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Boldness and Stress Responsiveness as Drivers of Nest-Site Selection in a Ground-Nesting Bird

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Abstract

Nest-site selection involves trade-offs between the probability of nest discovery by egg predators, danger to the incubating parent from predators and provision of an appropriate microclimate for incubation, and all three components are potentially influenced by nest concealment and distance to habitat edge. Personality traits also affect habitat choice, and the trade-off hypothesis suggests that variable stress-coping strategies may evolve because individuals prioritize either productivity (proactive coping) or survival (reactive coping), both of which cannot be simultaneously maximized. Applying this hypothesis to understand nest-site selection by female eider ducks (*Somateria mollissima*), we predicted that bold individuals with attenuated stress responsiveness should select concealed nests further away from the shore, thereby promoting clutch survival at the potential expense of reduced escape opportunities for themselves. In testing this prediction, we controlled for individual quality (female body condition and breeding experience) and verified that individual stress responses and nest-site preferences were consistent by analysing their repeatability. Finally, we analysed how the viable proportion of the clutch was related to nest-site and female characteristics. Our prediction was supported: bold females [short flight initiation distance (FID)] and those with lower handling-induced body temperature were found in concealed nests, and bold females and those with lower handling-induced corticosterone concentrations occupied nests farther from the shore. The viable proportion of the clutch peaked at intermediate proportional nest-cover and increased linearly with increasing nest distance from the shore. Stress coping styles may thus be related to nest-site selection, but their fitness consequences may be manifested indirectly through the nest-site characteristics.

Introduction

The selection of suitable breeding habitat is essential to the fitness of all animals, and selection should drive animals towards choosing an optimal breeding site (Jaenike & Holt 1991; Martin 1998; Clark & Shutler 1999). Habitat choice is intimately related to individual differences in personality traits (Sih et al. 2004), where personality (defined in the broad sense; Réale et al. 2010) refers to consistent individual behavioural differences which are likely to be influenced by or co-vary with individual quality measures (Luttbeg & Sih 2010). Despite the assumed link between habitat choice and personality, the consequences of personality-dependent habitat preferences remain understudied (but see Duckworth 2006; Boon et al. 2008). This is unfortunate as a non-random distribution of behavioural types in space implies that they will face different selection pressures on all aspects of their phenotype. Consequently, the influence of personality traits on habitat selection has been highlighted as one of the major themes in personality research (Wolf & Weissing 2012).

Predation is the dominant cause of nest failure in egg-laying animals (Martin 1993; Spencer 2002) and thus exerts a strong selection pressure on breeding habitat selection. Variation in nest attributes are likely to be associated with variable nest predation rates (Martin 1998). Nest sites that reduce the risk of predation on the adult or the young, however, might be less beneficial in terms of other qualities. These other nest-site qualities include the provision of a suitable thermal environment, influencing embryonic or postnatal development, and in birds incubation efficiency and the state of the incubating parent (Walsberg 1985). For birds, the requirements of nest safety and benign thermal conditions often cannot be maximized simultaneously (Amat & Masero 2004). It is conceivable, but as yet untested, that individuals differing in stress physiology and correlated risk-taking behaviours (bold and shy individuals *sensu* Réale et al. 2007) may place a different premium on safety from predation as opposed to other qualities of the breeding habitat (cf. Seltmann et al. 2012).

Conflicts may also arise regarding the safety of the parent as opposed to clutch safety, particularly in ground-nesting birds that have limited possibilities for escape. While nest concealment may reduce the chance of detection by a predator (Albrecht & Klvaňa 2004), thereby reducing clutch predation (Öst et al. 2008b), a parent in a concealed nest may in fact suffer from higher predation risk because the dense cover may interfere with its ability to escape, should a predator detect it (Öst & Steele 2010). Furthermore, nest cover will hamper the ability of the parent to gather information about nearby predators, thereby increasing its information deficit (Schneider & Griesser 2013). Hence, nest-site selection may involve a trade-off between low probability of detection vs. enhanced escape opportunities and information about potential predators (Götmark et al. 1995). Personality could play a central role in determining how individuals resolve this trade-off. Thus, bold and high risk-taking individuals may rely on crypsis and cope with the stress of hiding from predators in well-concealed nests, whereas shy and low-risk-taking individuals may place a higher premium on information about predators and ample escape opportunities (proactive vs. reactive coping *sensu* Koolhaas et al. 1999).

Besides depending on nest microhabitat features, the risk of nest predation may differ between interior and edge habitat (Donovan et al. 1997). For ground-nesting waterbirds, the shoreline represents a sharp boundary, likely to affect patterns of predation on adults and offspring alike. This is because clutch predation rates may peak at the habitat edge (in this case, the shoreline) (cf. Lloyd et al. 2005), whereas the survival of adults and hatched young may concurrently increase. The latter effect could arise because fleeing into the water from a shoreline nest may provide adults swift escape from aerial and mammalian predators (Bentzen et al. 2009), while also minimizing brood overland movements, when they are most vulnerable to predation (Gunness et al. 2001). Accordingly, we may speculate that bold and high risk-taking individuals might place a higher value on protecting their clutch at the potential expense of their own survival, and, hence, choose nest sites farther from the shoreline. However, to our knowledge, this possibility has never been tested.

