



## Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders

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Predation may drive differential selection among personality types, but the mechanism linking personality with predation risk is poorly understood. One such mechanism may be provided by stress hormones (corticosterone in birds), which are linked to boldness towards predators. However, because of feedbacks between boldness and future fitness expectations, the relationship between boldness and stress physiology may be modulated by individual quality. We investigated flight initiation distances (FIDs) of incubating eider, *Somateria mollissima*, females in relation to handling-induced corticosterone concentrations and individual quality (female breeding experience, body condition). We investigated whether FIDs were repeatable, and whether stress responsiveness and individual quality attributes, either independently or interactively, affected FIDs. We also analysed whether incubation duration, a period of peak predation pressure on females, would depend on female boldness towards predators (FID), controlling for individual quality. FIDs were repeatable within and between seasons, and females with higher handling-induced corticosterone concentrations generally had longer FIDs. However, this relationship was modulated by interactions between stress responsiveness and individual quality. High stress responsiveness was associated with longer FIDs in younger females, while the opposite was found for the oldest females. Furthermore, the FIDs of females in good body condition increased less strongly with increasing stress-induced circulating corticosterone. Shy females (long FIDs) and those in poor body condition had shorter incubation periods. Boldness is thus linked to stress responsiveness, helping to explain why stress responses may be correlated with survival. However, physiological stress effects on boldness cannot be understood in isolation from effects of individual quality.

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The relationship between personality and stress physiology is of primary importance for understanding the ontogeny of behaviour (e.g. Sih et al. 2004; Réale et al. 2010). Although some studies have already demonstrated a link between personality and stress physiology (e.g. Koolhaas et al. 1999; Carere et al. 2003), these interactions may be modulated and even controlled by individual state or status (e.g. breeding experience or body condition; Quinn & Cresswell 2005). Life history theory predicts that the value of current reproduction tends to increase relative to the value of future reproduction in older individuals (e.g. Stearns 1992). Since elevated stress hormone concentrations interfere with

reproduction (Silverin 1987; Kitaysky et al. 2001; Romero 2004), we can expect reproducing individuals to down-regulate their stress response towards the end of life (e.g. Wingfield & Sapolsky 2003) to ensure the success of the current reproductive event. Consistent with this hypothesis, some studies have found that older individuals show dampened stress responses (e.g. Heidinger et al. 2006); however, the published accounts are partly contradictory (Wilcoxon et al. 2011). Because older individuals are likely to put less emphasis on future fitness returns, life history theory predicts that these differences in fitness expectations should result in systematic differences in boldness towards predators (Clark 1994; Wolf et al. 2007; Biro & Stamps 2008). Paralleling the prediction for the relationship between stress response magnitude and age, older individuals may be bolder than younger ones (Wolf et al. 2007; Biro & Stamps 2008). However, it is unknown whether endocrine or behavioural modifications, or both, are responsible for potential age-related changes in boldness towards predators.

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Prey should also be able to assess their own vulnerability to predation and modify their antipredator behaviour accordingly (Ydenberg & Dill 1986; Lima & Dill 1990). Consequently, animals in poor body condition or health may be shyer when confronted with a predator than healthier animals or those in better condition (e.g. López et al. 2005; Martín et al. 2006). Such state-dependent escape decisions may be further amplified if predators preferentially target prey of inferior phenotypic quality (e.g. Cresswell & Quinn 2004; Quinn & Cresswell 2004). Condition-dependent avoidance of predation may also favour the evolution of personalities by reinforcing individual differences that arise from small differences in original 'assets' such as the amount of energy reserves (Luttbeg & Sih 2010). None the less, the link between personality and body condition is not straightforward and is poorly investigated. It is generally assumed that personality is independent of body condition (Réale et al. 2007) and this idea has some empirical support (David et al. 2011, 2012). However, because stress-induced levels of corticosterone may negatively correlate with body condition (e.g. Schwabl et al. 1991), body condition could affect both stress responsiveness and personality traits such as boldness.

