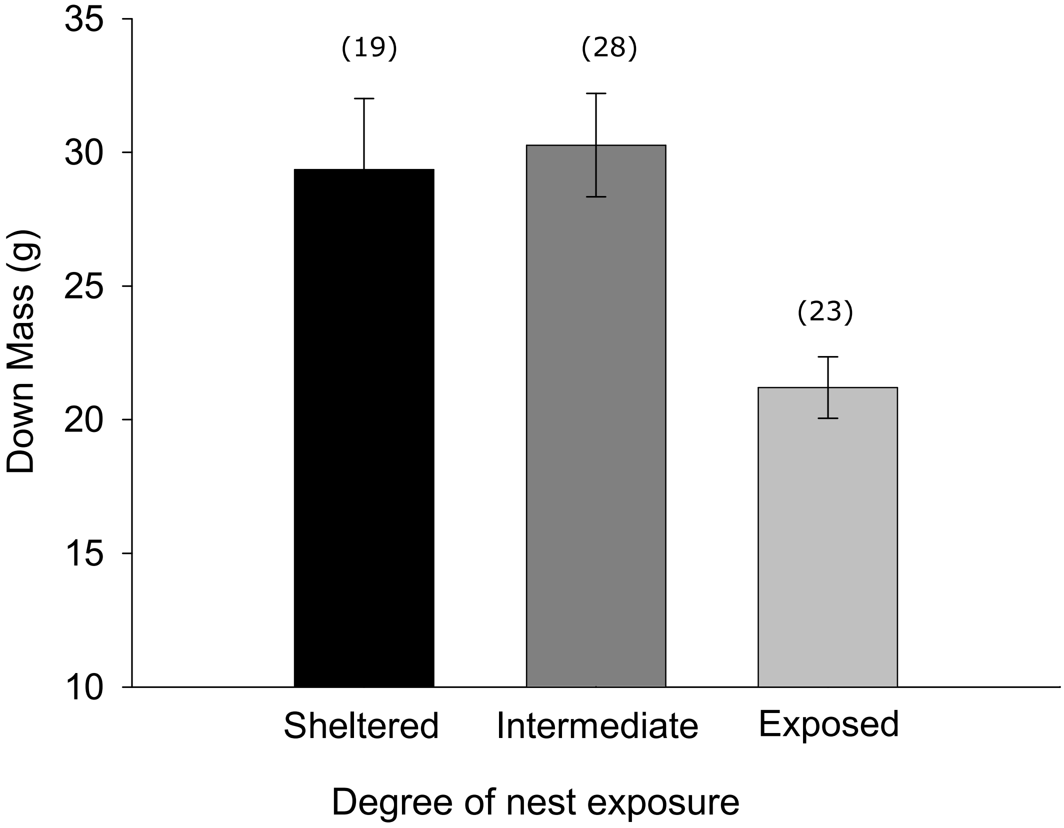


Figure 6.2. Incubation temperature as a function of the amount of down in nests with natural levels of down in 2004 (filled circles) and 2005 (open circles).

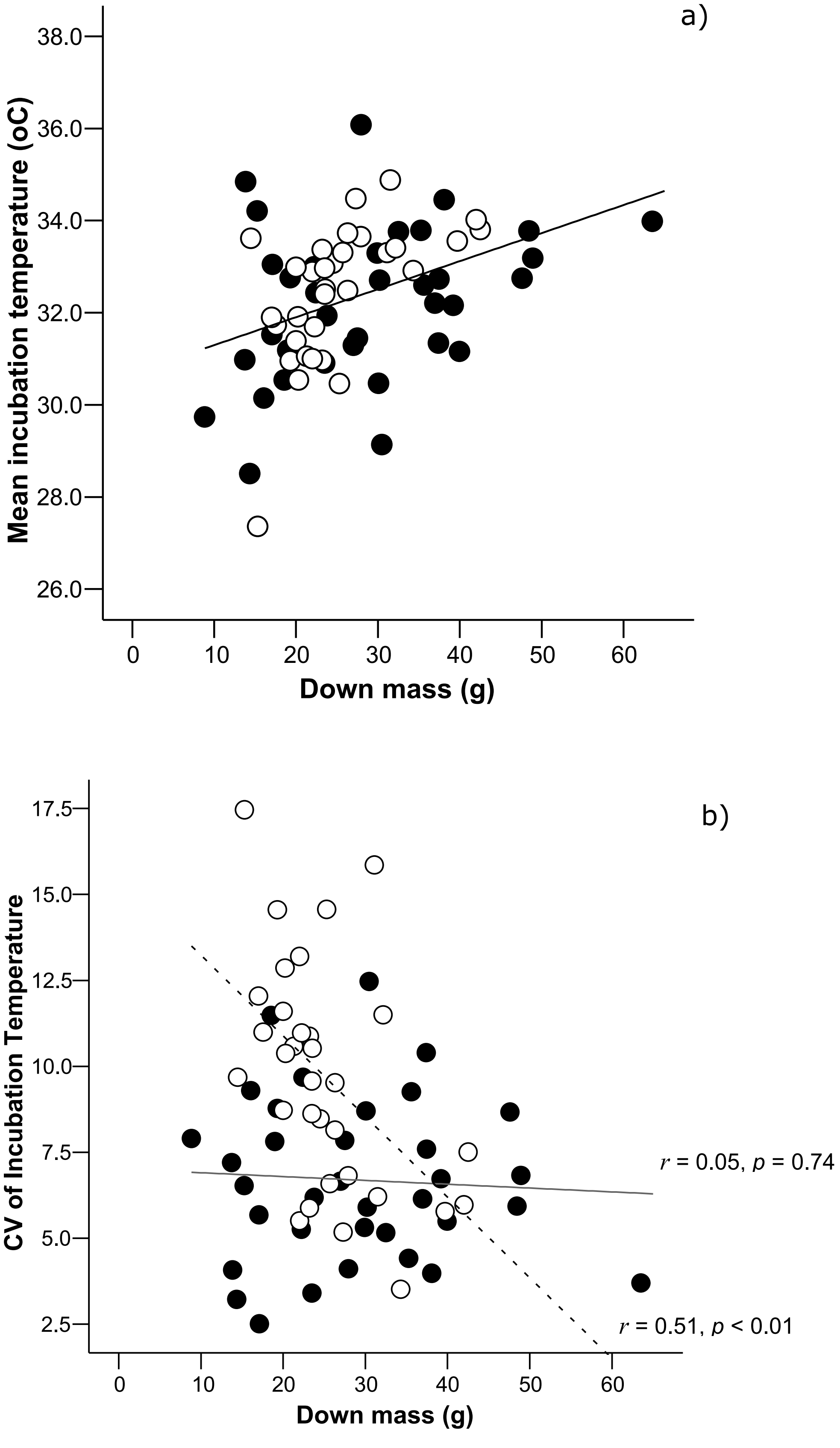
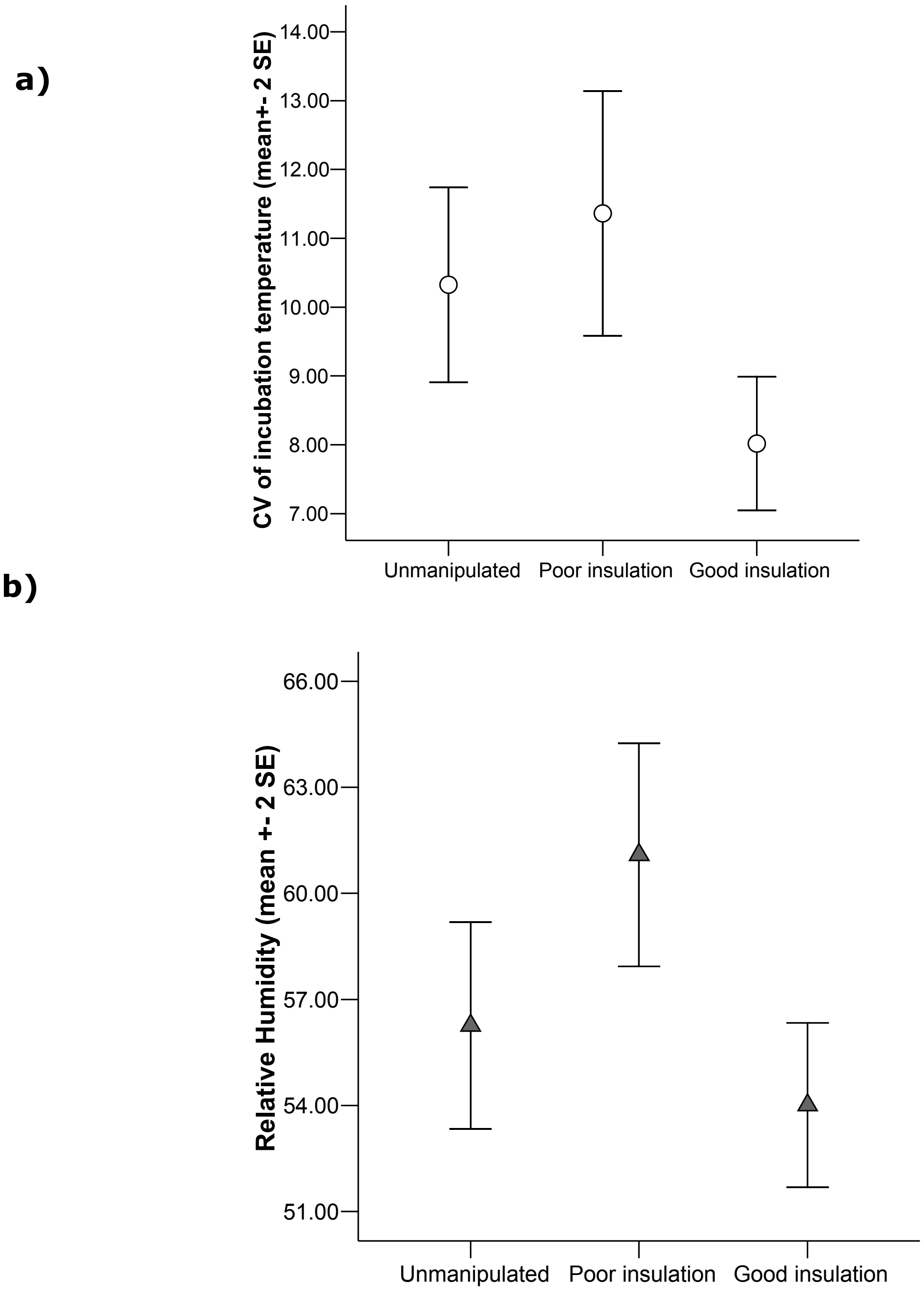