Several studies have investigated how nest-site characteristics affect risk-taking behaviours (Albrecht & Klvaňa 2004; Osiejuk & Kuczyński 2007) and stress physiology (D'Alba et al. 2011). However, experimental evidence in eider ducks *Somateria mollissima* suggests that the nest-site characteristics themselves may not directly influence the traits of the incubating parent, but rather that individuals may show consistent differences in their nest-site selection (D'Alba et al. 2011). Based on this experimental evidence, we therefore asked whether individuals of different personality types differ in their habitat preferences regarding nest concealment and distance to habitat edge, while acknowledging that our correlational study cannot infer causality between female and nest-site characteristics (see Discussion). Our study species, the eider, is well suited for this investigation, because it is a long-lived, precocial capital breeder, in which the female is the sole incubator, and in which both eggs (Öst et al. 2008b) and incubating females (Jaatinen et al. 2011; Ekroos et al. 2012) are subject to significant predation pressure. Nesting habitat characteristics vary greatly between females (Öst & Steele 2010), and this natural setup allowed us to study the influence of individual female characteristics on nest-site selection.

We tested the hypothesis that bold females with a short FID (Seltmann et al. 2012) and attenuated stress responsiveness (low handling-induced rise in corticosterone and body temperature) select concealed nests further away from the shore. To this end, we first verified that individuals actually responded to our handling procedure by a significant increase in corticosterone concentrations and body temperature, two measures which may be related to personality (Carere & van Oers 2004; Seltmann et al. 2012). We then analysed repeatabilities of nest-site characteristics and our two measures of stress responsiveness, as repeatability or individual consistency is a

pre-requisite for an effective selection acting on the trait. Next, we tested whether stress response profiles and preferences for nest-site characteristics were repeatable within individuals. Finally, we quantified the fitness effects, in terms of the viable proportion of the clutch, of nest-site characteristics and female-specific traits (boldness, stress responsiveness, individual quality). As there is evidence suggesting that the shape of selection on personality traits may vary depending on environmental conditions (e.g. Dingemanse et al. 2004), we also tested for the shape of selection (directional, stabilizing or disruptive) on the viable proportion of the clutch as a function of nest cover and distance to water.

Methods

Study Area

The study was conducted on a well-studied eider population in the archipelago surrounding Tvärminne Zoological Station (59°50′N, 23°15′E), on the Baltic Sea in south-western Finland, in 2010–2011. Female eiders breed in two contrasting habitats: on small open granite islands (n = 10), which are sparsely covered with patches of grasses, herbs or occasionally junipers (*Juniperus communis*) or on larger forested islands (n = 8), covered by closed stands of pine (*Pinus sylvestris*) and spruce (*Picea abies*) with an understory of juniper and other shrubs. Island area ranged from 0.18 ha to 10.49 ha (Lindström 2003). White-tailed sea eagle (*Haliaeetus albicilla)*, eagle owl (*Bubo bubo*), mink (*Neovison vison)* and raccoon dog (*Nyctereutes procyonoides)* are the main predators of incubating females, and hooded crows (*Corvus corone cornix*) and gulls (*Larus* spp.), the main egg predators. Females nest on the ground in two distinct habitats: large forested islands and small open islets. In both habitats, there is high variation in nest-site attributes, from completely uncovered nests on bare rock to hardly visible nests in dense shrubbery that are almost completely covered. Furthermore, female nest cups can be found along a gradient from shoreline to the centre of the islands. All study islands are protected by a prohibition on landing.

Measurement of Nest-Site Attributes

The coordinates of all nests were recorded using a Garmin Map76 GPS receiver (Garmin, Olathe, KS, USA). Nest cover was measured with a 42-mm Opteka fisheye lens mounted on an Olympus C-740 digital camera placed on a board level within the nest rim and aimed directly upwards. Photographs were analysed with the Image Tool program (v. 3.00; University of Texas Health Science Center, San Antonio). They were first converted to greyscale and then the pixels were converted to either black or white using a threshold controlled by the user. The threshold was adjusted so that all sky was white while all vegetation and rocks were black. This was impossible with a blue sky, so only photographs taken on a cloudy day were used. The program then counted black and white pixels giving an accurate measure of proportion cover. Photographs of all nests were taken in an as short an interval as possible after hatching to reduce any bias caused by vegetation growth during the field season. To evaluate the distance from the nest cup to the nearest shoreline, the GPS coordinates of each nest were entered into ESRI ArcGIS Version 9.3 and placed on to a spatially referenced base map of the 35 islands that border Tvärminne Zoological Station. Once in the right projection (Finland_*ZONE*_2), using the arc toolbox and editor, a poly-line was created from the nest site to the nearest edge of the island. Defining the edge was clear because the Baltic Sea has minimal tides. The distances of these lines were estimated by using the planar measurement type.

Female Trapping and Measurement Protocol

We captured incubating females on their nests using hand nets. Trapping took place predominantly during the end of the incubation period in May or early Jun to minimize nest desertion. Potential researcher-induced nest desertion is largely restricted to the early phases of incubation, whereas the frequency of nest visits does not influence the probability of nest desertion, provided that the first visit is timed to the later phases of incubation (Bolduc & Guillemette 2003). Female handling procedures were approved by the Animal Experiment Board/State Provincial Office of Southern Finland, the authority issuing the permit number ESLH-2009-02969/Ym-23 under which we performed this research. Female trapping procedures also complied with the specific regulations of the Tvärminne Zoological Station. A more detailed account of the ethics involved in female capture is given by Kilpi et al. (2001).