Some recent theoretical work has emphasized that life history productivity and boldness may be coupled: consistently highly fecund individuals should be bold, but this may come at the expense of reduced survival under predation risk (Stamps 2007; Biro & Stamps 2008). In this respect, the incubation period in birds provides a suitable testing ground, as incubation is energetically demanding (e.g. Williams 1996; Thomson et al. 1998) and exposes both parents and eggs to heightened predation risk (Martin 2002; Amat & Masero 2004; Lima 2009). Shy individuals may place a high premium on minimizing incubation time to shorten the period of exposure to predators, and such changes may be mediated by the main avian stress hormone corticosterone (CORT; Schmidt et al. 2009). However, this may only be achieved at the cost of reduced offspring quality (Hanssen et al. 2002; Brommer 2003; Shine & Olsson 2003). Thus, the possibility that incubation tactics are personality dependent could contribute to producing a fecundity–mortality trade-off assumed by theory (Stamps 2007; Biro & Stamps 2008). However, the relationship between boldness towards predators and incubation duration has not so far been systematically explored, while controlling for age- and state-dependent effects, which may also be important (e.g. Hanssen et al. 2002).

Prey boldness towards predators should preferably be observed during real or simulated attacks, when any differential fitness costs are likely to arise. Flight initiation distance (FID), the distance at which a focal animal flees from an approaching human, is a useful index for estimating boldness (Blumstein 2006; Carrete & Tella 2010; Carter et al. 2010). We investigated FIDs in incubating female eiders, *Somateria mollissima*. In this long-lived capital-breeding ground-nester, only females incubate; they show high nest attentiveness (Bolduc & Guillemette 2003a), thereby losing ca. 40% of their body mass during incubation (Gabrielsen et al. 1991). Female body condition when ducklings hatch is a proxy for individual quality, as it impacts longevity (Ekroos et al. 2012), hatching success (Lehikoinen et al. 2010) and the ability to rear broods successfully (Kilpi et al. 2001). Furthermore, both eggs (Andersson & Waldeck 2006) and females (Jaatinen et al. 2011; Ekroos et al. 2012) are subject to considerable predation pressure during incubation. We determined, first, whether FID qualifies as a personality trait, by exploring individual consistency (repeatability) in FIDs within and between breeding seasons. For each female, we measured baseline and handling-induced stress hormone (CORT) concentrations from blood samples taken at capture, and estimated the body condition and (minimum) years of maternal experience (cf. Jaatinen & Öst 2011). While the physiological mechanisms

associated with shy and bold behavioural profiles are typically unknown (Schjolden et al. 2005), individual differences in boldness resemble the proactive and reactive stress coping style described in the neuroendocrinological literature (Koolhaas et al. 1999). We hypothesized that low stress responders would be bolder, that is, show shorter FIDs (Réale et al. 2010). In keeping with the predictions from life history theory, we further hypothesized that older females should respond less strongly with reduced FIDs or lower CORT concentrations. This modulation could be achieved physiologically, by down-regulating the stress response with advancing age, and/or behaviourally, by a decoupling of boldness (FIDs) from the magnitude of the stress response. In line with the 'condition-dependent avoidance of predation' hypothesis (Luttbeg & Sih 2010), we hypothesized that for a given level of stress, females in poor condition would show longer FIDs. Lastly, we analysed whether FID affected incubation duration, controlling for female breeding experience and body condition. Here, we hypothesized that the relatively risk-insensitive bold females would show extended incubation periods.

## 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 southwestern Finland, in 2009–2011. All study islands are protected by a prohibition on landing.

### Trapping

We captured incubating females on their nests using hand nets, and the coordinates of all nests were recorded using a Garmin Map76 GPS receiver (Garmin, Olathe, KS, U.S.A.). Trapping took place predominantly during the end of the incubation period in May or early June 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 2003b). A detailed account of the ethics involved in female capture is presented in Kilpi et al. (2001), and female handling procedures were approved by the Animal Experiment Board/State Provincial Office of Southern Finland, number ESLH-2009-02969/Ym-23, and Tvärminne Zoological Station.

### Individual and Morphometric Measurements

Trapped females were ringed with a standard metal ring, weighed on a spring scale (to the nearest 10 g; average female weight at trapping 2009–2011: 1710 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 effort in 2003–2009: mean  $\pm$  SD = 55.8  $\pm$  0.14%; Jaatinen & Öst 2011), and annual trapping effort has been similar since 1996 (Öst et al. 2003). The incubation stage was estimated by egg flotation (Kilpi & Lindström 1997). Based on incubation stage, we estimated female body condition at hatching from regressions of 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). The validity of using this index for estimating body condition has been examined elsewhere (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 from regressions of the logarithm of body weight against the logarithm of incubation time and projected hatching date (Öst et al. 2008b). The duration of the incubation period was determined as the time difference (in days) between the real hatch date observed during nest visits (see below) and the estimated date of incubation onset determined by egg flotation at female capture.

