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Drivers of within- and among-individual variation in risk-taking behaviour during reproduction in a long-lived bird

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Plastic and selective mechanisms govern parental investment adjustments to predation threat. We investigated the relative importance of plasticity and selection in risk-taking propensity of incubating female common eiders *Somateria mollissima* facing unprecedented predation in SW Finland, Baltic Sea. Using a 12-year individual-based dataset, we examined within- and among-individual variation in flight initiation distance (FID), in relation to predation risk, nest detectability, individual traits and reproductive investment ($N_{FID} = 1009$; $N_{individual} = 559$). We expected females nesting in riskier environments (higher predation risk, lower nest concealment) to mitigate environmentally imposed risk by exhibiting longer FIDs, and females investing more in current reproduction (older, in better condition or laying larger clutches) to display shorter FIDs. The target of predation—adult or offspring—affected the mechanisms adapting risk-taking propensity; females plastically increased their FID under higher adult predation risk, while risk-avoiding breeders were predominant on islands with higher nest predation risk. Risk-taking females selected thicker nest cover, consistent with personality-matching habitat choice. Females plastically attenuated their anti-predator response (shorter FIDs) with advancing age, and females in better body condition were more risk-taking, a result explained by selection processes. Future research should consider predator type when investigating the fitness consequences of risk-taking strategies.

1. Background

Life-history theory predicts that prey should adjust their parental investment to the perceived predation threat [1]. Reproduction involves a trade-off between investing energy and resources in producing and caring for offspring, and saving resources for self-maintenance and survival [1–3]. This survival-reproduction trade-off is predicted to be stronger when parents are exposed to elevated predation risk [4]. To cope with predation threat, prey have developed anti-predator behaviours through natural selection and behavioural plasticity [5,6], both reflecting the fundamental trade-off between reproduction and survival.

Predator–prey interactions shape prey anti-predator traits and behaviours over time and space through selection processes [7,8]. Thus, lower quality or risk-taking prey may suffer higher predation mortality and/or reduced reproductive output under threat [9–11]. Such differences in survival or reproduction may induce phenotypic variation in survival rates and population

dynamics [12–15]. However, individuals may also plastically modulate their behavioural or physiological anti-predator responses depending on their internal state and extrinsic factors, including the level of nest and adult predation risk [7,16,17]. Consequently, phenotypic plasticity can confound patterns of selective (dis)appearance of risk-taking phenotypes, highlighting the need to account for both plasticity (within-individual processes) and selection (among-individual processes) in order to disentangle those responsible for population-level variation [18]. Identifying the drivers of variation in risk-taking behaviours is thus key to understanding their consequences for both life-history evolution and population dynamics, especially in a context of fluctuating predation threat. However, few studies have attempted to separate plasticity and selection of risk-taking phenotypes, given that such analyses require large longitudinal datasets covering a substantial part of the lifespan of the study organism, which are often difficult to obtain in the wild [19].

Flight initiation distance (FID), the distance at which prey start to flee from approaching potential predators [20], is a standardized measure to investigate risk-taking propensity and the relative roles of plasticity and selection in modulating risk-taking behaviour under fluctuating predation threat [21]. FID has been shown to be repeatable within individuals [22,–26]. On the one hand, fleeing from the nest may jeopardize reproductive success by disrupting incubation and by indicating offspring location to the approaching nest or adult predator [27]. On the other hand, delaying escape may reduce breeder survival [28]. Consequently, individuals investing more in the current reproductive event are expected to dampen their anti-predator response and delay escape to enhance offspring survival [29,30].

The evolutionary consequences of individual variation in risk-taking under predation threat depend on the relative magnitude of adaptive phenotypic plasticity (i.e. phenotypes actively matching prevailing risk) and selective disappearance effects (i.e. exclusion of certain phenotypes from the breeding pool) [31–33]. Our long-term longitudinal data on FIDs of incubating female common eiders *Somateria mollissima*, hereafter eiders, allowed us to improve knowledge on the relative influence of these mechanisms on risk-taking behaviour during reproduction. Specifically, we investigated how FID is modulated by phenotypic traits, parental investment, conspicuousness to predators and fluctuating predation pressure. The study was conducted amidst an unprecedented increase in predation pressure in our study population in the northern Baltic Sea, mainly attributed to the recent recovery of the white-tailed eagle *Haliaeetus albicilla*, the main predator of adult eiders [34]. This created an ideal backdrop to investigate individual plasticity and population-level selection processes involved in prey responses to a fluctuating predation regime [35].