Trapped females were ringed with a standard metal ring, weighed on a spring scale (to the nearest 10 g), and the length of the radius-ulna (to the nearest 1 mm) was recorded. We calculated the number of years since the bird was first ringed as a (minimum) estimate of years of maternal experience (Öst et al. 2008a; Öst & Steele 2010; Jaatinen & Öst 2011). This

is a reasonably accurate indicator of age because more than half of the successfully breeding females on our study islands are trapped annually (e.g. trapping success in 2003–2009: 55.8 ± 0.14%, (SD): Jaatinen & Öst 2011), females show almost absolute fidelity to their breeding island (Öst et al. 2011) and annual trapping effort has been similar since 1996 (Öst et al. 2003). The incubation stage was estimated by an egg floatation test (Kilpi & Lindström 1997). Based on incubation stage, we estimated female body condition at hatching by regressing the log-transformed projected weight at hatching against the log-transformed radius-ulna length and using the standardized residuals as a condition index (data from all years were pooled to obtain a global index). Females do not feed during incubation, and so the assumption of continued weight loss after female capture is valid in our study population, justifying our method for estimating body condition (Öst & Steele 2010). The projected weight at hatching was obtained by subtracting the expected weight loss (by calculating the expected number of days before hatching, based on incubation stage) from the body weight measured at capture. We caught females at different incubation stages, which enabled us to quantify average weight loss by regressing the logarithm of body weight against the logarithm of incubation time and projected hatching date (Öst et al. 2008b).

The FID of captured females, indicating their boldness (Seltmann et al. 2012), and the viable proportion of the clutch were determined while re-visiting the nests. We measured the proportion of eggs hatching rather than their absolute number, because undetected partial clutch predation during early egg laying, when the nest is completely unattended, is higher in nests offering little concealment (Öst et al. 2008b). We timed these nest visits so as to coincide with the estimated hatching date of the female's clutch, based on egg flotation when originally captured in that season (see above). FID was the distance at which the focal female fled following a standardized approach of an investigator (see Seltmann et al. 2012 for details), and it was measured to an accuracy of 10 cm. Because broods were not always completely hatched at our nest visits, we frequently obtained repeated FID measurements in the same season. Most females left their nests while we were approaching the nests, with only a small number of females that never left the nest. Females always returned to their nests, since we never encountered an abandoned nest during these repeated visits. There was no habituation effect on FIDs caused by repeated exposure to observers, because FIDs did not change systematically within individuals (Seltmann et al. 2012). Mean annual FIDs were used in the statistical analysis for birds for which repeated measures were available.

The viable clutch size was the number of live ducklings if the brood was still present in the nest (any unhatched or attacked eggs or dead ducklings were disregarded); in case the brood had left the nest based on signs of successful hatching, the number of unviable eggs or ducklings was subtracted from the clutch size at female capture, to get viable clutch size. Determining successfully hatched eggs was generally straightforward, because hatched eggs have an intact leathery membrane, while eggs attacked by predators typically leave shattered shells with the membrane, usually bloody, still attached to the shells (Öst & Steele 2010). While it is possible that eggs may have been attacked and carried away in between the brood leaving and us arriving at the nest, this is unlikely, because the time interval was short (usually <24 h) and because attacked eggs are typically eaten in the immediate nest surroundings, leaving plenty of shattered shell fragments.

We measured baseline and handling-induced serum corticosterone (CORT, the main avian stress hormone) concentrations and body temperatures. The blood samples were obtained by extracting approximately 1.5 ml of blood from the ulnar vein, and the timing of sampling since capture was monitored with a stopwatch. The first sample was taken immediately after female capture (usually within 3 min; mean ± SD = 2.8 ± 0.5 min, n = 142). The second sample was taken after all handling and marking procedures were complete (mean ± SD = 16 ± 4 min, n = 142). Blood samples were immediately stored on ice in a cool box, transported to the laboratory within 2–4 h and centrifuged (Sigma 3K12, B. Braun, Germany) at 1500 ***g*** for 10 min to separate the serum. The serum was then transferred into 1.5 ml reaction tubes (Micro tubes 1.5 ml PP, Sarstedt, Germany) and stored frozen at −20°C until analysis. Body temperature was measured twice from the cloaca, immediately after the first and just before the second blood sample, respectively, with a veterinary thermometer (VT 1831, Microlife AG, Switzerland) to the nearest 0.1°C.

Corticosterone Radioimmunoassay (RIA)

A validation of the serum corticosterone RIA kit (ImmuChem™ Double Antibody, Corticosterone, ^{125}I RIA Kit, MP Biomedicals, Orangeburg, NY, USA) for eiders is provided by Nilsson (2004). Intra-assay coefficients of variation were <10%, and mean assay sensitivity

was 13.1 ng/ml. Manufacturer cross-reactivity with other steroids were: desoxycorticosterone (0.34%), testosterone (0.10%), cortisol (0.05%), aldosterone (0.03%), progesterone (0.02%) and <0.01% for all other steroids tested. RIA values were corrected for dilution and extraction efficiency and expressed as ng/ml. The RIAs were performed according to the manufacturer's instructions with the exception that all volumes were halved (cf. Mashburn & Atkinson 2004).