#### *Collection of Serum Samples*

We measured baseline and handling-induced rise in CORT concentrations immediately after female capture. 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 second sample was taken after all handling and marking procedures were complete (mean  $\pm$  SD =  $15 \pm 4$  min,  $N = 477$ ). 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  $-20^\circ\text{C}$  until analysis.

#### *FID Assessment*

We measured FIDs of captured females while revisiting the nests for marking ducklings in conjunction with another study (also approved by the Animal Experiment Board/State Provincial Office of Southern Finland, number ESLH-2009-02969/Ym-23). 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). Determining FIDs at a similar phase of the incubation period has the advantage that the effect of variable incubation time on FIDs can be excluded (Forbes et al. 1994; Albrecht & Klvaňa 2004; Öst & Steele 2010). FIDs were determined in a standardized manner by first ensuring that the focal individual had noticed the approaching researcher, and then walking towards it following a direct trajectory at a constant low speed, and with no obstacles blocking the view between the bird and the observer. FIDs were always determined by the same observer wearing the same clothes to avoid bias resulting from differences in the physical appearance of investigators. FID was the distance between the nest and the approaching person when the female flushed away, and it was measured by a tape measure to the nearest 10 cm. Nests were revisited if the brood was not completely hatched or was still at the egg stage; in the latter case, the actual incubation stage was re-estimated by egg flotation. During these successive nest visits, we obtained repeated observations of the FID of focal females following the same procedures as described above. These repeated measurements allowed us to estimate the repeatability of FIDs within and between breeding seasons, as well as to evaluate the potential effect of habituation to the observer (cf. Rodríguez-Prieto et al. 2011). The potential for habituation to the observer was evaluated by exploring whether FIDs of individual females changed consistently with the number of previous encounters with the observer. For females observed at least twice within the same breeding season, FIDs were assessed  $2.4 \pm 0.6$  (mean  $\pm$  SD) times in 2009 (range 2–4,  $N = 154$ ),  $2.7 \pm 0.9$  times in

2010 (2–5,  $N = 166$ ) and  $2.6 \pm 0.7$  times in 2011 (2–5,  $N = 168$ ). Regarding repeated observations of FIDs between breeding seasons, FIDs were assessed  $3.9 \pm 1.1$  times between 2009 and 2010 (range 2–6,  $N = 101$  measurements of 26 individuals),  $4.4 \pm 1.6$  times between 2010 and 2011 (2–7,  $N = 97$  measurements of 22 individuals) and  $5.7 \pm 1.3$  times between 2009 and 2011 (4–8,  $N = 40$  measurements of seven individuals).

#### *Corticosterone Radioimmunoassay*

A validation of the serum corticosterone RIA kit (ImmuChem Double Antibody, Corticosterone,  $^{125}\text{I}$  RIA Kit, MP Biomedicals, Orangeburg, NY, U.S.A.) for eiders is provided by Nilsson (2004). Intra-assay coefficients of variation were less than 10% and mean assay sensitivity was 13.1 ng/ml. Manufacturer cross-reactivity with other steroids were as follows: desoxycorticosterone (0.34%), testosterone (0.10%), cortisol (0.05%), aldosterone (0.03%), progesterone (0.02%), and less than 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 Analyses*

We used the rpt.remlMM function from the R software package rptR (Nakagawa & Schielzeth 2010) to estimate the repeatability of FIDs within and between years. In order to adhere to the assumptions of this model, we  $\log(x + 1)$  transformed the FIDs. We only used stress-induced CORT concentrations in our analyses, since they measure the outcome of a standardized experimental challenge (reaction to our handling procedures) and they are less sensitive to uncontrolled external perturbations than are baseline CORTs (Breuner et al. 1999; Romero 2002; Angelier et al. 2007b). To assess the effects of the stress-induced CORT concentration, female minimum breeding experience, body condition, and the two-way interactions between stress responsiveness and the two individual quality measures on FID, we used a generalized linear mixed model (GLMM) with a Poisson error distribution and female identity as a random effect to account for repeated measurements of individuals. The model was fitted using Laplace approximation. To control for potential year effects and variable intervals between female capture and CORT sampling, year and the time between blood sampling and female capture were included as covariates in this analysis. Nonsignificant variables or interactions were removed from the final model. We did not correct for the effect of time of day in the analysis involving stress-induced concentrations of CORT, because time of day had no effect on this variable (linear mixed model (LMM) with female ID as a random effect:  $F_{1,129} = 0.01$ ,  $P = 0.93$ ). We tested for the effects of FID, the stress-induced CORT concentration, female minimum breeding experience, body condition, clutch size, and the two-way interactions between stress responsiveness and the two individual quality measures on incubation duration with an LMM, fitted using restricted maximum likelihood (REML) estimation and with female identity as a random effect. Nonsignificant variables and interactions were removed from the final model following a stepwise procedure. Egg flotation tends slightly to overestimate incubation date early in incubation and underestimate it later in incubation (e.g. Walter & Rusch 1997; Reiter & Andersen 2008). The year 2011 was phenologically later than the others, and because of this phenological difference, we captured females earlier in their incubation in 2011 compared to the other years. As a consequence of this methodological artefact, incubation durations were significantly longer in 2011 (LMM:  $t_{56} = 2.61$ ,  $P = 0.01$ ). We therefore restricted the incubation length