To this end, we first delineated the population-level trends in FID, female and nest characteristics, clutch size and predation risk over the entire study period (2008–2019). We then addressed whether FID was (i) related to female phenotypic traits, reproductive investment, nest conspicuousness and predation risk, (ii) repeatable and (iii) shaped by within-individual plasticity or among-individual selection. We assumed that FID would be affected by population-level selection against risk-taking phenotypes (i.e. displaying shorter FIDs) under the progressively increasing predation threat. In addition and according to life-history theory [1],

we expected females to be more risk-taking, i.e. display shorter FIDs, with advancing age (diminishing residual reproductive value), when the costs of reproduction are lower (good body condition) and when making a greater reproductive investment (large clutch). Given that nest conspicuousness can affect predation risk, we expected females to advance their escape response when breeding in nests offering little concealment, or on islands characterized by high adult and nest predation risk. Alternatively, but not exclusively, females characterized by shorter FIDs may avoid conspicuous nests and risky islands, hence mitigating environmentally imposed risk of predation. We further expected FID to be individually repeatable, but modulated by plastic adjustments to individual state, parental investment and perceived predation risk.

2. Methods

(a) Female monitoring

(i) Breeding female characteristics

The study was conducted in the western Gulf of Finland, in the archipelago surrounding Tvärminne Zoological Station (59°50′N, 23°15′E), in 2008–2019. Female eiders nest on diverse types of islands, including those covered by bare rocks, sparse patches of herbs, stands of juniper *Juniperus communis* or pine *Pinus sylvestris* dominated forest. Incubating female eiders at Tvärminne have been annually trapped on their nest with hand nets since 1990, and individually marked with a standard metal ring. Female weight was measured to the nearest 10 g with a Pesola spring balance, and radius-ulna length, a proxy of body size, was measured to the nearest 1 mm with a wing ruler. Females incubate for about 26 days [36], and females were trapped between May and early June during the later phase of incubation to minimize nest abandonment [37]. Hatching date was estimated using an egg floatation test [38], and the number of eggs was counted as a proxy of initial energetic investment in reproduction [39,40].

Eiders are long-lived (*ca* 21 years [41]) and philopatric [42,43] birds periodically relying on intermittent breeding [44]. Females were ringed when caught breeding for the first time, which typically occurs at three years-of-age [45]. As trapping success is high and trapping effort has been constant since 1996 [46], we used the number of years since the bird was first trapped and ringed as a proxy of female minimum age, also reflecting residual reproductive value. As capital breeders, eiders fast and rely on their body reserves both to produce eggs and for maintenance during incubation [47]. Maternal energy reserves are progressively depleted as incubation proceeds, necessitating the need to assess the amount of body reserves at a comparable time. We therefore estimated a body condition index at hatching, which corresponds to the time of FID measurement (see electronic supplementary material S1, [48]).

(ii) Risk-taking propensity

Animals usually respond to human approach as they would to an approaching natural predator [49]. We thus measured risk-taking propensity with a standardized FID protocol consisting of a unique observer approaching the nest at a constant slow gait and measuring the distance at which the incubating focal female fled [50]. Before starting the approach, the observer positioned himself so that the female had a free line of sight to him, ensuring that the focal female had noticed him and followed him with her gaze or slight head movements. Because a pilot study in 2012 showed that starting distance was not correlated with FID in this population (see electronic supplementary material S2),

Table 1. Number of FID measurements per incubating female common eider.

number of FID replicates (2008–2019)	1	2	3	4	5	6	7	8	9
number of females	310	131	73	23	13	5	2	1	1

starting distance was not recorded. As FID often decreases when the clutch nears hatching [28,51,52] but also to limit the risk of nest abandonment, FID was measured the day before the expected hatching date predicted by egg floatation. Once the female had fled from the nest, the observer immediately covered the nest to minimize the risk of detection and depredation by avian egg predators such as hooded crows *Corvus cornix* [53]. On average, 33.08 ± 5.94% of nests active at first encounter were annually sampled for FID (range: 24.19%–42.92%). This relatively low proportion was due to the fact that females whose eggs were depredated or hatched prior to FID measurement could not be sampled for FID (61.74 ± 13.79% of successful nests were on average annually sampled, range: 43.70%–87.50%). Coupled with a predation risk-induced increase in intermittent breeding strategies and premature mortality due to predation [34], the number of repeated measures per individual over time was lower than what one could expect from such a long-lived philopatric species (table 1). Overall, we measured 1009 FIDs to the closest 10 cm (later rounded to the closest meter (see §2(c)) to account for measurement imprecision and to meet model assumptions) on 559 incubating females over the 12-year study period.

(b) Perceived predation risk

(i) Nest concealment

Nest concealment was determined for each nest based on hemispherical photographs, aimed from the centre of each nest. Photographs were taken using a 42 mm semi-fisheye lens mounted on an Olympus C-740 digital camera [48], covering lateral and vertical nest surroundings. Each picture was converted to black and white, and the proportion of black pixels (corresponding to rocks or vegetation concealing the nest) was calculated using ImageJ [54].