Figure 6.3. Comparison of (a) variation (CV) in incubation temperature (circles) and (b) nest humidity (triangles) among nests with unmanipulated down, poor insulation (3g of down per egg) and good insulation (7g of down per egg). Data shown corresponds to experiment in 2005.



Discussion

There was considerable variation in the amount of down put into the nest by female Eider ducks. The amount of down was not related to the overall nest volume, laying date or clutch size. However, it was related to nest attributes, for example, females nesting in more sheltered sites put significantly more down into the nest. This suggests that the amount of down is not related to the thermal requirements at the nest site, but is linked to female quality or condition. In unmanipulated nests, down mass changed the microclimate of incubation both in terms of the average and the variability of incubation temperature; in nests with more down, nest attendance (incubation temperature) was higher and less variable. In experimental nests, the removal of down resulted in increased nest humidity; good nest insulation, on the other hand, was related to increase in nest attendance (more constant incubation temperature). Interestingly and in contrast with the results from unmanipulated nests, the average incubation temperature was not affected by reductions in down, suggesting first, that in compensating for a poor nest insulation females might have to increase heat production in order to maintain a constant incubation temperature. And secondly, that nest insulation alone is not responsible for determining the microclimate of incubation; nest attentiveness and variation in the level of heat transfer by the female are potentially the most important factors involved. No within-season reproductive benefits of the amount of down in the nest insulation were found either on the unmanipulated or the experimental nests.

One particularly interesting, and counter-intuitive finding was the positive relationship of nest quality (nest shelter) and the amount of down in the nest. In some birds it has been found that the amount of feathers put in the nest can be related to female body condition, because hens in a poorer state abstain from plucking feathers from their brood patches (*Gallus domesticus*; Brummermann and Reinertsen 1991). Eiders in this colony nesting in sheltered nests also lay larger clutches (Chapter 3), and it is reasonable to think then that the amount of down put in the nest could be reflecting an aspect of female quality. Nevertheless, our data showed no evidence of a relationship between initial female mass or body mass loss throughout incubation and the amount of down put in the nest. Further studies are needed to investigate, on one hand, the costs for females of supplying nests with down and second, to consider the link between maternal condition and nest insulation.

Does the amount of down matter?

Better nest insulation resulted in increased incubation temperature in unmanipulated nests. This is not surprising since it has been shown that down feathers have excellent insulating properties (Hilton et al. 2004). Some birds adjust their nesting behaviour according to the thermal environment by adding more feathers to the nest when temperatures are cooler (McGowan et al. 2004). Eider females however, did not replace the down removed from their nests and instead maintained a similar temperature regime in comparison with unmanipulated nests. This suggests in first place, that down feathers are valuable for females and in second place that females are able to counterbalance the heat that is lost from the eggs to the cold ground by producing more heat in order to maintain egg temperature within the optimal range. To our knowledge, there is only one other study showing similar results in Barn Swallows where egg temperature remained constant even when all the feathers were removed from the nest (Møller 1991). Maternal compensation for changes in the nest environment have been shown in the Pectoral Sandpiper (*Calidris melanotos*) where nest attendance increased as the costs of heating the eggs (in artificially heated nests) decreased (Cresswell et al. 2004).

As with data in Chapter 3, records of incubation temperature can be used as a measure of nest attendance. This was supported by the fact that date of measurement had a strong effect on incubation temperature (early in the season incubation temperature was lower). It is also possible that females cannot entirely buffer their clutches from environmental conditions and, that with incubation progression female attendance increases resulting in higher and less variable incubation temperature.

From our removal experiments in both years it was evident that, despite the unchanging incubation temperature, decreases in the amount of down in the nest resulted in increased nest humidity. High humidity can have a great impact on the development of embryos and ultimately in hatching success for example, by limiting the utilisation of egg components and therefore mechanically restricting the hatching process (Walsberg and Schmidt 1992). In addition, warm and humid conditions are optimal for bacterial reproduction and might increase the risk of eggs becoming infected with microbes (Bruce and Drysdale 1994). Thus, it is possible that by decreasing the amount of down in the nest, thermal properties remain the same but the viability of egg decreases due to high increments in humidity. In our study I did not find an effect of down removal on hatching success. However, future test of this hypothesis will require identifying the factors associated with nests microclimate that promotes bacterial infection of Eider eggs.

What are the benefits of having a well-insulated nest in eiders?

Studies of the importance of nest insulation are often problematic, since there may be a correlation between parent and nest quality, and the parents may compensate (as suggested by the unchanging incubation temperature across treatments in our data) from deficiencies in nest quality by increasing energy expenditure during incubation. Our data, however, did not support the idea that good nest insulation can help females reduce the energy spent during incubation.

In this study females that incubated in nests with reduced amounts of down did not significantly lose more mass. However, it is possible that differences in energy utilisation in relation to the degree of nest insulation might be subtle and not easily detected from the estimation of body mass loss. An alternative advantage of feathers in eider nests might be allowing the female to take longer or more frequent periods off the nest (Møller 1991). Therefore future studies on eiders should also try to investigate whether nest attentiveness is influenced by the quality of nest insulation.

