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*Published in:*

Proceedings of the Royal Society B: Biological Sciences

*DOI:*

[10.1098/rspb.2022.1338](https://doi.org/10.1098/rspb.2022.1338)

Published: 28/09/2022

*Document Version*

Accepted author manuscript

*Document License*

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*Please cite the original version:*

Mohring, B., Angelier, F., Jaatinen, K., Steele, B., Lönnberg, E., & Öst, M. (2022). Drivers of within- and among-individual variation in risk-taking behaviour during reproduction in a long-lived bird. *Proceedings of the Royal Society B: Biological Sciences*, 289(1983), Article 20221338. <https://doi.org/10.1098/rspb.2022.1338>

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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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15 **Keywords:**

16 Common eider; *Somateria mollissima*; flight initiation distance; phenotypic plasticity; predation risk;  
17 selection hypothesis

18 **1 Abstract**

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

## 35 2 Background

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

43 Predator-prey interactions shape prey antipredator traits and behaviours over time and space  
44 through selection processes [7,8]. Thus, lower-quality or risk-taking prey may suffer higher predation  
45 mortality and/or reduced reproductive output under threat [9–11]. Such differences in survival or  
46 reproduction may induce phenotypic variation in survival rates and population dynamics [12–15].  
47 However, individuals may also plastically modulate their behavioural or physiological antipredator  
48 responses depending on their internal state and extrinsic factors, including the level of nest and adult  
49 predation risk [7,16,17]. Consequently, phenotypic plasticity can confound patterns of selective  
50 (dis)appearance of risk-taking phenotypes, highlighting the need to account for both plasticity  
51 (within-individual processes) and selection (among-individual processes) in order to disentangle  
52 those responsible for population-level variation [18]. Identifying the drivers of variation in risk-  
53 taking behaviours is thus key to understanding their consequences for both life-history evolution and  
54 population dynamics, especially in a context of fluctuating predation threat. However, few studies  
55 have attempted to separate plasticity and selection of risk-taking phenotypes, given that such analyses  
56 require large longitudinal datasets covering a substantial part of the lifespan of the study organism,  
57 which are often difficult to obtain in the wild [19].

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

67 The evolutionary consequences of individual variation in risk-taking under predation threat  
68 depend on the relative magnitude of adaptive phenotypic plasticity (i.e., phenotypes actively  
69 matching prevailing risk) and selective disappearance effects (i.e., exclusion of certain phenotypes  
70 from the breeding pool) [31–33]. Our long-term longitudinal data on FIDs of incubating female  
71 common eiders *Somateria mollissima*, hereafter eiders, allowed us to improve knowledge on the  
72 relative influence of these mechanisms on risk-taking behaviour during reproduction. Specifically,  
73 we investigated how FID is modulated by phenotypic traits, parental investment, conspicuousness to  
74 predators and fluctuating predation pressure. The study was conducted amidst an unprecedented  
75 increase in predation pressure in our study population in the northern Baltic Sea, mainly attributed to  
76 the recent recovery of the white-tailed eagle *Haliaeetus albicilla*, the main predator of adult eiders  
77 [34]. This created an ideal backdrop to investigate individual plasticity and population-level selection  
78 processes involved in prey responses to a fluctuating predation regime [35].

79 To this end, we first delineated the population-level trends in FID, female and nest  
80 characteristics, clutch size and predation risk over the entire study period (2008-2019). We then  
81 addressed whether FID was (1) related to female phenotypic traits, reproductive investment, nest

82 conspicuousness and predation risk, (2) repeatable and, (3) shaped by within-individual plasticity or  
83 among-individual selection. We assumed that FID would be affected by population-level selection  
84 against risk-taking phenotypes (i.e., displaying shorter FIDs) under the progressively increasing  
85 predation threat. In addition and according to life-history theory [1], we expected females to be more  
86 risk taking, i.e., display shorter FIDs, with advancing age (diminishing residual reproductive value),  
87 when the costs of reproduction are lower (good body condition) and when making a greater  
88 reproductive investment (large clutch). Given that nest conspicuousness can affect predation risk, we  
89 expected females to advance their escape response when breeding in nests offering little  
90 concealment, or on islands characterised by high adult and nest predation risk. Alternatively, but not  
91 exclusively, females characterised by shorter FIDs may avoid conspicuous nests and risky islands,  
92 hence mitigating environmentally-imposed risk of predation. We further expected FID to be  
93 individually repeatable, but modulated by plastic adjustments to individual state, parental investment  
94 and perceived predation risk.