Data Analysis

To study potential changes in serum CORT concentrations and body temperatures in response to our handling procedure, we used a linear mixed model (LMM) fitted using restricted maximum likelihood (REML) estimation and treatment (before/after handling) nested in female identity as a random effect. Repeatabilities were analysed using the rpt.remlLMM, rpt.binomGLMM.multi and rpt.remlLMM.adj functions from the R software package rptR (Nakagawa & Schielzeth 2010). Adjusted repeatability (rpt.remlLMM.adj, Nakagawa & Schielzeth 2010) of nest distance to shore was used to correct for variation due to island identity, because, for example, some distances on larger islands were recorded that cannot be found on the smaller islets. In these repeatability analyses, we log-transformed the data on nest distance to shore and handling-induced CORT concentrations. Where available (cf. Table 1), we augmented our data with records from 2008 to 2009 and 2012 in the repeatability analyses to improve statistical power.

Baseline and handling-induced body temperatures were highly collinear ($r = 0.9$), and because only the latter variable has been linked with personality and stress responsiveness (Cabanac & Guillemette 2001; Carere & van Oers 2004), baseline body temperature was not included in further analyses. Likewise, because time of day did not affect baseline (LMM with female ID as a random effect: $F_{1,14} = 0.22$, p = 0.65, n = 142) or handling-induced CORT concentrations ($F_{1,14} = 0.14$, p = 0.72, n = 142), nor handling-induced body temperatures ($F_{1,14} = 1.70$, p = 0.21, n = 142), this variable was not considered further. There may be potential interactions between individual and habitat quality (D'Alba et al. 2011), between individual quality, stress responsiveness and personality traits (Luttbeg & Sih 2010, Seltmann et al. 2012) and between individual quality and hatching success (Lehikoinen et al. 2010; Öst & Steele 2010). We therefore controlled for individual quality measures (body condition, breeding experience) in all analyses. Initially, we tested for significant two-way interactions between personality traits (FID, handling-induced CORT concentration and body temperature) and individual quality attributes (female body condition, minimum breeding experience) on the response variables, but none were found.

We assessed the effects of FID, female body condition and minimum breeding experience, baseline and handling-induced serum CORT concentration, handling-induced body temperature and date of incubation onset on the amount of nest cover. To this end, we constructed a generalized linear mixed model (GLMM) with a binomial error distribution, fitted using Laplace estimation and female identity as a random effect to account for repeated measurements of the same individuals. In the analyses, we controlled for variation in capture-to-sampling durations by including the time elapsed between the first blood sampling and female capture and the second blood sampling and female capture as covariates (cf. Tables 2 and 3).

To test the effects of FID, female body condition and minimum breeding experience, baseline and handling-induced serum CORT concentration, handling-induced body temperature and date of incubation onset on nest distance from the shoreline, we used a LMM, fitted using REML estimation and female identity nested in island identity as a random effect. This random effect was used to account for repeated measurements of the same individuals and the fact that nest distance from the shoreline is strongly dependent

Table 1: Repeatability estimates for nest distance to shore (adjusted for island identity as a factor), proportional nest cover, handling-induced CORT concentration and handling-induced body temperature

Trait	Years	*R*	SE	CI	p	*n*
Nest distance to shore (adj)	2008–2012	0.20	0.04	0.11, 0.27	<0.001	531 (213)
Proportional nest cover	2008–2012	0.22	0.05	0.10, 0.24	<0.05	620 (238)
Handling-induced CORT	2009–2011	0.27	0.09	0.12, 0.42	<0.05	240 (110)
Handling-induced body temperature	2010–2012	0.25	0.07	0.09, 0.37	<0.01	320 (147)

Shown are the years of observation, the repeatabilities and their associated standard errors, 95% confidence intervals and p-values and the number of observations and individuals (in parentheses).

Table 2: Model selection and generalized linear mixed model (GLMM) (binomial error distribution, logit link function and female identity as random factor) to test the influence of a set of variables on proportional nest cover

Dependent variable	Independent variable	Parameter estimate	Standard error	p-value
Proportional nest cover	**Mean flight initiation distance (cm)**	−0.0014024	0.0006427	0.02
n = 142/127	Body condition	0.0704128	0.2156437	0.74
	Breeding experience (years)	0.0002455	0.0580641	0.99
	Baseline CORT (ng/ml)	0.0005146	0.0099779	0.95
	Time to first blood sample (s)	0.0108543	0.0086647	0.19
	Handling-induced CORT (ng/ml)	0.0008676	0.0046586	0.85
	Time to second blood sample (s)	−0.0002009	0.0011327	0.85
	Handling-induced body temperature (°C)	−0.4976738	0.2596587	0.049
	Incubation onset	−0.0148023	0.0399694	0.71

The final model (in bold) was selected by removing all non-significant variables using likelihood ratio tests. Parameter estimates and standard errors given in this table are derived from the starting model. p-values are derived from the likelihood ratio tests.

Table 3: Model selection and linear mixed model (LMM) (normal error distribution and female identity nested in island identity as random factor) to test the influence of a set of variables on nest distance to the shore

Dependent variable	Independent variable	Parameter estimate	Standard error	p-value
Log [Nest distance to shore (m)]	**Mean flight initiation distance (cm)**	−0.0007429	0.0001915	<0.001
n = 142/127	Body condition	−0.127666	0.068787	0.06
	Breeding experience (years)	0.011883	0.018498	0.50
	Baseline CORT (ng/ml)	0.001938	0.003046	0.51
	Time to first blood sample (s)	0.0041346	0.0023050	0.07
	Handling-induced CORT (ng/ml)	−0.0028551	0.0012650	0.02
	Time to second blood sample (s)	−0.000282	0.000354	0.40
	Handling-induced body temperature (°C)	−0.107063	0.083669	0.18
	Incubation onset	0.016546	0.012791	0.18

The final model (in bold) was selected by removing non-significant variables using likelihood ratio tests. Parameter estimates and standard errors given in this table are derived from the starting model. p-values are derived from the likelihood ratio tests.

on island identity which, amongst other things, includes information on island size. We log-transformed nest distance to shore in this analysis to meet the assumption of normality. We also controlled for variation in capture-to-sampling durations by including the time elapsed between blood samplings and female capture as covariates in the analysis.