In the unmanipulated nests, the incubation period was shortened on average by 0.5 days with approximate decreases of 10 g of down. Reducing the incubation period allow females to save energy (Parker and Holm 1990) which can be particularly important for females in poor condition. The fact that I did not find differences in the duration of incubation period among the experimental groups further supports the possibility that the amount of down is signalling individual quality where nests with smaller down mass are occupied by females in poor condition. Hanssen et al. (2002) proposed that eider females that lay large clutches (good quality) can afford longer incubation periods at the cost of higher energy expenditure to increase hatching success of eggs. Hence, incubation duration seems to depend on female condition rather than being constrained by the quality of the nest insulation.

In conclusion, down in the nest contributes to more stable incubation conditions. Females were able to counterbalance poor nest insulation and keep incubation temperature constant but the costs of doing this are unclear. No direct fitness benefits of nest down mass were found for the clutch or the female. However the advantages might be subtle and indirect benefits of good nest insulation such as shortening of incubation length and higher hatching synchrony should be considered in future studies. The down may also have other functions, for example influencing the level of bacterial growth in the nest.

Chapter 7

Macroclimate effects on population size and onset of laying in Common Eiders

Abstract

The thermal environment can affect birds at two levels: individual or at population level. At individual level the thermal environment influence the energy budgets of birds, so, it can constrain foraging activity, and determine the costs of thermoregulation and it can certainly influence the animal's allocation of energy to self-maintenance and parental care.

At population level the effects of climate on birds can be seen as changes in distribution and geographical range, changes in phenology and impacts on demographic factors.

Many studies have demonstrated direct links between change in weather conditions and phenology of migration, reproduction, reproductive outcome and adult survival of different species. Eiders are highly dependent on favourable climate conditions for reproduction and survival. Breeding performance depends to a large extent on female condition. This study investigates how climate over the past 30 years relates to population growth and onset of laying of Eiders breeding in Nordurkot, SW Iceland. Several linear models relating climate variables (including winter and summer temperature, NAO-index, wind and precipitation at the study site) and laying dates or population growth were run. Model selection was performed based on the AIC value of each model. Data showed that temperature at the study site, both in winter and summer, has increased over the past 30 years. Eiders have been laying increasingly earlier since 1977. The models showed that after mild temperatures during winter females lay early in the year perhaps because they to reach sooner the necessary body condition for egg formation and incubation. The Eider Population has shown a steep increase over the past 30 years. More importantly, in summer, milder temperatures contribute to increase in population perhaps through higher recruitment of eiders two years in the future. Evidence suggests that climate warming might benefit breeding success of eiders.

Introduction

The effect of weather on bird population dynamics has been long documented (Lack, 1966, Newton 1998, Crick 2004). Many studies have demonstrated direct links between change in weather conditions and phenology of migration and reproduction (Forchhammer et al. 2002, Sparks and Mason 2004, Croxton et al. 2006, Sparks et al 2002), reproductive outcome (Kitaysky and Golubova 2000, Thompson and Ollason 2001) and survival rates (Barbraud and Weimerskirch 2001) across different species.

Climatic variation can cause fluctuations in numbers via effects on adult survival during the non-breeding season. However, climate conditions during the breeding season can also have important effects on reproductive success and therefore impact the influx of recruits to the population in subsequent years (Durant et al. 2004*).* The effect of fluctuations in climate on breeding birds will vary according to their response to fluctuation in climate; this can be related to variation in costs associated with the amount of energy invested to different phases of reproduction. For instance, traits such as the onset of incubation or clutch size are constrained by the physiology of the individual and determine to a large extent the reproductive success for some species.

Food availability is largely determined by climate; consequently, changes in weather conditions can influence the acquisition of body reserves (Thompson and Ollason 2001). This in turn can affect performance in subsequent reproductive events (Marra et al. 1998, Norris et al. 2004). The severity of winter has the potential to exert a strong selective pressure on the timing of reproduction on birds, particularly those which depend to a large extent on stored body resources for egg production (capital breeders; Drent and Daan 1980). There is a vast amount of evidence showing that laying dates of birds can be influenced by weather. For example, in a long-term study, Dunn and Winkler (1999) found for the Tree Swallow (*Tachycineta bicolor*) a positive relationship between advancement of laying onset and ambient temperature. Similarly, in a review on the laying dates of 36 species, Crick and Sparks (1999) found that in 86% of the cases, onset of laying incubation was determined by temperature and rainfall.

The Common Eider (*Somateria mollissima*) meets its reproductive effort from stored reserves (Erikstad et al. 1993, Hanssen et al. 2003). Females do not feed during incubation. Therefore, they can lose up to 45% of their initial body mass (Korschgen 1977, Parker and Holm 1990). Incubating eiders are highly dependent on favourable climatic conditions for reproduction and survival. Timing of breeding in this species varies between years depending on weather conditions and can be delayed up to a month in years with late ice melt-down in the Arctic (Robertson 1995). It has been shown that severity of winter affects female condition and fledgling production on the subsequent reproductive event (Lehikonen et al. 2006). Chick survival and recruitment are, to a large extent, determined by the physiological condition obtained after hatching (Christensen 1999). Therefore, summer climate conditions, through indirect effects on food acquisition and directly on survival, might also bear an important influence on population parameters. In this study of incubating Common Eiders at a colony in Iceland, I investigated: a) the relationship between winter weather conditions and the onset of laying and b) whether fluctuations in population size among years can be explained by prevailing summer conditions, particularly during June (hatching peak in this population for 2004 and 2005 was 5 and 13 of June respectively; D'Alba unpublished data) where I expected the strongest correlation to occur.

Methods

Eider and climate data

The data for the population of Common Eiders (*Somateria mollissima*) used in this study were obtained from the owners of the land ("Nordurkot") where the birds breed. The owners annually harvest the down produced by eider females for commercial puposes. The study area is situated in the municipality of Reykjanesbær, SW Iceland (64^o01'3" N, 22^o 42' 27"W). Nordurkot holds ca. 2000 pairs. Data included the number of nests and the onset of laying (date when the first nest with eggs was found each year) from 1977 to 2006.

We used historic records of weather for 1975 - 2006 from the nearest weather station (4.7 km) at Keflavik airport at Reykjanesbær (http://www.vedur.is). Monthly climate indices were grouped in two categories: winter (December to February) and summer climate (May to July). The variables used were average temperature (^{o}C), precipitation (mm), wind speed (m/s) and sea surface temperature (SST). Records of monthly sea surface temperatures for the closest geographic area to the study site (64^o5' N, 22^o 5'W) were obtained from Rayner et al. (2006) and are expressed as departures from a based period (1961-1990) (data set: http://www.hadobs.org/). The winter North Atlantic Oscillation (NAO) index was obtained at http://www.cgd.ucar .edu/cas/jhurrell/ indices.html.

Statistical analysis

I looked at trends in all variables over time. The number of nests was ln-transformed in order to remove the heteroscedasticity in the data. Variables that showed a significant trend over time (laying onset, number of nests, ambient and sea surface temperatures) were detrended prior to all analysis (Chatfield 1996) by using the residuals from linear regressions on the temperature, laying onset and (ln) number of nests against year. The Sea Surface Temperature (SST) showed a non-linear trend over time, therefore, a quadratic regression was fitted in this case. Laying onset and population size (ln-number of nests) were used as dependent variables.

I performed a stepwise linear regression with laying onset as the dependent variable and climatic variables for winter NAO-index, SST and average temperature (^{o}C), mean precipitation (mm) and mean wind speed (m/s) as explanatory variables. The final model was selected based on the Akaike Information Criterion (Akaike 1973) corrected for small sample size (AICc). I bootstrapped (with replacement; number of repetitions = 1000) the regression involving the variables included in the final model in order to establish a confidence interval of the regression intercept and slope (Crawley, 2002).