(ii) Island-specific adult and nest predation risk

The main local predators of breeding females are the white-tailed eagle, the American mink *Neovison vison* and the raccoon dog *Nyctereutes procyonoides* [34,55]. In addition to predation on breeding females, eider eggs can be consumed either by primary predators of female eiders, or by avian predators like hooded crows or gulls *Larus* spp., usually depredating eggs during female absence from the nest [56]. In the study area, the numbers of killed females and depredated nests vary greatly over time and space (see electronic supplementary material S3). We thus calculated yearly indices of adult and nest predation risk for each of the 19 study islands over the 12-year study period.

First, island-specific adult predation risk index was defined as the proportion of killed nesting females, obtained by dividing the number of killed females on a given island and year by the number of breeding attempts on this island and year (see [55]). Breeding attempts included active nests ($N = 4097$ in 2008–2019), nests that had already been depredated ($N = 878$), and nests in which ducklings had already hatched ($N = 172$).

Second, island-specific nest predation risk index was obtained by dividing the number of failed breeding attempts at the final nest fate census on a given year and island by the number of nests on the island whose fate (success or failure) was known [57]. To this aim, we monitored each nest fate (failure or success) at the end of the breeding period. Eiders are precocial

birds and ducklings usually leave the nest within a day after hatching [58]. Successful nests were characterized by the presence of ducklings or hatched eggshells, recognizable by a leathery membrane. Depredated nests were characterized by the absence of eggshells or the presence of shells broken into pieces with a thin bloody membrane [48]. Nest failure was mainly due to depredation, and non-depredated but failed nests could be explained by females abandoning their nest or, occasionally, by females incubating unviable eggs. In some cases, nest depredation may result from the nest being depredated after the female had been killed, but as the number of depredated nests exceeded by many folds the number of females found killed and as the majority of females are observed in the study area after breeding failure, we believe that female depredation is not the main explanation for nest depredation. In addition, the correlation between our two island-specific predation risk indices was relatively low and variable over the study period (mean yearly correlation ± s.d. = 0.30 ± 0.19, range 0.05–0.62, see electronic supplementary material S4), suggesting that the two processes may be relatively independent from each other.

(c) Statistical analyses

Statistical analyses were conducted in R v.4.0.2. [59]. For all models, we ensured that the assumptions of normality and homoscedasticity of residuals were met. FID values were rounded to the closest meter to meet model assumptions and all explanatory variables were centred and scaled. We also checked for overdispersion after fitting Poisson generalized linear mixed models (GLMMs) [60]. We did not detect multi-collinearity among explanatory variables in any model (variance inflation factors, VIFs < 2.5 [61]).

First, we implemented GLMMs and linear mixed models (LMMs) to assess population-level temporal trends in focal variables ($N_{FID} = 1009$; $N_{individual} = 559$; $N_{island} = 19$). Female and island identity were included as random effects to account for the non-independence of observations from the same individual (FID, female minimum age, body condition, nest cover and clutch size) and/or island (all focal variables). GLMMs with a Poisson distribution were used to study annual variation in FID and female minimum age, and LMMs to assess variation in body condition, nest cover, clutch size, and island-specific nest and adult predation risk.

Second, we constructed a GLMM to investigate variation in FID in relation to environmental variables and intrinsic individual characteristics ($N_{FID} = 1009$; $N_{individual} = 559$). We constructed a Poisson GLMM with FID as the dependent variable and female age, body condition, nest cover, clutch size and island-specific adult and nest predation risk as explanatory variables. Female and island identity were included as random effects to account for the non-independence of observations from the same individual and island.