## 95 **3 Methods**

### 96 **3.1 Female monitoring**

#### 97 **Breeding female characteristics**

98 The study was conducted in the western Gulf of Finland, in the archipelago surrounding Tvärminne  
99 Zoological Station (59°50'N, 23°15'E), in 2008-2019. Female eiders nest on diverse types of islands,  
100 including those covered by bare rocks, sparse patches of herbs, stands of juniper *Juniperus communis*  
101 or pine *Pinus sylvestris* dominated forest. Incubating female eiders at Tvärminne have been annually  
102 trapped on their nest with hand nets since 1990, and individually marked with a standard metal ring.  
103 Female weight was measured to the nearest 10 g with a Pesola spring balance, and radius-ulna length,  
104 a proxy of body size, was measured to the nearest 1 mm with a wing ruler. Females incubate for

105 about 26 days [36], and females were trapped between May and early June during the later phase of  
106 incubation to minimize nest abandonment [37]. Hatching date was estimated using an egg floatation  
107 test [38], and the number of eggs was counted as a proxy of initial energetic investment in  
108 reproduction [39,40].

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

### 119 **Risk-taking propensity**

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

128 hatching [28,51,52] but also to limit the risk of nest abandonment, FID was measured the day before  
129 the expected hatching date predicted by egg floatation. Once the female had fled from the nest, the  
130 observer immediately covered the nest to minimize the risk of detection and depredation by avian egg  
131 predators such as hooded crows *Corvus cornix* [53]. On average,  $33.08 \pm 5.94$  % of nests active at  
132 first encounter were annually sampled for FID (range: 24.19 % - 42.92 %). This relatively low  
133 proportion was due to the fact that females whose eggs were depredated or hatched prior to FID  
134 measurement could not be sampled for FID ( $61.74 \pm 13.79$  % of successful nests were on average  
135 annually sampled, range: 43.70 % - 87.50%). Coupled with a predation risk-induced increase in  
136 intermittent breeding strategies and premature mortality due to predation [34], the number of  
137 repeated measures per individual over time was lower than what one could expect from such a long-  
138 lived philopatric species (table 1). Overall, we measured 1009 FIDs to the closest 10 cm (later  
139 rounded to the closest meter (see 3.3) to account for measurement imprecision and to meet model  
140 assumptions) on 559 incubating females over the 12-year study period.

## 141 **3.2 Perceived predation risk**

### 142 **Nest concealment**

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

### 148 **Island-specific adult and nest predation risk**

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

156 First, island-specific adult predation risk index was defined as the proportion of killed nesting  
157 females, obtained by dividing the number of killed females on a given island and year by the number  
158 of breeding attempts on this island and year (see [55]). Breeding attempts included active nests (N =  
159 4097 in 2008-2019), nests that had already been depredated (N = 878), and nests in which ducklings  
160 had already hatched (N = 172).

161 Second, island-specific nest predation risk index was obtained by dividing the number of failed  
162 breeding attempts at the final nest fate census on a given year and island by the number of nests on  
163 the island whose fate (success or failure) was known [58]. To this aim, we monitored each nest fate  
164 (failure or success) at the end of the breeding period. Eiders are precocial birds and ducklings usually  
165 leave the nest within a day after hatching [59]. Successful nests were characterized by the presence of  
166 ducklings or hatched eggshells, recognizable by a leathery membrane. Depredated nests were  
167 characterized by the absence of eggshells or the presence of shells broken into pieces with a thin  
168 bloody membrane [48]. Nest failure was mainly due to depredation, and non-depredated but failed  
169 nests could be explained by females abandoning their nest or, occasionally, by females incubating  
170 unviable eggs. In some cases, nest depredation may result from the nest being depredated after the  
171 female had been killed, but as the number of depredated nests exceeded by many folds the number of  
172 females found killed and as the majority of females are observed in the study area after breeding

173 failure, we believe that female depredation is not the main explanation for nest depredation. In  
174 addition, the correlation between our two island-specific predation risk indices was relatively low and  
175 variable over the study period (mean yearly correlation  $\pm$  SD =  $0.30 \pm 0.19$ , range 0.05 - 0.62, see  
176 electronic supplementary material S4), suggesting that the two processes may be relatively  
177 independent from each other.