To assess the effects of nest cover and distance to shore, FID, handling-induced CORT concentration, handling-induced body temperature, female body condition and minimum breeding experience on the viable proportion of the clutch, we constructed a GLMM with a binomial error distribution (viable eggs of a clutch were considered a success, non-viable eggs a failure), fitted using Laplace estimation and female identity as a random effect to account for repeated measurements of the same individuals. Because we were interested in determining the shape of selection acting on nest-site characteristics in terms of their effects on reproductive success (see Introduction), we also tested for possible non-linear effects. Before model selection, we compared the starting model with and without the quadratic terms of nest cover and nest distance to shore explaining the viable proportion of the clutch. We retained the quadratic term of nest cover (ANOVA: $\chi^2 = 7.57$, df = 1, $p < 0.01$) but not of nest distance to shore ($\chi^2 = 0.55$, df = 1, $p = 0.46$) in our starting model. In all three analyses described above, non-significant variables were removed from the final models using likelihood ratio tests. The residuals of all LMMs adhered to the assumption of normality. All statistical analyses were performed in the software R (version 2.15.1; R Core Team 2012), and data are reported as means and standard deviations and sample sizes as observations and individuals unless otherwise stated.

Results

Female Physiological Stress Responses to the Handling Procedure

Our handling procedure induced a significant rise in serum CORT concentrations (LMM: $b = 1.34$, $t =$

29.1, df = 141, p < 0.001, Fig. 1a) and body temperature (b = 0.30, t = 10.9, df = 141, p < 0.001, Fig. 1b). The mean CORT concentration before handling was 32.95 ± 21.28 and 114.53 ± 46.3 ng/ml after handling. Mean body temperature before handling was 40.52 ± 0.67°C and 40.82 ± 0.76°C after handling.

Repeatabilities

Handling-induced CORT concentration and body temperature, nest cover and nest distance to shore all showed significant, albeit moderate, repeatability within individuals, ranging from 0.20 to 0.27 (Table 1).

Nest Cover as a Function of FID and Handling-Induced Body Temperature

Mean proportional nest cover was 0.61 ± 0.29 and ranged from 0 to 0.94. Nest cover was associated with FID and handling-induced body temperature (Table 2): females with shorter FIDs (i.e. bold individuals; GLMM: b = −0.002, z = −2.63, p < 0.01, n = 142/127; Fig. 2a) and a lower handling-induced body temperature (b = −0.52, z = −2.11, p = 0.04, n = 142/127; Fig. 2b) occupied more concealed nests.

Nest Distance to Shore as a Function of FID and Handling-Induced CORT

Mean nest distance to shore was 28.22 ± 21.95 m and ranged from 1.02 m to 92.47 m. Nest distance to shore was associated with FID and handling-induced CORT concentration (Table 3): females with shorter FIDs (i.e. bold individuals; LMM: b = −0.0008, df = 122, p < 0.001; Fig. 3a) and lower handling-induced CORT concentration (b = −0.003, df = 122, p = 0.04; Fig. 3b) were found in nests farther from the shoreline.

Viable Proportion of the Clutch as a Function of Nest Cover and Nest Distance to Shore

Both the linear (GLMM: b = 15.15, z = 2.83, p < 0.01, n = 131/116) and quadratic term (b = −16.07, z = −2.86, p < 0.01, n = 131/116) of proportional nest cover and (linear) nest distance to shore (b = 0.05, z = 2.14, p = 0.03, n = 131/116) affected the viable proportion of the clutch (Table 4). The viable proportion of the clutch first increased with increasing nest cover, but then again decreased in the most concealed nests (Fig. 4a), whereas the observed proportional nest cover showed a bimodal frequency distribution, with many very open and very concealed nests (Fig. 4b). The viable proportion of the clutch also increased with increasing nest distance from the shore (Fig. 5).

Discussion

Our hypothesis that the boldness and stress responsiveness of female eiders would play an important role in determining their nest-site selection was supported by our results. Thus, bolder and less stress responsive individuals were found in more concealed nests farther from the shoreline (i.e. habitat edge). However, it is important to note here that we cannot infer causality between female and nest-site characteristics in the absence of experimental manipulations. Although our findings are correlational in nature and thus in need of confirmation by experimental work, they hinge on previous experimental evidence in eiders, suggesting that individuals consistently differ in their nest-site preferences, rather than the nest-site attributes themselves directly affecting female traits (D'Alba et al. 2011). Furthermore, our stress response measures (handling-induced rise in CORT levels and body temperature) were determined after removing the female from her nest, which lends some further

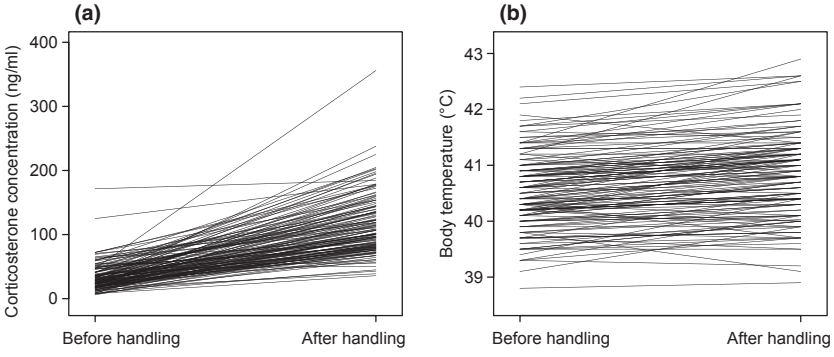

Fig. 1: Individual reaction norm slopes for (a) serum corticosterone and (b) body temperature for concentrations and temperatures before and after handling.