The age of first reproduction of eiders is on average 2 years for females and 3 for males (Ogilvie 2005). Therefore, I analysed the lagged (2 and 3 yr) effect of climate on the number of nests. Correlation coefficients were significant for June temperature at lag two; hence I included only the delayed June temperature as explanatory variable in the final model. The validity of the final model was checked testing the forecasting power of the model (Lindström 1996). I modelled population size Pt using previous densities (Pt–1, Pt–2) and June temperature (T-2). Model performances were compared using the AIC value. The best regression model was then built for only 24 years (1978- 2001; 1977 was not included because there was no value of Pt–1) not including the last five (2002-2006). Predicted values were obtained for the last 5 years and the corresponding values of SSE were calculated and compared to the SSE values for the same years obtained when the regression included all 29 years. The forecast of the model is considered successful when the observed values fit the 95% confidence limits of the forecast. All statistical tests are two-tailed and the criterion of significance is $P < 0.05$.

Results

Climate indices.

Neither the winter NAO-index nor precipitation showed a significant trend over time, whereas winter, summer, sea surface temperatures and wind speed have increased since 1977 (Table 7.1). None of the climate variables showed correlations among each other (Table 7.2).

Table 7.1. Descriptive statistics of the winter NAO-index, winter sea surface temperature (SST) for the closest area to the study site, and mean winter and summer temperature, precipitation and wind speed in Keflavik, Iceland, during the period 1977-2006.

Index	Mean ± SD	Range	Trend 1977-2006	P-value
Winter NAO-index	0.95± 2.03	-3.78 to 5.08	*r*s= 0.001	0.940
Winter SST	4.73 ± 0.37 oC	4.04 to 5.55 °C	*r*s= 0.535	0.002
Mean winter T°	0.49 ± 1.03 oC	-1.40 to 2.42 °C	*r*s= 0.451	0.012
Precipitation	106.87 ± 22.40 mm	51.35 to 152.32 mm	*r*s= 0.176	0.352
Wind speed	7.54 ± 0.69 m/seg	6.10 to 9.13 m/seg	*r*s= 0.614	0.001
Mean summer T°	8.49 ± 0.72 oC	6.43 to 9.73 °C	*r*s= 0.60	0.001

Trends are based on Spearman rank correlations for the entire data set.
NAO, North Atlantic Oscillation.

Table 7.2. Correlations among climate variables for winter (Dec-Feb) for the period 1977-2006.Values presented are Spearman rank correlation coefficients.

Index	Winter NAO-index	Winter SST	Mean winter temperature	Precipitation	Wind speed
Winter NAO-index	-	-0.251	-0.146	0.12	0.185
Winter SST	-	-	0.084	-0.055	-0.120
Mean winter temperature	-	-	-	0.267	-0.164
Precipitation	-	-	-	-	0.306

Onset of laying

The onset of laying has advanced since the past 30 years (Range: 22nd April to 13th May trend over time: $r_s = -0.43$ $p = 0.01$ Fig 7.1). Laying dates were not related to the NAO index, SST, rain or wind speed (Table 3). However, there was significant negative relationship between laying onset and the average winter temperature, when winters are mild eiders start laying early ($r = -0.47$ $p = 0.009$, $\alpha = -6.88e-7$, $\beta = -0.397$; bootstrap ± 95%CI for intercept = -0.3535 , 0.318; for slope = -0.708, -0.041; Table 7.3, Fig 7.2).

Fig 7.1. Trend in the onset of laying of the study colony (1977-2006).

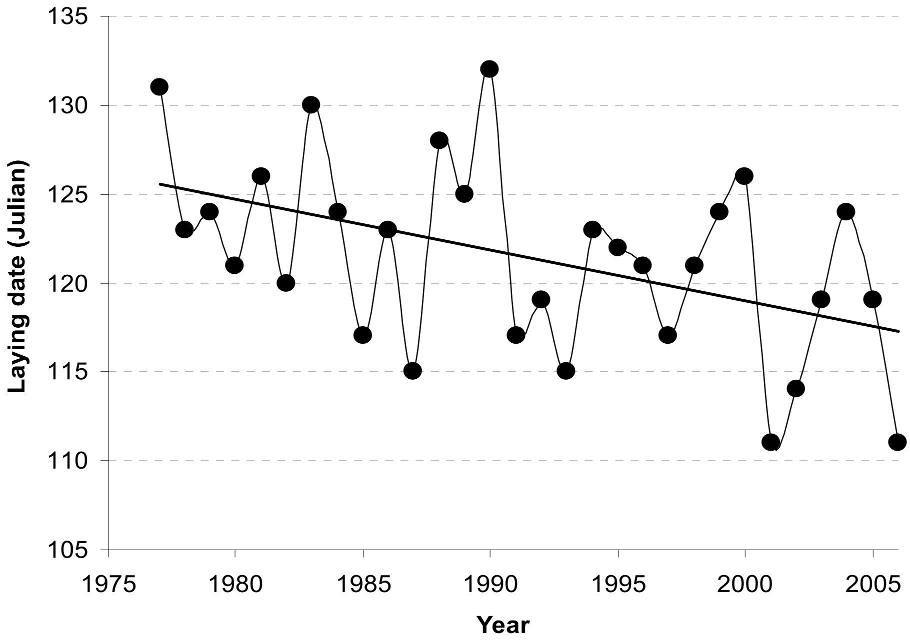
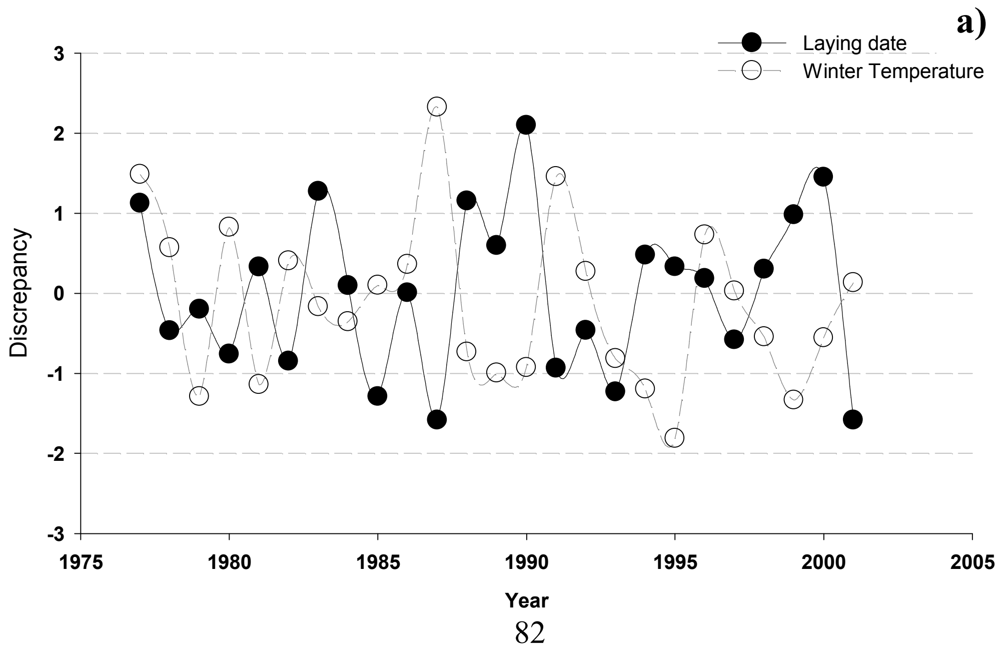


Fig 7.2. Time series (a) and relationship (b) between the laying onset and winter mean temperature. Y axis presents the deviation (discrepancy) of expected and observed values of the variables (detrended data).