**Table 1**

Repeatabilities ( $R$ ) of flight initiation distances of female eiders within and between years

Year(s)	$R$	SE	CI	$P$	$N$
2009	0.80	0.04	0.73, 0.84	<0.001	154 (65)
2010	0.76	0.04	0.70, 0.81	<0.001	166 (60)
2011	0.76	0.04	0.67, 0.79	<0.001	168 (66)
2009–2010	0.69	0.06	0.57, 0.74	<0.001	101 (26)
2010–2011	0.54	0.12	0.32, 0.67	<0.001	97 (22)
2009–2011	0.37	0.14	0.15, 0.57	<0.05	40 (7)

CI: 95% confidence interval;  $P$ : significance of repeatability;  $N$ : observations (individuals).

analysis to the phenologically similar years 2009 and 2010, when incubation lengths (mean  $\pm$  SD) were also similar ( $26.9 \pm 1.8$  and  $27.3 \pm 2.1$  days, respectively; LMM:  $t_{56} = 1.23$ ,  $P = 0.21$ ). The residuals of all LMMs adhered to the assumption of normality. All statistical analyses were performed in the software R (version 2.10.1; R Development Core Team 2009).

## RESULTS

### Repeatability of Flight Initiation Distance

FID showed a high and significant repeatability within years, as well as between 2 and between 3 consecutive years (Table 1, Fig. 1). The repeatability of FIDs for females encountered in all 3 years was also significant, yet slightly lower, in comparison (Table 1). There was no habituation effect on FIDs caused by repeated exposure to observers, since FIDs did not change systematically within individuals (LMM:  $b = -0.006$ ,  $F_{1,332} = 0.08$ ,  $P = 0.78$ ,  $N = 178$  individuals/511 observations).

### Effect of CORT, Body Condition and Breeding Experience

We found that stress-induced CORT concentrations, female body condition and breeding experience were all significantly correlated with FIDs (Table 2). There was also an effect of time elapsed between capture and blood sampling (GLMM:  $b = 0.002$ ,  $z = -18.7$ ,  $N = 251$ ,  $P < 0.001$ ) and a significant year effect ( $z = 6.72$ ,  $P < 0.001$ ) on FIDs; the mean FIDs  $\pm$  SD were  $2.4 \pm 3.2$  m,  $3.3 \pm 3.9$  m and  $2.7 \pm 3.4$  m in 2009, 2010 and 2011, respectively. The relationship between stress-induced CORT concentrations and FIDs was modulated by female breeding experience and female body condition. Higher stress-induced CORT concentrations were

**Table 2**

Model selection and GLMM (Poisson error distribution, log link function and female identity as a random factor) to test the influence of a number of variables on flight initiation distance

Dependent variable	Independent variable
Mean flight initiation distance (cm)	<b>Body condition</b>
$N = 251/204$	<b>Breeding experience (years)</b>
	<b>Stress-induced CORT (ng/ml)</b>
	<b>Year</b>
	<b>Time to second blood sample (s)</b>
	<b>Stress-induced CORT*breeding experience</b>
	<b>Stress-induced CORT*body condition</b>