Third, to elucidate the relative contributions of within- and among-individual changes in the explanatory variables on FID, we used within-subject centring [18,62] on a subset of individuals measured at least twice ($N_{FID} = 691$; $N_{individual} = 245$). Each explanatory variable was partitioned into its within-individual component, calculated by mean-centring the focal variable within each individual, and its among-individual component, calculated as the mean value of the focal variable for each
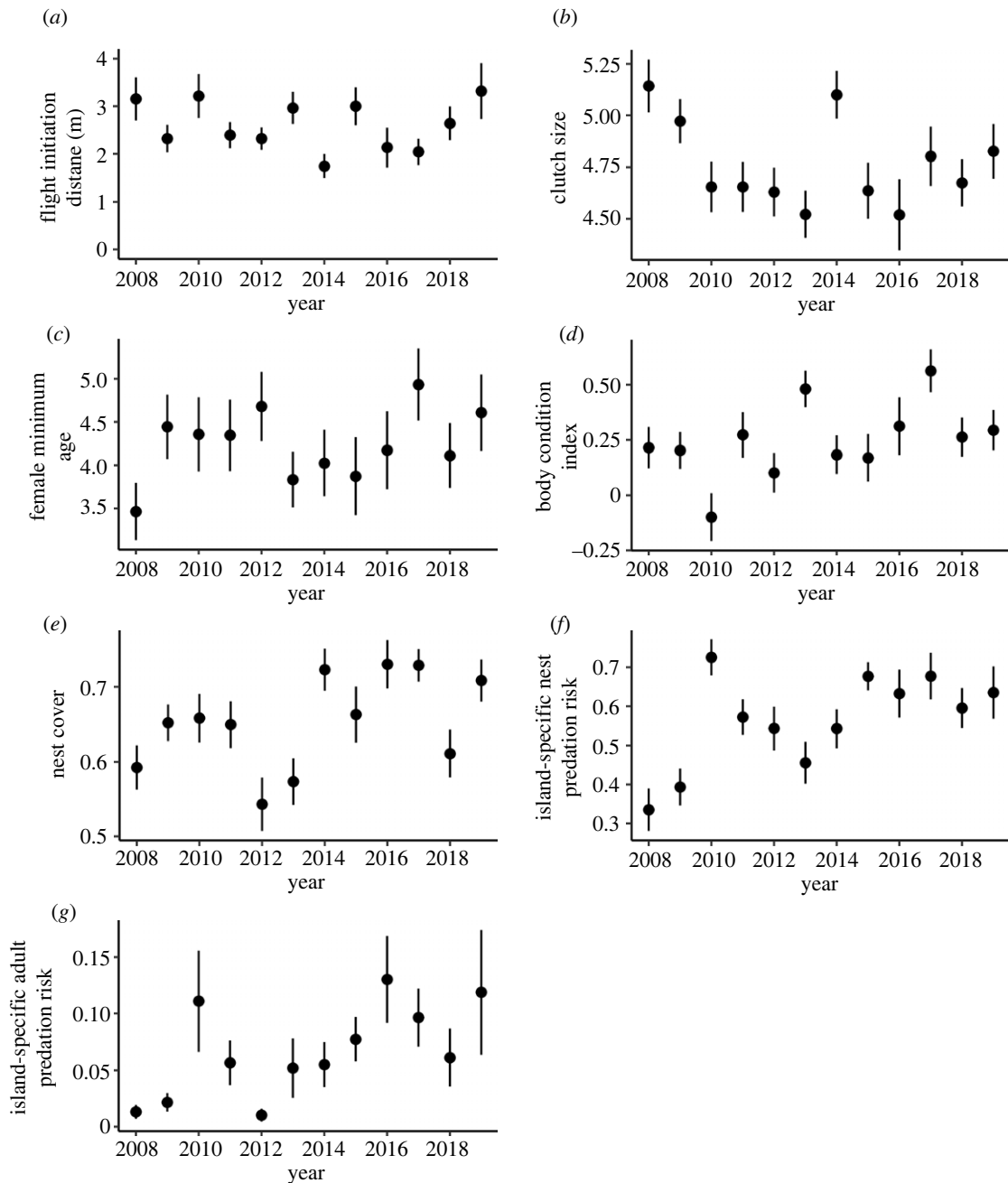
Figure 1. Yearly fluctuations in female eider (*a*) flight initiation distance, (*b*) clutch size, (*c*) minimum age, (*d*) body condition index, (*e*) nest cover and island-specific (*f*) nest and (*g*) adult predation risk over the 12-year study period. Black dots correspond to yearly population-level mean values of the focal variables and bars account for yearly population-level standard errors.

observed individual (see equation 2 in [62]). The within-individual component describes how each repeated observation deviates from the individual's mean (suggesting plastic behavioural responses) and the among-individual component describes how each individual differs from the population mean (suggesting non-random distribution of phenotypes potentially induced by directional selection on the focal trait) [62]. We thus constructed a Poisson GLMM with FID as the dependent variable and within-individual and among-individual components of age, body condition, nest cover, clutch size, and island-specific adult and nest predation risk as explanatory variables, and female and island identity as random effects. We further calculated adjusted within-individual repeatability of FID from this model [63]. Additionally, when both within- and among-individual effects were significant, we tested whether the within- and among-individual effects significantly differed from each other (see equation 3 in [62]). Within-individual

variance and repeatability of explanatory variables are further detailed in the electronic supplementary material S5 and S6.