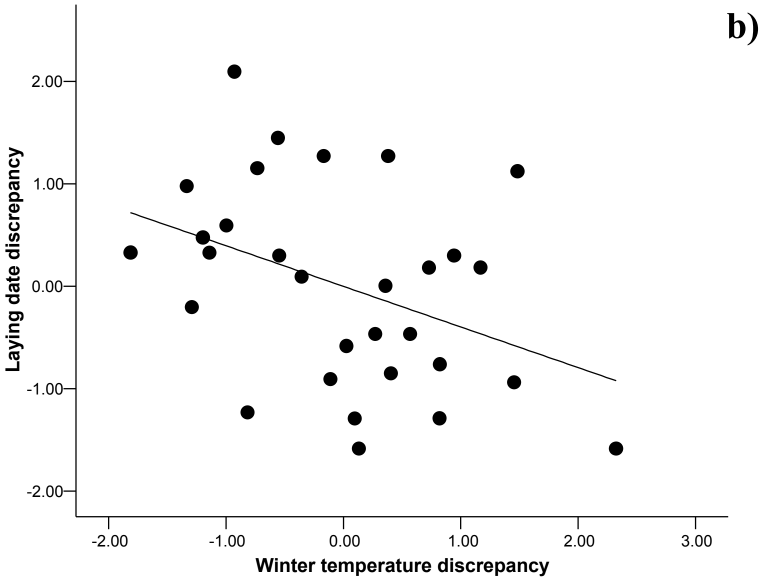


Table 7.3. Model fitting results of the stepwise multiple regression to test the effects of climate on the laying dates of Common Eiders breeding at Nordurkot during 1977-2006.

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Model	R	R^2	Df reg/residual	AICc	SSE	F	p
WinT, SST Wind,NAO,Rain,	0.45	0.03	6,23	92.66	22.26	1.23	0.32
WinT, SST,NAO,Rain	0.44	0.07	5,24	89.90	22.37	1.57	0.21
WinT, SST,NAO	0.44	0.10	4,25	87.30	22.43	2.15	0.11
WinT, SST	0.42	0.11	3,26	85.53	22.96	2.95	0.07
WinT	0.39	0.12	2,27	84.03	23.59	5.23	0.03

—

R^2 Adjusted coefficient of determination

Breeding numbers

The colony size at Nordurkot has increased from 530 nests in 1977 to 2010 nests in 2006 ($r = 0.92$, $p<0.001$, $n = 30$). Population growth was not associated to the NAO index, or climatic conditions (average summer temperature, wind speed, precipitation or sea surface temperature; Table 7.4). However, temperature during June showed a 2-year delayed correlation with the number of nests (Fig 7.3). Consequently, I built our models of population size including June temperature (*Tt-2*) along with the one and two-previous years population size (*Pt-1*) and (*Pt-2*). The model that best described the variation in number of nests was that including June temperature (*Tt-2*) and the population size in the previous year (*Pt-1*), so that the colony size in a current year is influenced by colony size on the previous year and June temperature two years ago (Table 7.5). This model was fairly accurate in predicting short-term fluctuations in population size in particular after 1995 where the predicted values were more similar to the observed ones (Fig 7.4). The forecast of our model (where the last 5 years were dropped) seems to have been successful since all observed points for the period 2002-2006 were within the 95% confidence limits of the forecast (Fig 7.4).

Table 7.4 Cross-correlations between climate indices and population size (all detrended data). Numbers in bold represent significant values at *P*<0.05 level

Lag	Winter NAO-index	SST	Summer temperature	June temperature
-3	0.35	0.13	0.13	0.34
-2	0.30	0.20	0.35	**0.45**
-1	0.24	0.19	0.24	0.33
0	0.08	0.13	0.09	0.21
1	0.006	-0.07	0.13	0.17
2	-0.08	0.11	0.23	0.25
3	0.23	0.13	0.10	0.11

Table 7.5. **a)** Results of forecast linear models describing the population size (detrended ln-number of nests "*Pt*") as a function of previous population size (*Pt*–1and *Pt*–2) and June temperature of two years ago (*Tt*-2). Bold AIC value denote the most parsimonious models **b)** regression coefficients of most parsimonious model, numbers in bold denote significant coefficients at *P*<0.05 level.

a) Model terms	AIC	SSE	DF	F	Adjusted R^2
Pt–1	53.39	9.59	27	51.07	0.64
Pt–1+ *Pt*–2	53.34	8.27	25	27.02	0.65
Pt–1+ *Pt*–1+ *Tt*-2	49.73	6.77	24	22.91	0.70
Pt–1+ *Tt*-2	**49.64**	7.54	26	34.81	0.70

b) regression	β	se	± 95% CI	t
constant	-0.01	0.10	-0.22 ± 0.18	-0.17
Number of nests (*Pt*−1)	**0.73**	0.10	0.51 ± 0.95	**6.82**
June temperature (*Tt*-2)	**0.30**	0.11	0.06 ± 0.53	**2.66**

Fig 7.3. Time series of population size (ln) number of nests) and June mean temperature. Y axis presents the deviation (discrepancy) of expected and observed values of the variables (detrended data). June temperature shows 2-year delayed effect on the population size (cross-correlation lag 2 r = 0.44 ± 0.19 SE p = 0.01).

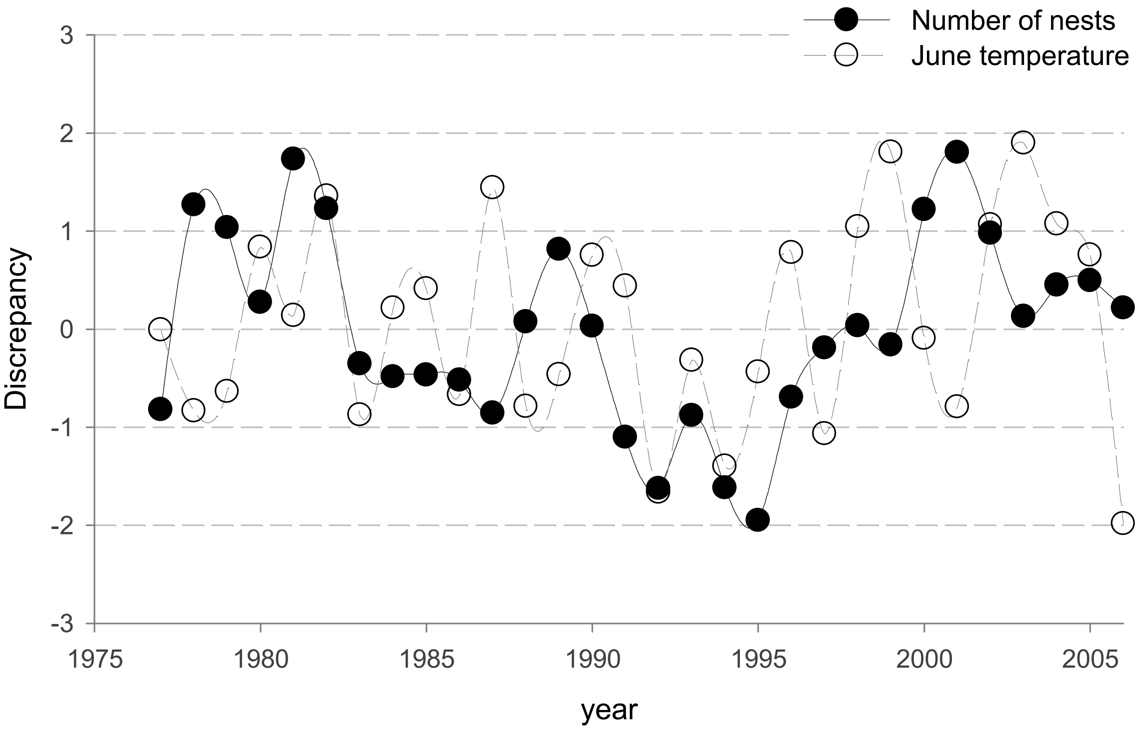


Fig 7.4. Forecasting power of the model with June temperature data and population size. Y axis shows the deviation of expected and observed population size (number of nests). The dotted line represents observed population size for 1977-2006. The fit of the model ($Pt = {}_{\alpha 1} Pt-1 + {}_{\alpha 2} Tt-2 + \in$) for 1976-2001 is indicated by the solid line and circles. Predicted values ± 95% confidence limits of the forecast for 2002-2006 are shown in gray squares. See methods for details.