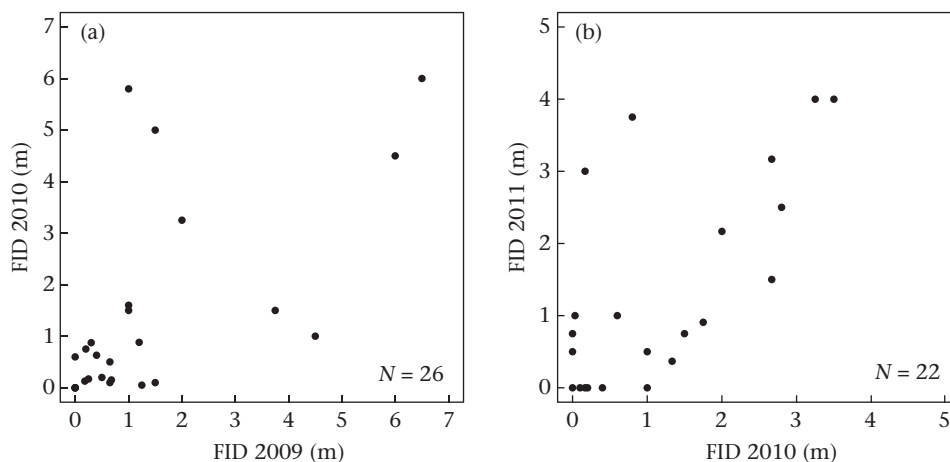
All independent variables and the two-way interactions between stress responsiveness and the two individual quality measurements were significant and remained in the final model (in bold).

positively correlated with longer FIDs in the youngest females, but the response of FIDs to increasing stress-induced CORT concentrations gradually declined, and eventually reversed, with advancing breeding experience (stress-induced CORT \* minimum breeding experience: GLMM:  $b = -0.004$ ,  $z = -23.4$ ,  $N = 251$ ,  $P < 0.001$ ; Fig. 2a). FIDs of females in better body condition increased less strongly with increasing concentrations of stress-induced CORT (stress-induced CORT \* body condition: GLMM:  $b = -0.001$ ,  $z = -3.15$ ,  $N = 251$ ,  $P < 0.01$ ; Fig. 2b).

We additionally tested for a direct relationship between stress responsiveness and individual quality, by analysing whether female breeding experience or body condition explained stress-induced CORT concentrations, either linearly or in a curvilinear manner (cf. Goutte et al. 2010; Wilcoxon et al. 2011). We did not find any significant effects of female breeding experience (LMM with female identity as a random effect:  $F_{1,106} = 1.26$ ,  $P = 0.26$ ) or body condition ( $F_{1,106} = 0.16$ ,  $P = 0.69$ ), or their quadratic terms (both  $P$ s  $> 0.11$ ) on stress-induced CORT concentrations.

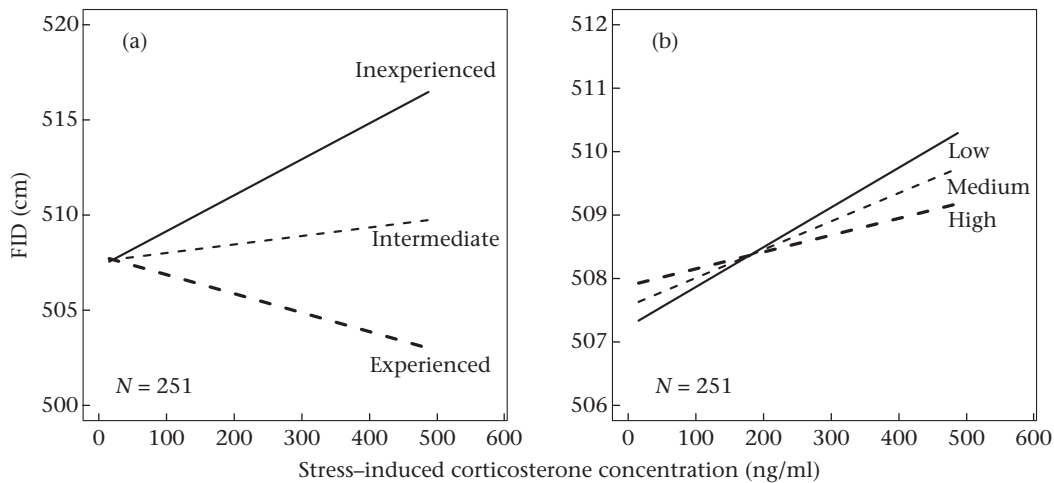
### Incubation Length as a Function of FID and Body Condition

Incubation duration was affected only by female body condition and FID (Table 3). Females incubated for longer when they were in better body condition (LMM:  $b = 0.774$ ,  $F_{1,17} = 29.19$ ,  $P < 0.001$ ; Fig. 3a) and when they showed shorter FIDs ( $b = -0.001$ ,  $F_{1,17} = 8.36$ ,  $P = 0.01$ ; Fig. 3b). In contrast, no interactions between the stress-induced CORT concentration and female breeding experience ( $b = -0.0008$ ,  $F_{1,8} = 1.31$ ,  $P = 0.29$ ) or body condition ( $b = 0.002$ ,  $F_{1,11} = 0.19$ ,  $P = 0.67$ ) on incubation duration were



**Figure 1.** The relationship between mean flight initiation distances (FIDs) of the same female eiders captured in (a) 2009 and 2010, (b) 2010 and 2011.