3. Results

(a) Population-level temporal trends in focal variables

Annual fluctuation in the focal variables is presented in figure 1, and further description of the variable-specific variation over time is given in the electronic supplementary material S7. FID decreased over time (GLMM: estimate ± standard error (E ± s.e.) = −0.245 ± 0.034; $z = −7.169$, $p < 0.001$, electronic supplementary material S7A), as did clutch size (LMM: E ± s.e. = −0.096 ± 0.039, $t = −2.436$, $p = 0.015$, electronic supplementary material S7B). On the contrary, female minimum age

(GLMM: E ± s.e. = 0.586 ± 0.032, z = 18.246, p < 0.001, electronic supplementary material S7C), body condition (LMM: E ± s.e. = 0.155 ± 0.028, t = 5.604, p < 0.001, electronic supplementary material S7D) and nest cover (LMM: E ± s.e. = 0.036 ± 0.006, t = 5.719, p < 0.001, electronic supplementary material S7E) showed a positive time trend, as did nest (LMM: 0.067 ± 0.016; t = 4.080, p < 0.001, electronic supplementary material S7F) and adult (LMM: 0.024 ± 0.008; t = 3.074, p = 0.002, electronic supplementary material S7G) predation risk.

(b) Intrinsic and extrinsic determinants of flight initiation distance

Shorter FIDs were associated with advancing female (minimum) age (table 2, figure 2a), better body condition (table 2, figure 2b) and greater nest concealment (table 2, figure 2c). By contrast, increased island-specific adult predation risk was linked to longer FIDs (table 2, figure 2d).

(c) Flight initiation distance repeatability and within- and among-individual variation in flight initiation distance predictors

FID was significantly and moderately repeatable within individuals (adjusted repeatability, r = 0.400, 95% confidence interval, CI = [0.317, 0.527]). Shorter FIDs were associated with advancing age (table 3). As the within-individual slope was not steeper than the between-individual slope (non-significant difference between among- and within-individual slopes; z = 1.121; p = 0.262; see equation 3 in [62]), our results are in favour of a plastic response to ageing, but do not allow us to confirm selective disappearance of old breeders with long FIDs [64]. Shorter FIDs were also associated with good body condition and high nest concealment, these effects occurring only on the among-individual level (table 3). Interestingly, although high island-specific adult and nest predation risk were both significantly associated with longer FIDs, the FID response to adult predation risk was due to within-individual variation (table 3), whereas that to nest predation risk was confined to the among-individual level (table 3).

4. Discussion

Here, we investigated the patterns and drivers of variation in a standardized measure of risk-taking propensity (FID) in incubating female eiders experiencing increasing predator-induced mortality over 12 years. The temporal increase in adult and nest predation risk was accompanied by an increase in nest concealment, which presumably reflects the combined effect of adaptive responses, such as behavioural compensation to reduce detection by the visually hunting white-tailed eagle, and direct predator-induced selection against open nesting (see §4(a)). Contrary to our expectations, a concomitant decrease, rather than increase, in FID was observed, conceivably due to the action of overcompensatory intrinsic and extrinsic mechanisms (see §4(a)). Our most novel finding was that the prime target of predation—adult versus offspring—had a profound influence on individual variation in escape decision. Indeed, females plastically adjusted their risk-taking propensity to the level of perceived threat to themselves, while individuals with different risk-taking profiles settled on islands characterized by different

Table 2. GLMM explaining variation in FID in relation to individual (minimum age, body condition, nest cover and clutch size) and environmental (island-specific adult and nest predation risk) explanatory variables. Female and island identity were included as random effects. Significant parameter estimates (p < 0.05) are in italics.

fixed effect	estimate ± s.e.	z	p
intercept	0.63 ± 0.09	6.713	<0.001
female minimum age	*−0.46 ± 0.04*	*−11.736*	*<0.001*
body condition index	*−0.08 ± 0.03*	*−2.599*	*0.009*
nest cover	*−0.13 ± 0.04*	*−3.220*	*0.001*
clutch size	−0.00 ± 0.3	−0.069	0.943
island-specific adult predation risk	*0.07 ± 0.03*	*2.104*	*0.035*
island-specific nest predation risk	−0.00 ± 0.3	−0.071	0.945

levels of threat to their nest. Thus, risk-avoiding phenotypes were predominant on islands with high nest predation risk, while breeding females plastically adjusted their anti-predator behaviour to perceived predation threat on themselves. These differential predator type-specific mechanisms linking FID responses to predation threat are consistent with the fundamental life-history trade-off between reproduction and survival (see §4(c)).