### 178 **3.3 Statistical analyses**

179 Statistical analyses were conducted in R 4.0.2. [60]. For all models, we ensured that the assumptions  
180 of normality and homoscedasticity of residuals were met. FID values were rounded to the closest  
181 meter to meet model assumptions and all explanatory variables were centred and scaled. We also  
182 checked for overdispersion after fitting Poisson generalized linear mixed models (GLMMs) [61]. We  
183 did not detect multicollinearity among explanatory variables in any model (variance inflation factors,  
184 VIFs < 2.5 [62]).

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

192 Second, we constructed a GLMM to investigate variation in FID in relation to environmental  
193 variables and intrinsic individual characteristics, ( $N_{\text{FID}} = 1009$ ;  $N_{\text{individual}} = 559$ ). We constructed a  
194 Poisson GLMM with FID as the dependent variable and female age, body condition, nest cover,  
195 clutch size, and island-specific adult and nest predation risk as explanatory variables. Female and

196 island identity were included as random effects to account for the non-independence of observations  
197 from the same individual and island.

198 Third, to elucidate the relative contributions of within- and among-individual changes in the  
199 explanatory variables on FID, we used within-subject centring [18,63] on a subset of individuals  
200 measured at least twice ( $N_{\text{FID}} = 691$ ;  $N_{\text{individual}} = 245$ ). Each explanatory variable was partitioned into  
201 its within-individual component, calculated by mean-centring the focal variable within each  
202 individual, and its among-individual component, calculated as the mean value of the focal variable  
203 for each observed individual (see equation 2 in [63]). The within-individual component describes  
204 how each repeated observation deviates from the individual's mean (suggesting plastic behavioural  
205 responses) and the among-individual component describes how each individual differs from the  
206 population mean (suggesting non-random distribution of phenotypes potentially induced by  
207 directional selection on the focal trait) [63]. We thus constructed a Poisson GLMM with FID as the  
208 dependent variable and within-individual and among-individual components of age, body condition,  
209 nest cover, clutch size, and island-specific adult and nest predation risk as explanatory variables, and  
210 female and island identity as random effects. We further calculated adjusted within-individual  
211 repeatability of FID from this model [64]. Additionally, when both within- and among-individual  
212 effects were significant, we tested whether the within- and among-individual effects significantly  
213 differed from each other (see equation 3 in [63]). Within-individual variance and repeatability of  
214 explanatory variables are further detailed in electronic supplementary materials S5 and S6.

## 215 **4 Results**

### 216 **4.1 Population-level temporal trends in focal variables**

217 Annual fluctuation in the focal variables is presented in figure 1, and further description of the  
218 variable-specific variation over time is given in the electronic supplementary material S7. FID

219 decreased over time (GLMM: estimate  $\pm$  standard error (E  $\pm$  SE) =  $-0.245 \pm 0.034$ ;  $z = -7.169$ ,  $p <$   
220  $0.001$ , electronic supplementary material S7A), as did clutch size (LMM: E  $\pm$  SE =  $-0.096 \pm 0.039$ ,  $t$   
221 =  $-2.436$ ,  $p = 0.015$ , electronic supplementary material S7B). On the contrary, female minimum age  
222 (GLMM: E  $\pm$  SE =  $0.586 \pm 0.032$ ,  $z = 18.246$ ,  $p < 0.001$ , electronic supplementary material S7C),  
223 body condition (LMM: E  $\pm$  SE =  $0.155 \pm 0.028$ ,  $t = 5.604$ ,  $p < 0.001$ , electronic supplementary  
224 material S7D) and nest cover (LMM: E  $\pm$  SE =  $0.036 \pm 0.006$ ,  $t = 5.719$ ,  $p < 0.001$ , electronic  
225 supplementary material S7E) showed a positive time trend, as did nest (LMM:  $0.067 \pm 0.016$ ;  $t =$   
226  $4.080$ ,  $p < 0.001$ , electronic supplementary material S7F) and adult (LMM:  $0.024 \pm 0.008$ ;  $t = 3.074$ ,  
227  $p = 0.002$ , electronic supplementary material S7G) predation risk.