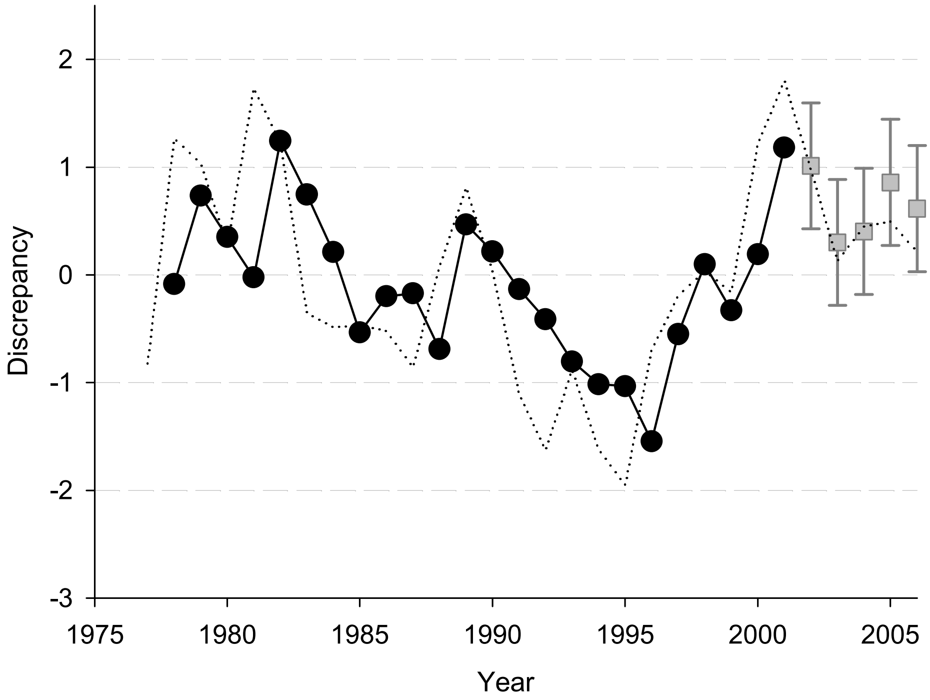
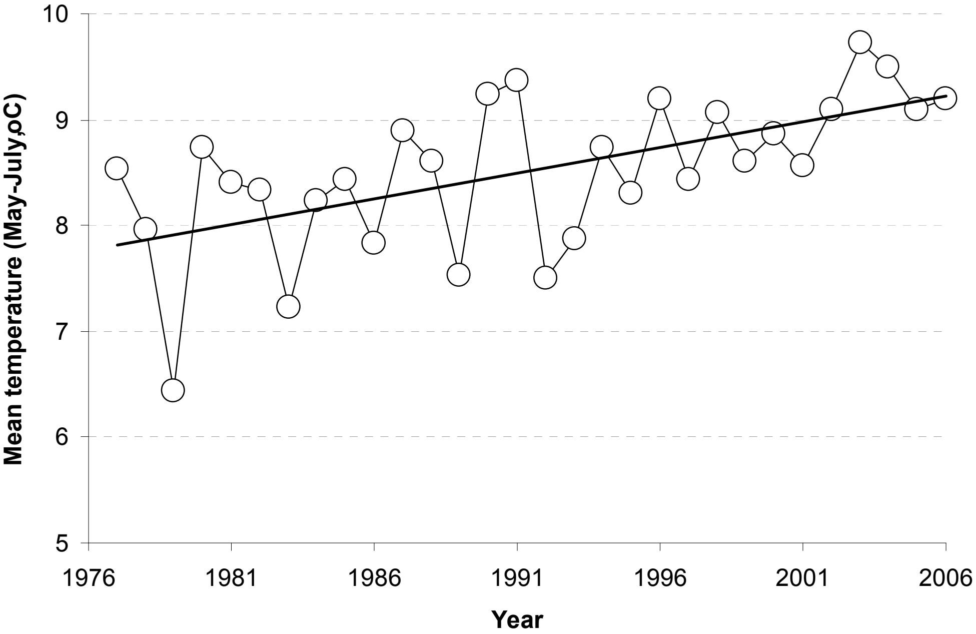


Fig 7.5. Average May-July temperature in Reykjanesbær, SW Iceland from 1977 to 2006. Temperature has increased ($r_s = 0.60$, $p < 0.01$, regression coefficients: $\alpha = -87.83$ $\beta = 0.05$) and the increment has become steeper after 1994 ($\alpha = -122.18$ $\beta = 0.07$).



Discussion

The main aim of our study was to assess the influence of environmental variability on the onset of incubation and short-term fluctuations in population size of Common Eiders. In agreement with large scale studies demonstrating that many birds have advanced laying over the past 25 years (Crick et al 1997), I found that Eiders breeding in this colony in Iceland have shifted their egg laying towards earlier dates. In addition, I found evidence indicating that winter temperature is positively associated with onset of laying. No relationship with the NAO index or SST were found.

Variation in climate conditions, and its influence on food availability, has been found to relate to the phenology of reproduction in many bird species (Crick and Sparks 1999). In particular for Common Eiders, winter conditions affect female body condition during reproduction and, presumably as a consequence of this, also affect the variability of laying onset (Lehikoinen et al. 2006). Our data showed that after mild winters egg laying commenced early. It is possible that by decreasing the energetic costs associated with thermoregulation and investment in self-maintenance (Rauter and Reyer 2000), milder winter conditions could allow females to acquire the necessary body condition to initiate reproduction sooner. Nesting early could be beneficial if offspring survival is increased if the fledged young have a prolonged period before winter. Further investigation is needed in order to reveal the potential costs and consequences of advanced egg-laying in eiders.

The colony size showed a general increase with marked oscillations over the past 30 years. Overall, worldwide populations of Common eiders have been reported to be either stable or in slow decline except in Iceland where numbers have increased since the last decades (CAFF 1997, Petersen 2002) The protective action of Icelandic farmers most likely accounts for a high proportion of the increase in eider numbers.

I hypothesized that weather conditions during the breeding season could explain short-term fluctuations in the number of nests at the colony via effects on reproductive success in a particular year. For example, females in poor condition tend to abandon the clutch in the final stages of incubation (Bustnes and Erikstad 1991) and this effect could be more marked particularly during cold years, resulting in decreased reproductive success on that particular event. No relationship of the NAO index, SST or wind and precipitation with population size were found. However, I found that temperature during the hatching period (2yr lagged effect) could explain annual fluctuations in colony size. I interpret this finding as an environmental effect on hatching success and/or survival of hatchlings, which is likely to influence recruitment rate into the population in subsequent years. Although I do not have a direct measure of the yearly number of recruits for this population, lagged effects of climate variation on recruitment rate and consequent population size have been reported previously for other seabird species (*Fulmarus glacialis*; Thompson and Ollason 2001).

On the other hand, although adult survival is likely to be influenced by climate conditions in many seabird species (Newton 1998), weather is likely to have greater impacts on post hatching stages particularly of offspring in precocial species (Sæther et al. 2004). In eiders, ambient temperature around the hatching peak could determine offspring survival through effects on hypothermia, predation or chick starvation. High duckling mortality is common in this species and explains most of the variation on reproductive success up to the fledging stage (Swennen 1991).

It is noteworthy that our model was able to predict short-term fluctuations in population size reasonably well, particularly after 1995. Interestingly, after this year a steeper increase in summer temperatures was evident in the data series (Fig 7.5). It is possible that the effect of temperature on population size becomes accentuated in the last 10 years due to this pronounced increment in temperature. However the biological processes underlying this effect are at the moment unknown.

In summary, the results show that Common Eiders are likely to be strongly influenced by their thermal environment both for reproduction and survival. Conditions during the breeding season can influence the dynamics of the population through effects on early survival on our study species. The lagged effect of weather is likely to be explained by the delayed maturity presented by Common Eiders, showing the importance of considering the species life history when carrying out studies of the effect of climate change on avian populations. Based on my findings, I propose that, populations of Eiders breeding in Iceland are likely to benefit to a certain extent from rises in temperatures in the northern hemisphere.