(a) Population-level temporal trends in focal variables

Intriguingly, and in contrast with findings in other species [65–67], higher adult and nest predation risk correlated with lower—rather than higher—population-level FID. The statistically significant decrease in FID over the study period is not visible when viewing mean annual population-level FID (figure 1a), becoming evident only by the use of random effects, which correct for pseudoreplication and provide a phenotypic estimate that blends within- and among-individual effects [68]. Two co-occurring compensatory mechanisms could mask and even negate the detection of a population-level increase in FID in response to increasing threat. First, nest cover has significantly increased over the study period, which, all else equal, should translate into shorter FIDs (figure 2c). This temporal shift in nest concealment likely represents an adaptive response to escalating predation by the visually hunting white-tailed eagle, which prefers open habitats, in which incubating females consequently suffer higher mortality [34,69]. At the macrohabitat scale, nesting on open islands may gradually decline because of higher predation [69,70] and lower breeding propensity linked to increased predation risk [34,71]. However, because females are highly philopatric to their nesting site [42,43], also behavioural compensation through microhabitat selection of concealed nest-sites within islands is likely involved. Second, consistent with previous findings, female body condition has increased over time [34,55] and in addition, the population has aged [55], probably contributing to a population-level shift towards shorter FIDs (figure 2a,b). The temporal increase in body condition of breeders may partly be due to more frequent predation-induced nest failure
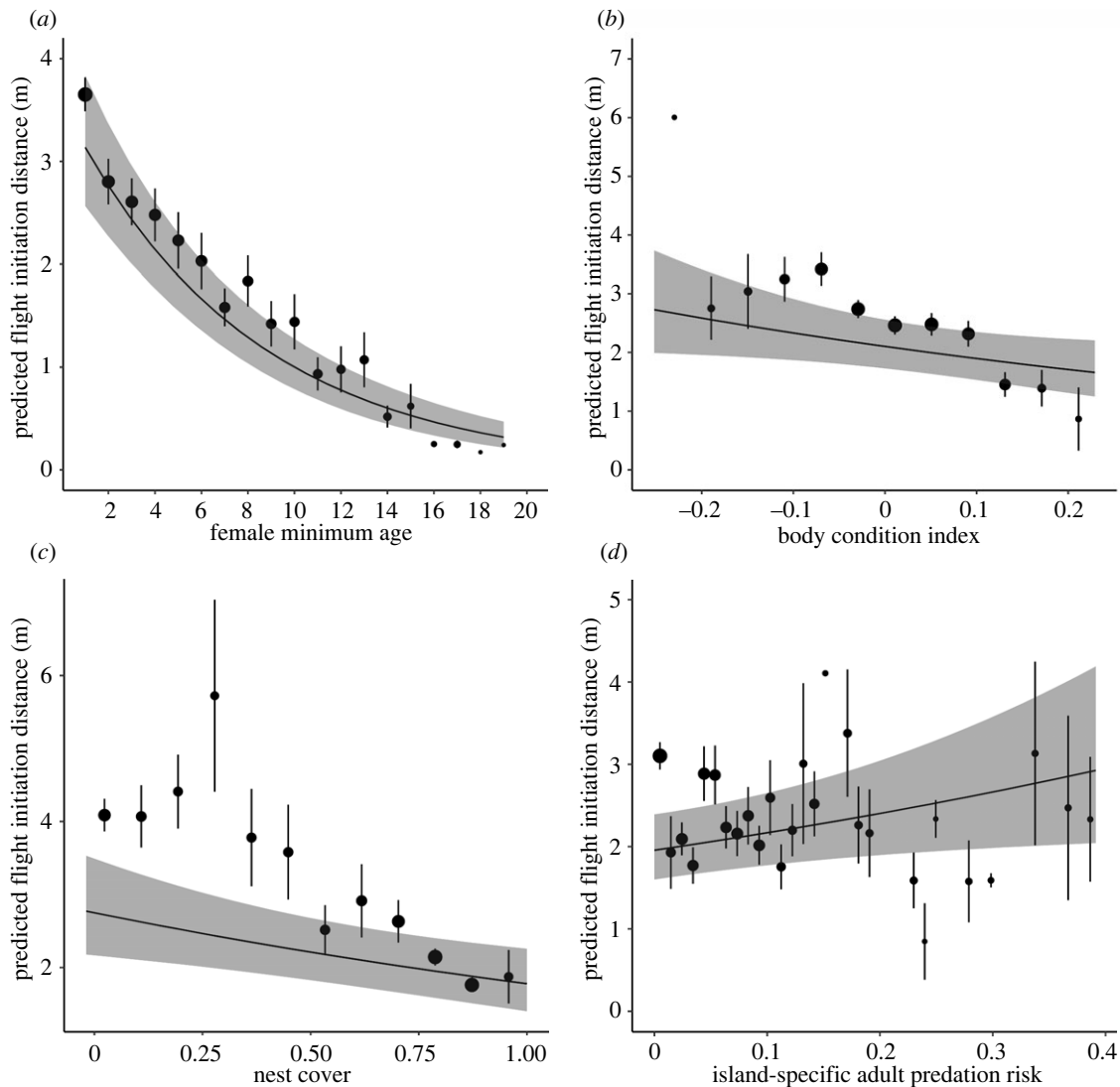
Figure 2. Relationship between predicted flight initiation distance of incubating female eiders and (*a*) female age, (*b*) body condition, (*c*) nest concealment and (*d*) island-specific adult predation risk. Black dots correspond to mean values of the explanatory variable over regular intervals with dot size being proportional to the number of available data points for each interval, and bars account for standard errors. Regression lines depict the population response without integrating random effects, while the grey areas account for 95% confidence intervals.