## 228 **4.2 Intrinsic and extrinsic determinants of FID**

229 Shorter FIDs were associated with advancing female (minimum) age (table 2, figure 2A), better body  
230 condition (table 2, figure 2B) and greater nest concealment (table 2, figure 2C). In contrast, increased  
231 island-specific adult predation risk was linked to longer FIDs (table 2, figure 2D).

## 232 **4.3 FID repeatability and within- and among-individual variation in FID predictors**

233 FID was significantly and moderately repeatable within individuals (adjusted repeatability,  $r = 0.400$ ,  
234 95% confidence interval, CI =  $[0.317, 0.527]$ ). Shorter FIDs were associated with advancing age  
235 (table 3). As the within-individual slope was not steeper than the between-individual slope (non-  
236 significant difference between among- and within-individual slopes;  $z = 1.121$ ;  $p = 0.262$ , see  
237 equation 3 in [63]), our results are in favour of a plastic response to ageing, but do not allow us to  
238 confirm selective disappearance of old breeders with long FIDs [65]. Shorter FIDs were also  
239 associated with good body condition and high nest concealment, these effects occurring only on the  
240 among-individual level (table 3). Interestingly, although high island-specific adult and nest predation  
241 risk were both significantly associated with longer FIDs, the FID response to adult predation risk was

242 due to within-individual variation (table 3), whereas that to nest predation risk was confined to the  
243 among-individual level (table 3).

## 244 **5 Discussion**

245 Here, we investigated the patterns and drivers of variation in a standardised measure of risk-taking  
246 propensity (FID) in incubating female eiders experiencing increasing predator-induced mortality over  
247 12 years. The temporal increase in adult and nest predation risk was accompanied by an increase in  
248 nest concealment, which presumably reflects the combined effect of adaptive responses, such as  
249 behavioural compensation to reduce detection by the visually hunting white-tailed eagle, and direct  
250 predator-induced selection against open nesting (see 5.1). Contrary to our expectations, a  
251 concomitant decrease, rather than increase, in FID was observed, conceivably due to the action of  
252 overcompensatory intrinsic and extrinsic mechanisms (see 5.1). Our most novel finding was that the  
253 prime target of predation – adult versus offspring – had a profound influence on individual variation  
254 in escape decision. Indeed, females plastically adjusted their risk-taking propensity to the level of  
255 perceived threat to themselves, while individuals with different risk-taking profiles settled on islands  
256 characterised by different levels of threat to their nest. Thus, risk-avoiding phenotypes were  
257 predominant on islands with high nest predation risk, while breeding females plastically adjusted  
258 their antipredator behaviour to perceived predation threat on themselves. These differential predator  
259 type-specific mechanisms linking FID responses to predation threat are consistent with the  
260 fundamental life-history trade-off between reproduction and survival (see 5.3).

### 261 **5.1 Population-level temporal trends in focal variables**

262 Intriguingly, and in contrast to findings in other species [66–68], higher adult and nest predation risk  
263 correlated with lower – rather than higher – population-level FID. The statistically significant  
264 decrease in FID over the study period is not visible when viewing mean annual population-level FID

265 (figure 1A), becoming evident only by the use of random effects, which correct for pseudoreplication  
266 and provide a phenotypic estimate that blends within- and among-individual effects [69]. Two co-  
267 occurring compensatory mechanisms could mask and even negate the detection of a population-level  
268 increase in FID in response to increasing threat. First, nest cover has significantly increased over the  
269 study period, which, all else equal, should translate into shorter FIDs (figure 2C). This temporal shift  
270 in nest concealment likely represents an adaptive response to escalating predation by the visually  
271 hunting white-tailed eagle, which prefers open habitats, in which incubating females consequently  
272 suffer higher mortality [34,70]. At the macrohabitat scale, nesting on open islands may gradually  
273 decline because of higher predation [70,71] and lower breeding propensity linked to increased  
274 predation risk [34,72]. However, because females are highly philopatric to their nesting site [42,43],  
275 also behavioural compensation through microhabitat selection of concealed nest-sites within islands  
276 is likely involved. Second, consistent with previous findings, female body condition has increased  
277 over time [34,55] and in addition, the population has aged [55], likely contributing to a population-  
278 level shift towards shorter FIDs (figures 2B, 2A). The temporal increase in body condition of  
279 breeders may partly be due to more frequent predation-induced nest failure by poor-condition  
280 individuals before monitoring onset, as good body condition is associated with higher nest success  
281 [58,73–75]. Poor-condition individuals may also be more likely to refrain from breeding [34,73] or  
282 suffer higher predation-induced mortality [70]. For example, in blue petrels *Halobaena caerulea*,  
283 poor body condition early in the season was associated with lower breeding success and a higher  
284 proportion of non-breeders [73]. In addition, increasing nest predation risk may reduce the  
285 production and recruitment of new breeders, and eventually translate into the observed ageing of the  
286 population (electronic supplementary material S7C), which has also previously been identified [55].