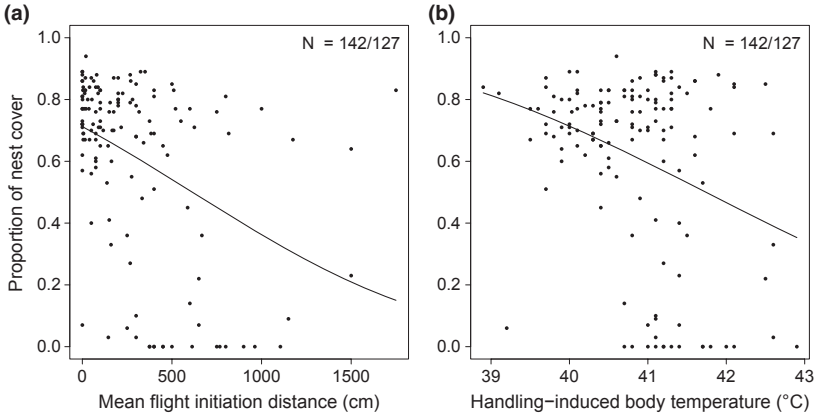

Fig. 2: Proportional nest cover as a function of (a) mean flight initiation distance and (b) handling-induced body temperature. The number of observations/individuals is shown in the upper right-hand corner of each panel.

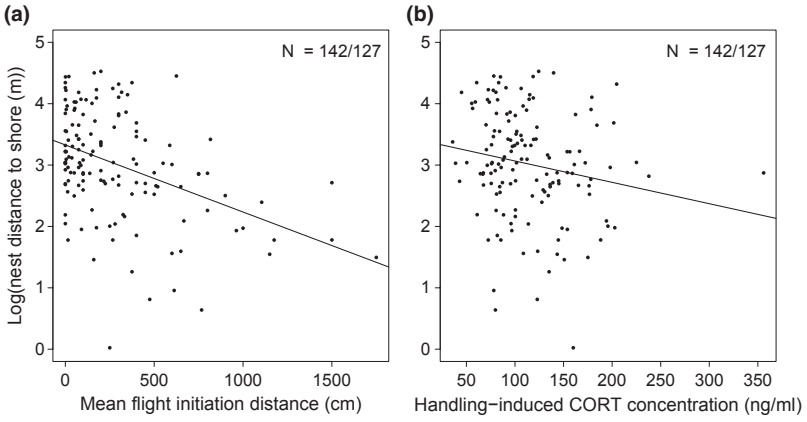

Fig. 3: Nest distance to shore as a function of (a) mean flight initiation distance and (b) handling-induced corticosterone concentration. The number of observations/individuals is shown in the upper right-hand corner of each panel. The line represents the line of best fit for the regression.

Table 4: Model selection and generalized linear mixed model (GLMM) (binomial error distribution, logit link function and female identity as random factor) to test the influence of a set of variables on the viable proportion of the clutch

Dependent variable	Independent variable	Parameter estimate	Standard error	p-value
Viable proportion of clutch	**Proportional nest cover**	15.057792	5.663616	<0.01
n = 131/116	**Proportional nest cover^2**	−15.961348	5.762552	<0.01
	Nest distance to shore (m)	0.040544	0.022907	0.03
	Mean flight initiation distance (cm)	−0.001324	0.001605	0.38
	Handling-induced body temperature (°C)	−0.201465	0.656596	0.73
	Handling-induced CORT concentration (ng/ml)	−0.009595	0.009336	0.26
	Minimum maternal experience (years)	−0.161954	0.140686	0.21
	Body condition	−0.226672	0.441547	0.58

The final model (in bold) was selected by removing non-significant variables using likelihood ratio tests. Parameter estimates and standard errors given in this table are derived from the starting model. p-values are derived from the likelihood ratio tests.

credence to the hypothesis that females with different stress-coping styles may differ regarding their nest-site selection. Interestingly, nest-site choice had fitness consequences which resulted from differences in nest-site characteristics rather from differences in personality traits or state of the females. Thus, nests further away from the shoreline had a higher viable proportion of the clutch. The relationship between nest cover and the viable proportion of the clutch was non-linear, with the highest viable proportion of the clutch produced in nests with intermediate cover, indicating the possibility of stabilizing selection acting on nest concealment. We have previously shown that FID, our measure of boldness towards predators, is highly repeatable (Seltmann et al. 2012). Our present results show that handling-induced CORT concentration and body temperature, as well as nest concealment and distance to shore, were also repeatable