by poor-condition individuals before monitoring onset, as good body condition is associated with higher nest success [57,72–74]. Poor-condition individuals may also be more likely to refrain from breeding [34,72] or suffer higher predation-induced mortality [69]. For example, in blue petrels *Halobaena caerulea*, poor body condition early in the season was associated with lower breeding success and a higher proportion of non-breeders [72]. In addition, increasing nest predation risk may reduce the production and recruitment of new breeders, and eventually translate into the observed ageing of the population (electronic supplementary material S7C), which has also previously been identified [55].

(b) Parental investment and phenotypic traits as drivers of plasticity and selection in risk-taking behaviour

The moderate within-individual repeatability of FID (*r* = 0.400) leaves room for differential selective disappearance of individuals depending on risk-taking propensity, but also for individually flexible adjustments of anti-predator behaviours according to internal state and environmental

conditions. The repeatability of FID is at the lower end of published estimates, typically ranging from 0.34 to 0.88 [22–26], and lower than the one previously reported for eiders over a shorter portion of the species' lifespan [50], probably reflecting the fact that repeatability tends to decline with time between samplings [75].

Two mutually non-exclusive mechanisms could explain the dampened anti-predator response with increasing individual quality and parental investment (age and body condition effects, table 2, figure 2). First, empirical evidence suggests that individuals in better health or condition tolerate closer approaches from potential predators [76,77]. Thus, assuming that shorter FIDs are correlated with higher individual quality, selection processes could explain the among-individual correlation between good body condition and short FIDs (figure 2*b*). Higher-quality individuals may face a lower rate of predation (e.g. due to possessing superior escape abilities [78,79]). Indeed, the survival of female eiders increases with body condition in our study population [69]. Selective disappearance effects may also be manifested through differences in breeding propensity. Increased predation risk is linked to

Table 3. GLMM explaining variation in FID in relation to within- and among-individual changes in explanatory variables (minimum age, body condition, nest cover, clutch size and island-specific adult and nest predation risk). Female and island identity were included as random effects. Significant parameter estimates ($p < 0.05$) are in italics.

fixed effect	estimate ± s.e.	z	p
intercept	0.49 ± 0.12	4.266	<0.001
age$_{Within}$	*−0.26 ± 0.03*	*−9.062*	*<0.001*
age$_{Among}$	*−0.34 ± 0.07*	*−4.810*	*<0.001*
body condition$_{Within}$	−0.04 ± 0.03	−1.340	0.180
body condition$_{Among}$	*−0.13 ± 0.06*	*−2.185*	*0.029*
nest cover$_{Within}$	−0.03 ± 0.02	−1.277	0.202
nest cover$_{Among}$	*−0.25 ± 0.07*	*−3.306*	*<0.001*
clutch size$_{Within}$	0.03 ± 0.03	1.233	0.217
clutch size$_{Among}$	−0.01 ± 0.06	−0.247	0.805
island-specific adult predation risk$_{Within}$	*0.10 ± 0.03*	*3.445*	*<0.001*
island-specific adult predation risk$_{Among}$	0.02 ± 0.07	0.288	0.77
island-specific nest predation risk$_{Within}$	−0.02 ± 0.03	−0.641	0.521
island-specific nest predation risk$_{Among}$	*0.15 ± 0.03*	*2.404*	*0.016*

a higher incidence of non-breeding in long-lived species [34,70,71], and we may hypothesize that risk-avoiding breeders with low body reserves (associated with longer FIDs), are particularly reluctant to jeopardize their own survival prospects and therefore more frequently skip breeding. A similar effect was not found for females laying larger clutches, but the low repeatability of clutch size ($r = 0.072$; electronic supplementary material S6) may not allow us to detect a potential among-individual effect of clutch size on FID.

Second, females could plastically adjust their risk-taking propensity to their level of parental investment. Females should be more willing to take risks to favour current reproduction as they age and the prospects of future reproduction diminish ('restraint hypothesis' [80]), supported by ample empirical evidence [7,26,29,81]. Indeed, females plastically decreased their FID with advancing age (figure 2a). However, we also expected current brood value to be higher for good-condition mothers and for females laying larger clutches, reflected in a reduced FID response. This argument hinges on the fact that mothers in good body condition produce larger clutches [82,83], incubate more constantly [84,85] and guard offspring more intensely [86]. Intriguingly, we did not find any evidence of females plastically adjusting their FID to their current body condition or clutch size. One plausible explanation could be that body condition is not as individually labile as often envisaged [73,86]. Supporting this hypothesis, female body condition was repeatable within individuals (repeatability, $r = 0.484$; electronic supplementary material S6). Similarly, undetected partial clutch predation, potentially contributing to the temporal association between decreasing clutch size and increasing nest predation risk, may obscure the link between actual reproductive investment and maternal anti-predator responses. Conspecific brood parasitism may also be involved [87,88], although it is only a marginal phenomenon in this low-density population [87].