Chapter 8

General discussion

This thesis addressed several issues concerning the study of the interactions between organisms and their physical environment during reproduction. I have shown that reproductive success is related to nest site preferences (Chapter 2) and that, by choosing a suitable nest site, individuals can gain control of the microclimate conditions that can exert a great influence on reproductive performance (Chapter 2). I explored some of the effects of microclimate on individual physiology and use of energy during incubation (Chapters 3 and 4). I presented evidence as to how parents and nests form part of an incubation unit; behaviours like building and maintaining the nest in good condition represent a form of parental care which can have subtle but important effects on the incubation environment (Chapters 3, 5 and 6). In an attempt to link individual responses to climate with population dynamics (Chapter 7), I discussed how the thermal environment, through its effects on physiology, can affect reproduction and survival thus influencing populations as a whole. In this section I will place the results obtained in this study within the broader picture of habitat selection and the evolution of life histories.

An assumption of life history theory is that individuals select an appropriate breeding site at an appropriate time. However, mothers often are presented with a wide selection of potential nest patches varying in quality. Often, the choice that an individual makes does not necessarily reflect its ideal habitat preference. Generally, constraints such as time limitations or poor physiological condition (and therefore decreased competitive ability to access resources) may inhibit their selectiveness and ultimately shape nest site choice. Heterogeneity in habitat can lead to differential selection of patches. When prospective nest users search for a new place to breed, they rely on biotic (e.g. presence of conspecifics, abundance of predators) and abiotic (e.g. microclimate) cues to assess the suitability of that particular site (Martin 2001).

The effect of microclimate of incubation/gestation on neonate phenotype has been studied extensively on many vertebrates. In reptiles, mothers choose nest sites in relation to specific thermal and hydric conditions (Hughes and Brooks 2006), which influence the incubation period and size of hatchlings (Janzen 1993, Brown and Shine 2004). The rate of neonate development of Karoo rats (*Otomys unisulcatus*), depends on the lodge selection by mothers, which provide a favourable microclimate (Pillay 2001). In mound-builder birds (Megapodiidae), Booth and Jones (2002) showed that incubation periods increase with low temperatures, and in addition eggs used 74% more energy than eggs incubated at high temperatures (Booth 1987). In Starlings (*Sturnus vulgaris*), low temperatures lead to extended incubation periods and smaller hatchlings (Reid et al. 2002).

Common Eider nesting preferences have been examined on numerous occasions. All those studies can provide valuable information about the existence of variation between individuals and populations living in different environments. Eiders in this study seemed to form aggregations of nests with high similarity in female attributes (but not nest characteristics) (Chapter 1) suggesting that biotic factors (for example social stimuli) can be important when choosing a nest site. That Eider females tend to nest in close proximity to kin and form family coalitions during reproduction (McKinnon et al. 2006) suggests that nest selection and associated reproductive success could have a genetic component.

Presence of conspecifics can promote selection of a particular habitat by increasing its suitability (for example by increasing protection against predators). High density of conspecifics, on the other hand, can increase the level of competition on a site thereby reducing its value (Krause and Ruxton 2002).

Predation as another important selective pressure shaping nest choices in Eiders has been documented previously (Schamel 1977, Robertson 1995). This has been examined in comparison with selection based on microclimate and energy use (Kilpi and Lindstrom 1997). The conflict between choosing a nest with an optimal microclimate or one that provides protection from predators is often documented in the literature. For example, for Kentish Plovers (*Charadrius alexandrinus*) it was shown that they prefer exposed sites with higher visibility (and lower predation risk) at the expense of heat stress at the nest site (Amat and Masero 2004) as opposed to Ptarmigans (*Lagopus leucurus*), which select sheltered nest sites at the expense of increased risk of predation (Wiebe and Martin 1998). For many Eider populations around the world, predation an important cause of nesting failure (Gerell 1985, Robertson 1995) and population decline (Andersson 2002). In environments where predators are numerous Eiders preferably choose sites without any cover at the expense of deteriorated microclimate (Divoky and Suydam 1995; Noel et al. 2005).

The system used of my study provided a good opportunity to test the effects of microclimate on nest selection in an environment where predation risk is low. Due to the protective measures of the farmers the number of nests lost to predators inside the confinement of the farms is generally negligible and although this most certainly do not exempt females from perceiving predation as a hazard, decreased nesting failure over time could drive individuals of this population to give priority to microclimate properties of nests when choosing a site. As shown in Chapter 2, a large number of females breeding in the area nested in sites that were completely or partially covered (Appendix 1). However, also a large proportion of individuals nested in completely exposed areas, which were in all cases, close to the sea.

Factors like weather and predator abundance may fluctuate in unpredictable ways or choosing individuals might not be capable of assessing accurately their impact on a particular reproductive season. Nevertheless, nest site choice is a context-dependent dynamic process, and as such individuals can improve upon their initial selection. For example, Pinyon Jays *Gymnorhinus cyanocephalus* select nest location favouring concealment or microclimate depending on past experience (Marzluff 1988). Within this study population, nest site selection may reflect long-term optima that may not be advantageous in the short-term (Clark and Shutler 1999). This makes it difficult to create an image of the possible mechanisms through which nest site preferences arise. Despite the fact that in this species the thermal environment has a great impact on body condition and reproduction. The evidence so far suggests that female eiders are well adapted to face environmental demands and decisions made when selecting a nest site based on biotic factors seem to be of higher importance than abiotic factors for Common Eiders in this population.

The habitat determines the microclimate experienced by organisms influencing its physiological condition and consequently its performance through different stages of the life cycle (Huey 1991). Fig.8.1 provides a schematic representation of the interaction between organisms and their physical environments, which is mediated by physiological processes in several ways: in the first place, individuals in better condition are more able to compete for access to breeding sites. In turn, the nest site (by establishing the accessibility to resources) has the potential to influence the energy gain and (through its effects on microclimate) the energetic costs associated with thermoregulation. Furthermore, variation in physiological condition of females determines reproductive success in Eiders (Kilpi et al. 2001, Ost et al. 2003) and many other bird species (Nager et al. 2000, Moe et al. 2002, Parker 2002).

Maternal consequences of the constrains on the selection of a nest patch is that energy expended during incubation can increase if an unsuitable site is chosen (Chapter 2). For the offspring, consequences of poor microclimate can include slow developmental rates, e.g. longer incubation period (Chapter 2). However, individuals in good condition are able to compensate for suboptimal incubation conditions by allocating more time (increasing attentiveness) or energy in order to keep a favourable environment of incubation. In Chapter 5, for example, I showed that even when nest insulation was deteriorated, females were able to maintain incubation temperature within optimal levels. It is generally considered that eggs are isolated from the external environment by the parents who act as a buffer, setting the microenvironment to which the eggs are exposed (Deeming 2002). However it was evident from my data that this is not always the case and that ambient conditions can be experienced by embryos and, depending on the level of parental attentiveness, even when mothers are present in the nest. In this case, it becomes more apparent that mothers can determine the offspring's environment not only by selecting the nest location but also by adjusting their behaviour and therefore both can be considered as maternal effects (Roitberg 1998).

Some nest characteristics (like proximity to water) affected the reproductive success. Nevertheless, the correlations between site characteristics and reproductive success do not necessarily reveal whether they are due to the sites themselves or to attributes of the organisms (Porter 1990; Ens et al. 1992). In Eiders, settlement patterns could be explained by the social structure presented during reproduction, where, family groupings arriving to the breeding grounds choose the highest quality nesting area available at time of arrival (McKinnon et al. 2006). In this case, differences in nesting productivity observed in the study could arise in part with genetic diversity.

Overall, I was not able to detect broad patterns of adaptive responses to nest location or design, and the capacity of eiders to adjust nesting strategies between years needs further investigation. However, effects of nests on fitness are probably detected on the long-term. For long-lived organisms like Eiders it has been proposed that even a small reduction in adult survival would reduce the number of subsequent breeding attempts, thereby greatly lowering lifetime reproductive success (Charlesworth 1980, Curio 1988, Wooller et al. 1992).