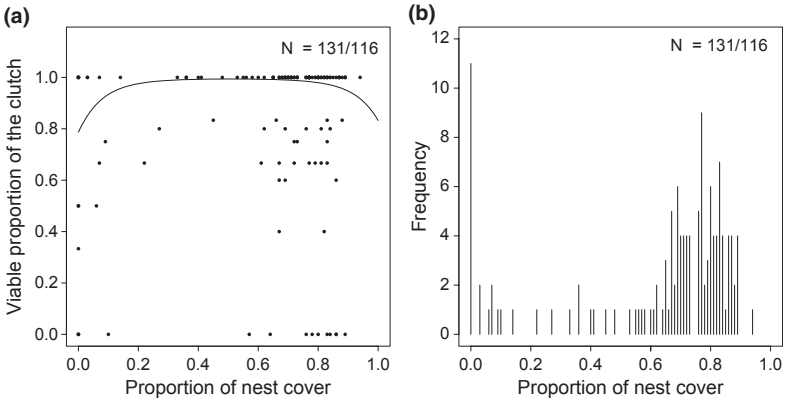

Fig. 4: The viable proportion of the clutch as a function of proportional nest cover (a) and the observed frequency distribution of proportional nest cover (b). The number of observations/individuals is shown in the upper right-hand corner of each panel.

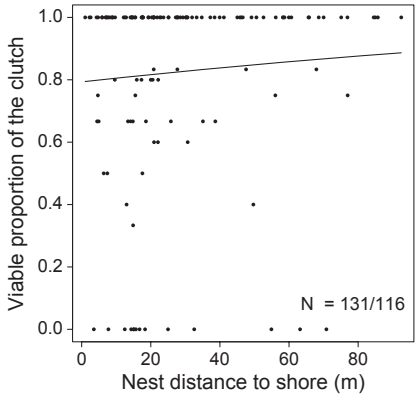

Fig. 5: The viable proportion of the clutch as a function of nest distance to shore. The number of observations/individuals is shown in the lower right-hand corner of the graph.

within individuals over breeding seasons, and thus there is potential for these traits to evolve under natural selection (e.g. Lynch & Walsh 1998). The repeatability of nest-site characteristics is perhaps not entirely unexpected, considering the high breeding philopatry in the population, with a median breeding dispersal distance of only 21 m between seasons (Öst et al. 2011). Although significant, the repeatability of nest-site characteristics was still relatively low. One reason could be that we did not control for nest success in these analyses; breeding dispersal increases after nest failure (Öst et al. 2011), which can potentially reduce the repeatability of nest-site characteristics between seasons. Repeatabilities of stress-induced CORT concentrations have been reported before, under laboratory conditions as in the wild (Cockrem & Silverin 2002; Cockrem et al. 2009; Rensel & Schoech 2011), but to our knowledge, repeatability of stress-induced rise in body temperature has only been studied once recently (Careau et al. 2012).

Whereas CORT responsiveness and female risk-taking propensity (FID) are linked in eiders (Seltmann et al. 2012), we found no correlation between FID and handling-induced body temperature (GLMM: $b = -0.06$, $z = -1.43$, p = 0.15, n = 142/127). Adding to this apparent inconsistency, the handling-induced body temperature and CORT concentration of females explained different aspects of their chosen nest site (nest cover and distance to shore, respectively). These apparent inconsistencies might suggest that body temperature and CORT responses to stress may in fact capture different dimensions of the complex and composite trait 'boldness'. Thus, Carere & van Oers (2004), who showed that shy great tits (*Parus major*) demonstrated a greater body temperature response, defined boldness using responses to a novel object rather than to threatening stimuli, as we have done here. While these two types of boldness measures may indeed be correlated with each other (Albrecht & Klvaňa 2004; Van Oers et al. 2004), this may not always be the case. For example, in baboons (*Papio ursinus*), Carter et al. (2012) demonstrated that boldness measures based on novel object tests and exposure to simulated predation threat were not correlated with each other. In the light of our data, we encourage further studies specifically aimed at testing whether stress-induced hyperthermia is correlated with variation in how individuals deal with novelties, threatening stimuli or both.

Why did the majority of females nest in sites offering either very little or high concealment considering that nests with intermediate cover actually produced the highest proportion of hatched young? To answer this question, it should first be noted that we cannot verify that nests of intermediate concealment were actively avoided by females without directly comparing the availability (e.g. via random plots) and actual choice of nest concealment (cf. Clark & Shutler 1999). If most available nest sites are located either on densely forested or very open islands and genetic inheri-

tance and/or imprinting on the choice of nest concealment is strong, as perhaps indicated by the significant repeatability of this trait, observed nest-site choices may not involve any active selection of extreme types of concealment. Furthermore, the timing of incubation onset had no significant effect on any of the measured habitat characteristics. In agreement with earlier studies on this population (Öst et al. 2008b; Öst & Steele 2010; Ekroos et al. 2012), this finding also suggests that females have no preference for a special nesting habitat type, and that late breeders are not forced into less desirable sites.