(c) Predation as a driver of plasticity and selection in risk-taking propensity

Females breeding in concealed nests displayed shorter FIDs. This confirms previous evidence that well-hidden prey in sheltered habitats tolerate a closer approach before fleeing [28,52,89–92], including eiders [93]. However, there is ongoing debate on whether individuals adjust their behaviour according to their local environment [94], or settle in habitats providing the best match to their behavioural profile ('personality-matching hypothesis' [95]), or phenotype in general [32]. Our results are more consistent with the personality-matching hypothesis. We conclude this because female eiders did not plastically adjust their anti-predator behaviour to their level of nest concealment over years (no within-individual effect), while there was a predominance of risk-taking females in concealed nests (significant among-individual effect). Our findings parallel those of D'Alba *et al.* [96]: female eiders varying in their physiological stress-coping phenotypes preferred nests with different shelter, rather than nest shelter directly affecting maternal stress levels. However, because the low within-individual variation in nest cover (electronic supplementary material, table S2) may prevent the detection of a significant within-individual effect of variation in nest cover on FID, our findings of support for the personality-matching hypothesis should be interpreted with some caution.

We provide, to our knowledge, the first demonstration that the target of predation determines the mechanisms adapting risk-taking propensity to the perceived level of threat. Thus, females plastically adjusted their escape responses to the perceived predation risk on themselves but not on their nests, whereas nest predation risk affected the relative distribution of risk-taking phenotypes in the population. Fundamental life-history trade-offs may explain these seemingly counterintuitive findings. Adult survival in long-lived iteroparous animals is typically high and canalized against environmental perturbations, and thus species should prioritize their own survival at the expense of current reproductive success (e.g. [97,98]). Higher individual risk should therefore advance escape responses, as indeed found here (figure 2d). However, the low average individual variance in island-specific nest predation risk (see electronic supplementary material S5) may limit the detection of within-individual effects, and so we encourage research aimed at further disentangling plastic effects of predation risk on offspring or adults, respectively. Our results also highlight a predominance of risk-avoiding females (longer FIDs) on islands with high nest predation risk. We hypothesize that the observed non-random distribution of risk-taking phenotypes may be linked with habitat-specific directional selection. Open treeless islands have previously been shown to suffer from higher nest predation risk [34], and to offer less concealed nest-sites, in which females display longer FIDs ([93]; this study). Importantly, in open nest-sites, higher stress-sensitivity (commonly associated with risk-avoidance) has been shown to be associated with lower nest depredation under high predation threat [56]. Consequently, one may expect reproductive selection for risk-

avoiding phenotypes on sparsely vegetated islands characterized by high nest predation risk. As the low repeatability of island-specific adult predation risk ($r = 0.103$, electronic supplementary material S6) may render it difficult to detect a significant among-individual effect, we encourage future studies using more replicates to confirm the absence of an among-individual effect of predation risk on adults on FID.

5. Conclusion

Our long-term study showed that risk-taking propensity can increase at the population level despite increasing predation pressure, likely due to compensatory changes in nest-site selection and breeder quality overcoming the direct effects of predation threat on prey behaviour. Nevertheless, at the individual level, female eiders did show the expected increase in FID with increasing predation risk. Importantly, our results suggest that the underlying mechanism—behavioural plasticity or selective (dis)appearance—may differ depending on the target of predation (adults or offspring), in line with the theoretically predicted reluctance of parents in long-lived species to trade their own survival for that of their offspring. In addition, greater propensity for risk-taking in concealed nests was likely a consequence of personality-matching [95], rather than mirroring individual plasticity. We also highlighted that older and better-condition females engaged in greater risk-taking. An important insight arises from the current backdrop of unprecedented increase in predation risk. Selective (dis)appearance effects are typically underestimated in captive populations or in species experiencing low-extrinsic mortality [35]. By contrast, our results suggest that individual quality-dependent mortality and reproductive output may be important drivers of individual plasticity in anti-predator responses in natural populations experiencing high predation risk and the strength of predator-induced selection may even

affect the direction of selection [99]. Important next steps will be to elucidate the lifetime fitness consequences of differential risk-taking strategies under variable predation risk and, as highlighted by our study, such endeavours should strive to isolate the effects of adult and nest predation in wild animals.

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