**Figure 2.** Stress-induced CORT concentrations and flight initiation distances (FID) of female eiders in relation to (a) (minimum) years of breeding experience and (b) body condition. In (a), the solid line denotes females with little breeding experience (mean – 1 SD), the dotted line females with intermediate breeding experience (mean) and the dashed line females with a long previous breeding experience (mean + 1 SD; see Aiken & West 1991 for more details on plotting interaction terms). In (b), the solid line denotes females in poor body condition (mean – 1 SD), the dotted line females in intermediate body condition (mean) and the dashed line females in good body condition (mean + 1 SD).

detected. Likewise, female breeding experience ( $b = 0.08$ ,  $F_{1,8} < 0.01$ ,  $P = 0.96$ ), stress-induced CORT concentrations ( $b = -0.0005$ ,  $F_{1,11} = 0.84$ ,  $P = 0.38$ ) or clutch size ( $b = 0.02$ ,  $F_{1,10} = 0.19$ ,  $P = 0.86$ ) did not significantly affect incubation duration.

## DISCUSSION

Our finding of highly repeatable FIDs of females both within and between breeding seasons suggests that boldness is a valid personality trait, and thus it could cause differential selection on personality types (cf. Biro & Post 2008). So far only a few studies have assessed the repeatability of FID in the wild, finding that repeatability is high, ranging from 0.76 to 0.95 (Carrete & Tella 2010; Carter et al. 2010; Evans et al. 2010). However, strong individual consistency in predator avoidance behaviour appears to be a general phenomenon (birds: Carrete & Tella 2010; mammals: Malmkvist & Hansen 2002; fish: Coleman & Wilson 1998; reptiles: Carter et al. 2010).

Recent studies have shown that corticosterone is an important factor in mediating escape behaviours (e.g. Thaker et al. 2010). It is noteworthy that the link between boldness and stress responsiveness in female eiders runs opposite to the conventional definition of proactive and reactive stress coping styles. According to the prevailing view, the response patterns of proactive individuals correspond to those of bold ones; such individuals are characterized by a small stress-induced increase in CORTs and an active flight/

flight response, whereas reactive, ‘shy’ individuals show high stress responsiveness and respond to challenges with immobility and lack of initiative (e.g. Koolhaas et al. 1999; Schjolden et al. 2005). In contrast, we found that high stress responders had longer FIDs. This pattern appears to be a robust consequence of inherent differences in boldness rather than, for example, differences in the time needed to detect and react to a predator (i.e. the approaching observer). Thus, when determining FIDs, we always ensured that females were able to see us before approaching the focal individual. Furthermore, considering that such potentially slow reactors are expected to show a reactive stress coping style associated with high stress responsiveness (cf. Quinn & Cresswell 2005), we actually found that females with short FIDs had a lower handling-induced stress response. The simplest explanation for the apparently aberrant stress coping styles of female eiders may reflect their great reliance on crypsis during incubation, which may prevent the activation of the flight response in bold individuals. In contrast, most of the existing studies on proactive and reactive stress coping styles have been done in mammals in which crypsis for avoiding predation is less important (reviewed in Koolhaas et al. 1999).