The considerable variability in nest-site characteristics is enigmatic, considering that both directional selection, which may be operating on nest distance to shore (Fig. 5), and stabilizing selection, as implied for nest concealment (Fig. 4a), will generally tend to eliminate behavioural variation, preserving only those types closest to the optimum (Bulmer 1973; Carere et al. 2010). One simple explanation could be that selection for intermediate nest cover was rather weak (Fig. 4a). Alternatively, a mixture of behavioural types may coexist if proactive and reactive stress-coping styles have differential adaptive value depending on the environmental context (Cockrem 2005; Blas et al. 2007; Breuner et al. 2008). In particular, it has been suggested that low responders perform better in constant environments, while high responders are more successful in variable environments (Cockrem 2005). This argument may also apply here. It is conceivable, and in fact likely, that the amplitude of environmental variation increases with decreasing nest concealment and closeness to the shoreline. Females incubating in open nests are subject to more variable thermal regimes during incubation due to their more direct exposure to wind, rain and sunlight, which may increase heat loss (Kilpi & Lindström 1997) or cause heat stress (Fast et al. 2007; Öst et al. 2008b). Likewise, nests closer to the shore may be disproportionately affected by extreme weather events such as flooding (cf. Van de Pol et al. 2010), which may partly explain the lower hatchability of eggs at such sites (Fig. 5). Furthermore, partial clutch predation on especially early-laid eggs is higher in open nests (Öst et al. 2008b). Correspondingly, nesting close to water may increase the likelihood of detection by particularly aerial nest predators, with a concomitant increase in clutch predation rates at habitat edges (cf. Lloyd et al. 2005). Considering the way we determined the viable proportion of the clutch (see Methods), partial predation can be ruled out as a factor for habitat-dependent differences in viable clutch size. However, the mere presence of predators can induce sustained psychological stress, which may influence stress response magnitude (Clinchy et al. 2013) and result in increased body temperature (Campeau et al. 2008), with a concomitant reduction in the proportion of eggs hatching successfully (Zanette et al. 2011).

Although the choice of an open nest close to the shoreline is thus likely to come at an expense of current reproductive success, short-term reproductive success is but one component of fitness. Individual differences in personality traits can be favoured when those traits contribute to consistent individual differences in how animals resolve the life-history trade-off between fecundity and survivorship (e.g. Stamps 2007; Wolf et al. 2007). Individuals may prioritize either productivity or survival, both of which cannot be simultaneously maximized. Empirical evidence indeed suggests that proactive individuals tend to sustain high productivity at a potential cost to survival (reviewed by Smith & Blumstein 2008). The observed differences in nest-site selection criteria of female eiders exhibiting consistent differences in boldness and stress responsiveness may fit with this trade-off hypothesis. Bold individuals (shorter FID, weaker stress response) may put a higher premium on clutch survival by nesting in covered nests further away from the shore. However, they may thereby put themselves at greater risk of predation, as a product of compromised chances of detecting a predator in time (cf. Schneider & Griesser 2013) and reduced escape opportunities, should the predator attack. Thus, females in concealed nests are more easily caught by us (Öst & Steele 2010), presumably reflecting their greater vulnerability to real predation; increased predation mortality in concealed nests has also been documented in shorebirds (Amat & Masero 2004). We cannot completely rule out that the relationship between FID and nest cover may have been affected by reduced visibility in covered nests. However, we find this explanation unlikely because we made sure that females on the nest had recognized the approaching researcher, and thus females almost invariably either turned to look at the approaching observer or ducked their head to make themselves less visible in the nest. Furthermore, female eiders that nest closer to the shore can increase their odds of surviving a predator attack by having a quicker escape route to the water (Bentzen et al. 2009) or benefit from reduced (mammalian) predation on adults (Spencer 2002). However, it should be emphasized that we cannot draw definite conclusions regarding whether the observed correlations between nest-site selection, boldness and stress responsiveness may be explained

by the trade-off hypothesis. To adequately evaluate this hypothesis, we would also need to analyse how female survival depends on nest-site characteristics. This is currently impossible given that we only have 2 yrs of overlapping data on nest-site characteristics, personality traits, stress response profiles and reproductive success. However, with additional years of data available, we intend to pursue this question in the future. While we did not find significant effects of individual quality on nest-site characteristics or on the viable proportion of the clutch, this does not mean that such relationships do not exist. In eiders, individual and habitat quality may be linked (D'Alba et al. 2011), and clutch size is related to maternal experience and body condition (Öst & Steele 2010). Maternal experience and body condition could also indirectly influence nest-site choice by modulating the association between FID and stress-induced CORT (Seltmann et al. 2012). Nonetheless, the magnitude of any such effects appears small in our study, as we did not detect any significant collinearity between the individual quality measures and personality and stress-related variables (all Pearson correlation coefficients ≤ 0.4).

Alternatively, the link between nesting habitat and stress-coping styles could arise if nest success is spatially predictable, as has previously been suggested (Öst et al. 2011). Thus, the boldness and low stress responsiveness of females occupying concealed nests in the centre of islands may reflect their confidence in having found a safe nest location. In apparent support of this idea, experienced female eiders may be found in more concealed and centrally located nests (Öst & Steele 2010), and these females also show a weaker escape response (FID) with increased handling-induced CORT secretion (Seltmann et al. 2012). However, we consider this possibility less likely because female breeding experience did not significantly explain variation in nest concealment nor nest distance to the shore in our analyses, which incorporated a more comprehensive set of predictors than that used by Öst & Steele (2010).

Our study is one of the first to show that personality and stress-coping style are related to nest-site choice, in a manner that may be consistent with the trade-off hypothesis for the evolution of personality (e.g. Wolf et al. 2007). The non-random spatial distribution of different personality types revealed by our work may, in turn, provide a basis for differential selection acting on these types (cf. Wolf & Weissing 2012). Our results also demonstrate that individual differences in risk taking and stress-coping style may affect fitness indirectly through breeding habitat selection. As a next step, we encourage studies investigating how survival and breeding success, and ultimately lifetime reproductive success, is shaped by potential interactions between the preferred breeding habitat and stress-coping style. Our study population of eiders may offer particularly exciting possibilities to evaluate the adaptive value of contrasting stress-coping styles in different environments, as these environments are also associated with differences in female survival (Ekroos et al. 2012).

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