General and Comparative Endocrinology 172 (2011) 218–224

Contents lists available at ScienceDirect

General and Comparative Endocrinology

journal homepage: www.elsevier.com/locate/ygcen

State dependent effects of elevated hormone: Nest site quality, corticosterone levels and reproductive performance in the common eider

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ARTICLE INFO

Article history:
Received 20 April 2010
Revised 7 March 2011
Accepted 9 March 2011
Available online 16 March 2011

Keywords:
Nest shelter
Baseline corticosterone
Reproductive success
Common eider

ABSTRACT

Nest shelter in incubating birds is of major importance in providing protection against unfavourable conditions such as harshness of the environment and exposure to predators. We examined the link between nest shelter, baseline corticosterone (CORT) levels and hatching success in common eiders (*Somateria mollissima*) incubating at nest sites with different levels of shelter. Since more sheltered nest sites could be occupied by better-quality females, we also used an experimental manipulation of nest shelter to separate the effects of the physical attributes of the nest site from those of individual quality. We compared birds with naturally sheltered nests, exposed nests and exposed nests provided with artificial nest shelters and measured clutch size, body condition, CORT levels at the end of incubation and hatching success. If nest shelter reduces CORT levels, we predicted that CORT levels would be highest at the least sheltered sites, and that the provision of artificial shelter would reduce CORT levels. We found that nest shelter was not related to CORT levels in incubating eiders. Nest shelter, however, affected body condition, with females at exposed sites losing more body mass during incubation than females at naturally and artificially sheltered nests. Interestingly however, in those birds nesting at the exposed sites, with and without artificial shelter, those with the highest CORT levels had the lowest hatching success. This relationship was not evident in females nesting at naturally sheltered sites. These results suggest that the level of nest shelter does not directly affect CORT levels in females. Instead, we suggest that the relationship between CORT levels and hatching success is state-dependent. Exposed sites are occupied by individuals that laid smaller clutches, and hence are likely to be of lower quality, and the negative effects of elevated CORT on hatching success are more pronounced in these females.

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1. Introduction

Nest site quality affects both avian reproductive success and the costs to parents of achieving this success [28,52]. This is because attributes of the nest and the nest site can have a considerable influence on the harshness of the conditions experienced by breeding birds [25,38,42,50]. Nest shelter, for example, can provide valuable protection from extreme weather [49,64], safety in social conflicts with neighbours [7] and protection from predators [8,23]. Consequently, birds at exposed sites might be subjected to more stressful conditions during breeding, which could negatively affect their reproductive success.

Exposure to stressful conditions promotes the release of glucocorticoid hormones, mainly corticosterone (CORT) in birds, via the activation of the hypothalamic pituitary adrenal or 'stress' axis [58,59]. This hormonal response to environmental stimuli ensures an adaptive regulation of energy balance in suboptimal conditions [18,60]. However, prolonged elevation of baseline CORT can alter the physiology and behaviour of breeding birds resulting in reallocation of resources from reproduction to self-maintenance [51,61]. Few studies have investigated the relationship between CORT and reproductive success and only some of these have found the predicted negative correlation between elevated CORT levels and health and/or reproductive performance (reviewed in [2,5]. Relationships between CORT and fitness might not be causal, but arise because CORT levels covary with other factors that influence fitness, for example access to food, body condition and habitat quality (e.g. [30,32,45,55]. Accordingly, the relationship between CORT levels and fitness could be context-dependent and vary amongst different fractions of the population [2,4].

Quality of the nest site is one such factor that could influence both reproductive success and circulating CORT levels. Low temperatures [31] and increased predation risk [12] produce elevations of baseline CORT. By locating their nests in well-sheltered areas, parents could ameliorate these stressful conditions during incubation (exposure to low temperatures, [16,36] and/or preda-

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0016-6480/$ - see front matter Published by Elsevier Inc.
doi:10.1016/j.ygcen.2011.03.006

tion risk, [20] and, by experiencing less environmentally induced stress, increase their reproductive performance [16,36]. However, competition for access to better quality sites often occurs and better quality or older individuals may occupy the best nest sites [46]. Hence, potentially confounding effects of a positive covariation in nest site and individual quality need to be taken into account.

Here we examine whether the relationship between nest site quality and reproductive performance could be mediated via variation in circulating levels of baseline CORT in the common eider (*Somateria mollissima*). The present study aimed specifically to examine the extent to which reduced nest site quality, in terms of reduced nest shelter, is associated with increased circulating CORT levels in incubating birds and how variation in circulating CORT levels are related to variation in fitness as indicated by measures of reproductive performance. Eider ducks are capital breeders and incubation is carried out by females only; females fast throughout the incubation period [39,48] and can lose up to 40% of their initial body mass [24]. Breeding success in eiders has been linked to stress hormone exposure, with experimental elevation of CORT levels in incubating female common eiders leading to a higher rate of egg loss [15]. There is large variation in nest site quality amongst females [16,35,50]. Exposure of incubating eiders to environmental stressors is likely to be influenced by nest site quality. Shelter at the nest site, usually provided by vegetation, offers more favourable thermal conditions for females leading to lower body mass loss during incubation and a higher hatching success compared to more exposed nest sites [16].