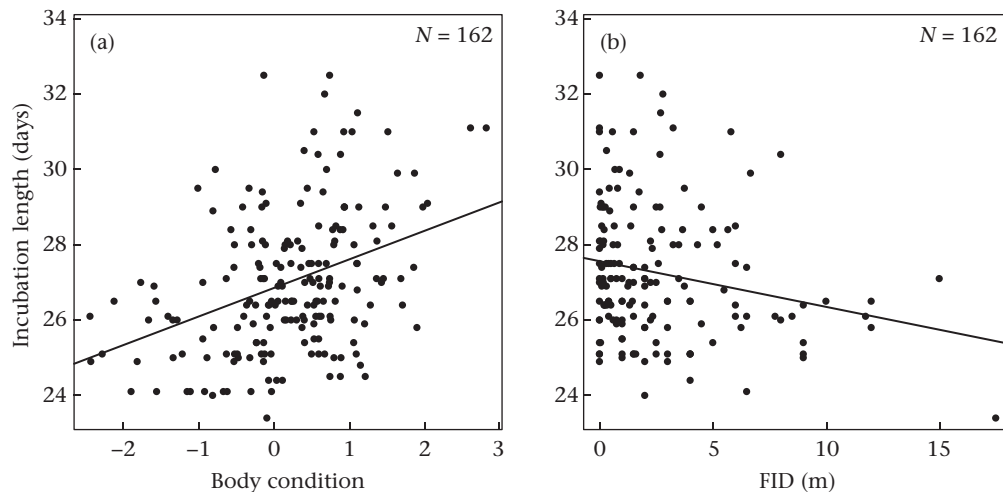
Despite the relative consistency of individual flight responses, our results also revealed that FIDs can be flexible and modulated by stress-induced CORT concentrations, female breeding experience and body condition, and also year effects were apparent. Perhaps the most striking finding was that whereas young breeders showed the expected increase in FIDs with increasing magnitude of the stress response, the direction of the relationship was reversed in the oldest breeders. One explanation could be that this may reflect a direct effect of senescence. Some studies have indicated that the relationship between stress responsiveness and age may be curvilinear (Goutte et al. 2010; Wilcoxon et al. 2011), so that the very oldest individuals are unable to dampen their physiological response to acute stressors. If physiological stress responsiveness begins to rise with the advent of senescence, while behavioural responses (FIDs) steadily decline over the lifetime of an individual, this could explain the disparate antipredator responses to increasing stress-induced CORT concentrations depending on breeding experience. Although FIDs indeed declined with advancing breeding experience according to a single-variable model with breeding experience as the sole predictor and female identity as a random effect ( $b = -0.239$ ; GLMM:  $z = -24.75$ ,  $N = 286$  observations of 229 females,  $P < 0.001$ ), this explanation

**Table 3**

Model selection and LMM (normal error distribution and female identity as a random factor) to test the influence of a number of variables on incubation duration

Dependent variable	Independent variable
Incubation duration (days) $N = 162/143$	<b>Body condition</b>
	<b>Mean flight initiation distance (cm)</b>
	Breeding experience (years)
	Stress-induced CORT (ng/ml)
	Clutch size
	Breeding experience*stress-induced CORT
	Body condition*stress-induced CORT

The final model (in bold) was selected by removing nonsignificant variables and interactions following a stepwise procedure.



**Figure 3.** The relationship between the incubation length of female eiders and their (a) body condition and (b) flight initiation distance (FID).

none the less seems unlikely. Thus, we found no evidence of either linear or curvilinear effects of female breeding experience on the stress-induced CORT concentrations. This relative age insensitivity of the CORT stress response agrees with studies conducted on other seabirds (e.g. Angelier et al. 2007b). Alternatively, only a small fraction of the females included in our study may have reached a stage of senescence associated with declining physiological function. Eiders are long-lived with an estimated life expectancy of 21 years and the first indications of rising mortality rates become apparent only after 17 years of age (Coulson 1984), whereas the oldest females in our study had an estimated minimum maternal experience of 16 years.

However, there are other, not mutually exclusive, explanations for the interactive effects of stress responsiveness and female breeding experience on boldness. From a proximate physiological perspective, it is possible that although stress may trigger the release of similar amounts of CORTs into the blood irrespective of female age, CORT receptors may be progressively down-regulated with advancing age (e.g. Stein-Behrens & Sapolsky 1992), and the concomitant attenuation of the stress response may facilitate an increase in reproductive performance with age (Heidinger et al. 2006). Second, CORT-mediated stress responses may be balanced or even overridden by the action of other hormones, particularly prolactin, a major hormone promoting mother–offspring bonding. Both baseline and stress-induced prolactin levels typically increase with advancing age in seabirds (e.g. Angelier et al. 2007a, 2007b), and such interactive hormonal regulation may tend to inhibit flight reactions of incubating older females. Third, from an ecological perspective, female breeding experience in eiders is likely to be correlated with the ability to assess local predation risk (Öst & Steele 2010), which may directly influence boldness. Thus, nest site safety is moderately spatially predictable in our study area and breeding dispersal decreases with advancing breeding experience (Öst et al. 2011), presumably owing to older females having successfully located a safe nest site. Consequently, the hatching success of experienced females exceeds that of younger ones (Öst & Steele 2010). We may hypothesize that older females may become habituated to their relatively ‘safe’ nest surroundings, which may in turn increase their boldness, acting to decouple physiological stress responses from actual boldness under threat of predation. Such effects may be enhanced by the differential social environment faced by different-aged female eiders. Thus, older females select more centrally located nests on islands, where nest densities are higher (Öst & Steele 2010). Not only can nests in the interior of

clusters experience lower nest predation (e.g. Lima 2009), but also the boldness of individuals nesting in these denser breeding aggregations may be higher, because boldness tends to increase in social situations (e.g. van Oers et al. 2005).