Subtle fitness consequences of nest quality were perceived from the experiments where by modifying the thermal regime of an individual, nest design influenced body temperature and thus short-term physiological performance. Although I was not able to measure the effects of nest manipulations on the level of investment in current reproduction, it has been shown that females in poor condition abandoned their chicks, which leads to lower survival (Bustnes and Erikstad 1991, Kilpi et al. 2001). Poor physiological condition of mothers at the end of a breeding season increases the reproductive costs in terms of future reproduction, as a consequence, individuals might have to adjust their reproductive strategies, decreasing clutch size or even not breeding in particular years (Yoccoz et al. 2002). However, fluctuations in the thermal environment can lead to annual variations in factors such as resource availability and population density, making difficult the prediction of optimal reproductive strategies (McNamara et al. 1995). Furthermore, it is likely that switching strategies have adaptive benefits (Martin 1988), which in my study may also explain some of the variability in nest site choices that I documented.

Breeding success in birds depends on the variability of individual life-history traits (female body weight, clutch size, incubation period), environmental conditions and covariations between these parameters (Fig 1), Climate as and environmental factor has a strong impact on populations of long-lived birds. Through the different chapters of this thesis I tried to include a dual level (individual and population) in my analysis of the environmental effect on reproduction of Eiders. I found that temperature influenced at the individual level, the incubation period, incubation effort, and at the population level it was correlated with onset of laying and fluctuation in colony size, clearly indicating (as in previous studies; Gabrielsen et al. 1991, Lehikonen et al. 2006) that this species relies on favourable climate conditions for reproduction. While this study investigated the interaction between environmental variability on reproductive performance and demography of a capital breeder species, it did not consider effects of climate on adult survival, which is a very responsive parameter in population dynamics of long-lived organisms (Stearns 1992). Future work investigating fitness consequences of environmental conditions during reproductive stages needs to assess the influence of food availability in conjunction with habitat quality on breeding success and adult survival.

The recognition that investigating about the decisions that animals make when selecting habitats is important for conservation is not new but much work still has to be done to determine the influence of the environment on habitat choice and other life history traits. This acquires more importance as the vast evidence of the increasing unpredictability in climate has shown in recent decades. There is much work to be done on this topic but this thesis illustrated some ways in which individuals can respond to changes in environmental conditions. This is essential in developing strategies aimed at habitat protection and species conservation (Sutherland 1998). Many Eider populations around the world are in decline, and although the causes have been mainly ascribed to human-related activities their relative importance probably varies among populations and is still largely unknown (CAFF 1997).

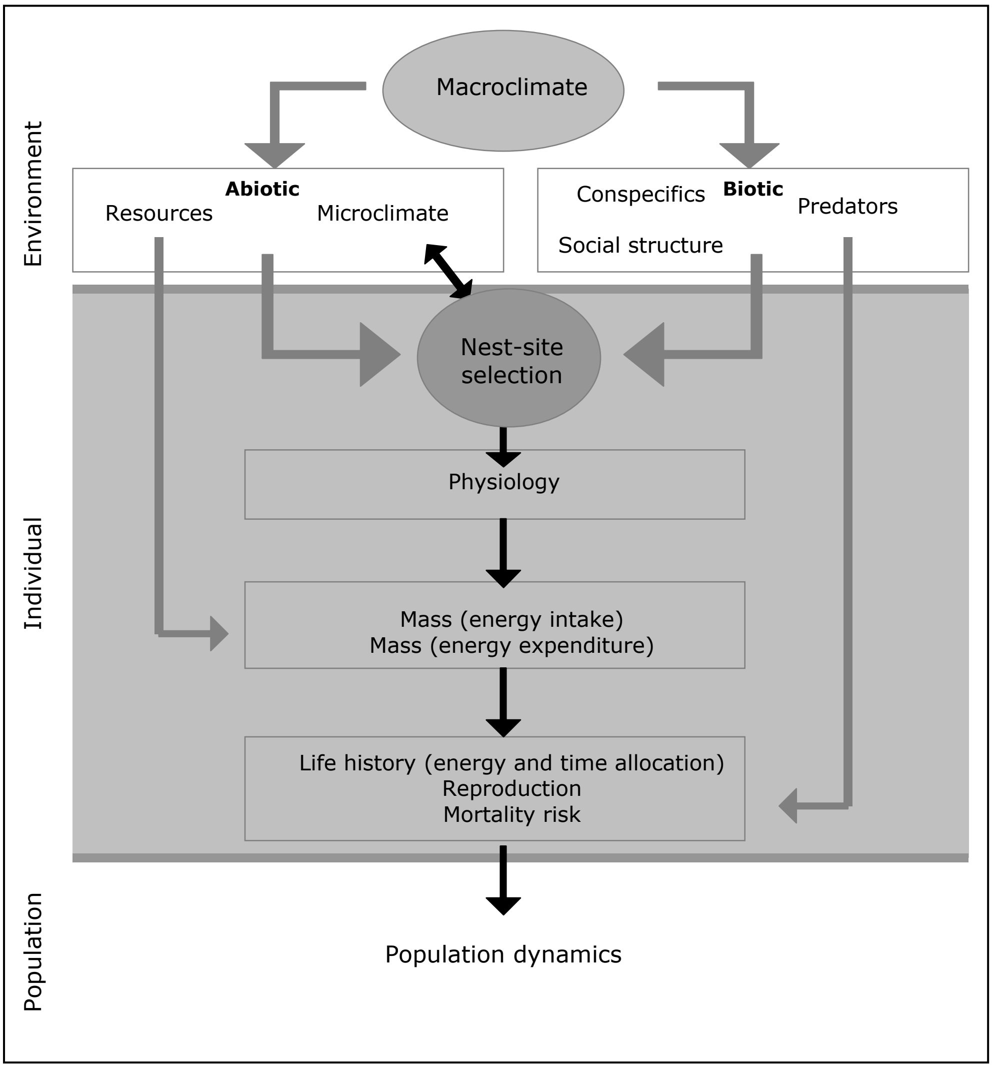


Fig 8.1. Associations between climate, individual properties and population dynamics. Nest influences microclimate, which in turn determines energetics of incubation and ultimately reproductive performance. These effects are mediated by physiology of the organism. By modifying life history of individuals, nesting habitats can impact population processes. Modified from Porter et al. (2000).

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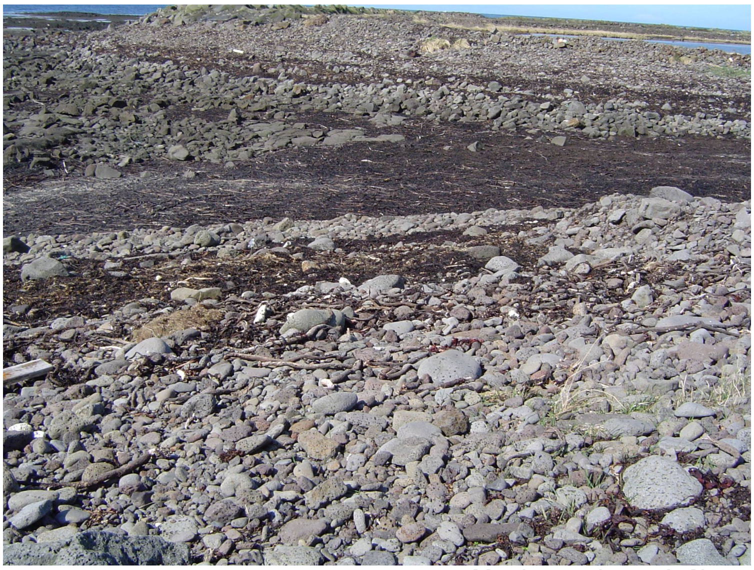
APPENDIX 1

Map of the study area
Nordurkot is located in the municipality of Reykjanesbær, SW Iceland, the large re large rectangle (broken line) shows the area from which the nests were sampled for the entire study in 2004 and 2005. The small rectangle denotes the study plot used in Chapter 1. Image was obtained from Google Earth (V3.0, 2005)

APPENDIX 2

Types of nesting sites found in Nordurkot, Iceland.



All Photos by LD'Alba

Examples of types of nesting sites chosen by female Eiders in the study area.

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