The relationship between nest site quality, baseline CORT levels and hatching success (a measure of reproductive success during the incubation period) was investigated in two ways. Firstly, we compared the CORT levels of females incubating at naturally sheltered and exposed nest sites. We predicted that females nesting at exposed sites would have higher levels of CORT than females nesting at sheltered sites since they experience consistently higher levels of external stressors. Secondly, to control for the fact that nest site quality may be linked to female quality, we experimentally provided artificial nest shelters to a sample of birds nesting at exposed sites. If the hypothesis that exposure to harsh conditions at nest sites is stressful is correct, we would expect that the provision of shelter to females incubating at such sites would reduce their baseline CORT levels. We also examined the extent to which baseline CORT levels were related to hatching success in females in all groups.

2. Methods

The study was performed from April to June 2005 at Norðdurkot (Reykjanes Peninsula, SW-Iceland). Every year ca. 2000 eider pairs nest in an area that varies greatly in the amount of vegetation cover, from salt marsh grasses dominated by *Agrostis stolonifera* and *Puccinellia maritima* to patches lined exclusively with brown algae *Pelvetia canaliculata*. Nesting birds in the area are accustomed to close and regular presence of farmers, who collect the down lining of the nests at the end of the incubation period for commercial purposes. The study area was searched daily for newly-constructed nests and marked with inconspicuous numbered sticks. Nests were selected randomly for inclusion in the study and selected nests were visited daily from the nest building stage throughout laying and incubation until the entire clutch hatched (usually 26 days after the first egg in the clutch being laid; [47]. We recorded the fate of all eggs in a clutch (i.e. hatched or not), and inspected all unhatched eggs for signs of embryo development and microbial infection (presence of gas and/or black-green colouration when opening the egg) to obtain the cause of hatching failure: loss to predation, infection or abandonment.

2.1. Nest shelter

At the beginning of incubation, before females were caught, we assessed the degree of natural nest shelter for all nests following the methods given in [16]. Briefly, we analysed pictures (using ImageJ software v.1.36) taken from above each nest to measure the percentage of the nest circumference covered by surrounding vegetation and/or rocks within a 0.5 m radius of the nest cup. Vegetation around nests did not change 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 (D'Alba, pers. obs.). Nests were classified into two categories: exposed (no vegetation and/or rocks within 0.5 m radius of the nest cup) and sheltered (mean coverage 58 ± 4.21% (min–max: 25–84%); mean vegetation height 20 ± 1.49 cm (min–max: 12–23 cm, $N = 14$). About a fifth of female eiders nest at exposed sites although there seemed to be plenty of unoccupied sheltered nest sites and they did not start breeding later than females nesting at sheltered sites [16]. The sample of nests included in this study comprised 37 nests that were evenly distributed across the colony; fourteen nests were sheltered and 23 were exposed. A larger sample of exposed sites was used to enable experimental manipulation within this group.

2.2. Female state

Females were caught at each of the study nests early in incubation and again shortly before hatching using a landing net. Only one female nesting at a sheltered site that was caught during early incubation abandoned her clutch after a bad storm and before she was caught a second time, and was therefore not included in the sample of 37 study nests. Female birds were caught for the first time, measured (head-bill, tarsus and wing length) and weighed all by the same person (L.D'A) on average 5 ± 0.36 days ($N = 37$) after the first egg was laid. At the time of first capture, artificial shelters at the experimental nests (see below) had been in place for approximately two days. Incubation in eiders generally starts after the third egg is laid [26,44]. We considered the start of incubation as the day on which the fourth egg was laid. There was no difference between the three nest shelter groups in the incubation stage at the time of first capture of the females ($F_{2,34} = 0.22$, $P = 0.80$). All females were caught again 18.3 ± 0.39 days ($N = 37$) after the first capture (on average two days before the eggs hatched) and there was no difference in the time of capture between the shelter groups ($F_{2,34} = 0.49$, $P = 0.61$). At the second capture, a single blood sample (100 μl) was taken from the brachial vein with a 25 gauge needle within 3 min of approaching the nest to determine baseline levels of corticosterone [62]. Blood was collected in heparinised capillary tubes, centrifuged and the plasma stored at −20 °C for subsequent hormone assays. Female mass loss between the two capture events was expressed as a percentage of the body mass at the first capture. In order to have a single measure of female structural size, we ran a Principal Component Analysis (PCA) on three body size measurements (tarsus, head-and-bill, and wing length); the first principal component PC1 was positively related to the three body size measurements ($r > 0.70$) and explained 63% of the variance. PC1 was therefore used as an integrated measure of body size. We estimated female condition at the start and end of incubation using the residuals of a regression between female mass at first ($r = 0.50$, $P = 0.001$, $N = 37$) or second ($r = 0.54$, $P = 0.001$, $N = 37$) capture and body size.

Corticosterone (CORT) concentrations were measured in these blood samples after extraction of 20 μl aliquots of plasma in diethyl ether by radioimmunoassay [41,58] using anti-corticosterone antiserum code B3-163 (Esoterix, USA) and "1,2,6,7-3H"-