For a given concentration of stress-induced CORT, females in poor body condition showed a stronger relationship between CORT and FID than females in good body condition. This result may imply that only females in good body condition can afford to delay fleeing from a threat (cf. Martín et al. 2006; but see Hawlena et al. 2009). Females in poor condition may have low expected fitness value of the current reproductive event, and hence they may be expected to prioritize their own rather than their offspring’s survival (e.g. Stearns 1992). In support of this prediction of life history theory, eider females in poor condition have lower odds of successfully hatching a clutch (Lehikoinen et al. 2010), and also more often abandon their brood shortly after hatching (e.g. Bustnes & Erikstad 1991; Kilpi et al. 2001). Individual body condition could also be maintained over the long term because of high annual repeatability (over 40% of the total variation is explained by female identity; Jaatinen & Öst 2011), and so it seems plausible that body condition could influence individual boldness in this species (cf. Luttbegg & Sih 2010).

Overall FIDs peaked in 2010, followed by 2011, while FIDs were shortest in 2009. The ranking of predation rates on incubating adult females in 2009–2011 mirrors the rank order found for FIDs. The sum total of females found killed at their nests divided by the total number of nests counted can be used as an annual index of predation pressure on females (e.g. Jaatinen et al. 2011). This annual index of predation pressure was by far the highest in 2010 (0.14), followed by 2011 (0.06) and 2009 (0.05). The concordance between annual predation pressure and average FIDs may indicate that boldness may display flexibility in response to variable predation risk (but see Bell & Sih 2007). Eider females are indeed capable of flexible behavioural adjustments in response to variable predation risk. For example, communal brood-rearing decisions of females respond to the predation risk experienced during incubation (Jaatinen et al. 2011).

Both energetic considerations and predator avoidance affected incubation duration in female eiders. Females in poor body condition had a shorter incubation period, which is consistent with the idea that such females can reduce mass loss by minimizing incubation time, which can be achieved by laying earlier in the season and/or by producing smaller eggs (Hanssen et al. 2002). Conversely, females in good body condition may afford the cost of longer

incubation time with its associated increase in mass loss, thereby producing good-quality offspring with higher survival prospects (Hanssen et al. 2002). We also found that females with longer FIDs (shy individuals) had an abbreviated incubation period, which agrees with our hypothesis that less bold individuals should strive to minimize incubation time, when the predation pressure on females is highest (Ekroos et al. 2012). This is one of the first demonstrations that shy individuals may put a higher premium on their own survival during incubation. However, this may also be achieved by other means; longer-lived species may show reduced incubation constancy, that is, a smaller proportion of time spent actively incubating the eggs, resulting in a prolonged incubation period (cf. Martin & Schwabl 2008). There are few previous studies assessing the effect of FIDs on incubation behaviour, however, and thus many unresolved questions remain. For example, it is unclear whether offspring quality differs with respect to parental boldness, and whether such potential differences may depend on incubation length. With respect to potential physiological mechanisms steering the observed patterns, our results suggest that although shy individuals showed higher stress responsiveness, stress-induced CORT concentrations do not seem to influence incubation duration directly. However, this preliminary finding does not serve to exclude the possibility that CORTs play a role in regulating incubation duration; under captive conditions, CORT-implanted Japanese quail, *Coturnix coturnix japonica*, hens had an abbreviated incubation period (Schmidt et al. 2009).

To conclude, we have shown that individual boldness is linked to stress responsiveness in female eiders, an observation that may help to explain why stress responsiveness may correlate with survival, as has been shown in some birds (e.g. Angelier et al. 2009). Our study also clearly demonstrated that the effects of individual quality and stress physiology on personality traits should not be studied in isolation, because their effects are likely to be intertwined. Our study also identified some important gaps in our current knowledge. We encourage studies assessing whether different environments may favour different levels of boldness, and whether intraspecific social interactions potentially modulate stress responsiveness and boldness. From a physiological perspective, research aimed at pinpointing the potentially interactive effects of different hormonal control mechanisms on boldness would be particularly desirable.

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