## 287 **5.2 Parental investment and phenotypic traits as drivers of plasticity and selection in risk-** 288 **taking behaviour**

289 The moderate within-individual repeatability of FID ( $r = 0.400$ ) leaves room for differential selective  
290 disappearance of individuals depending on risk-taking propensity, but also for individually flexible  
291 adjustments of antipredator behaviours according to internal state and environmental conditions. The  
292 repeatability of FID is at the lower end of published estimates, typically ranging from 0.34 to 0.88  
293 [22–26], and lower than the one previously reported for eiders over a shorter portion of the species’  
294 lifespan [50], probably reflecting the fact that repeatability tends to decline with time between  
295 samplings [76].

296 Two mutually non-exclusive mechanisms could explain the dampened antipredator response  
297 with increasing individual quality and parental investment (age and body condition effects, table 2,  
298 figure 2). First, empirical evidence suggests that individuals in better health or condition tolerate  
299 closer approaches from potential predators [77,78]. Thus, assuming that shorter FIDs are correlated  
300 with higher individual quality, selection processes could explain the among-individual correlation  
301 between good body condition and short FIDs (figure 2B). Higher-quality individuals may face a  
302 lower rate of predation, e.g., due to possessing superior escape abilities [79,80]. Indeed, survival of  
303 female eiders increases with body condition in our study population [70]. Selective disappearance  
304 effects may also be manifested through differences in breeding propensity. Increased predation risk is  
305 linked to a higher incidence of non-breeding in long-lived species [34,71,72], and we may  
306 hypothesize that risk-avoiding breeders with low body reserves (associated with longer FIDs), are  
307 particularly reluctant to jeopardize their own survival prospects and therefore more frequently skip  
308 breeding. A similar effect was not found for females laying larger clutches, but the low repeatability  
309 of clutch size ( $r = 0.072$ , electronic supplementary material S6) may not allow us to detect a potential  
310 among-individual effect of clutch size on FID.

311 Second, females could plastically adjust their risk-taking propensity to their level of parental  
312 investment. Females should be more willing to take risks to favour current reproduction as they age

313 and the prospects of future reproduction diminish ('restraint hypothesis' [81]), supported by ample  
314 empirical evidence [7,26,29,82]. Indeed, females plastically decreased their FID with advancing age  
315 (figure 2A). However, we also expected current brood value to be higher for good-condition mothers  
316 and for females laying larger clutches, reflected in a reduced FID response. This argument hinges on  
317 the fact that mothers in good body condition produce larger clutches [83,84], incubate more  
318 constantly [85,86], and guard offspring more intensely [87]. Intriguingly, we did not find any  
319 evidence of females plastically adjusting their FID to their current body condition or clutch size. One  
320 plausible explanation could be that body condition is not as individually labile as often envisaged  
321 [74,87]. Supporting this hypothesis, female body condition was repeatable within individuals  
322 (repeatability,  $r = 0.484$ , electronic supplementary material S6). Similarly, undetected partial clutch  
323 predation, potentially contributing to the temporal association between decreasing clutch size and  
324 increasing nest predation risk, may obscure the link between actual reproductive investment and  
325 maternal antipredator responses. Conspecific brood parasitism may also be involved [88,89],  
326 although it is only a marginal phenomenon in this low-density population [88].

### 327 **5.3 Predation as a driver of plasticity and selection in risk-taking propensity**

328 Females breeding in concealed nests displayed shorter FIDs. This confirms previous evidence that  
329 well-hidden prey in sheltered habitats tolerate a closer approach before fleeing [28,52,90–93],  
330 including eiders [94]. However, there is ongoing debate on whether individuals adjust their behaviour  
331 according to their local environment [95], or settle in habitats providing the best match to their  
332 behavioural profile ('personality-matching hypothesis' [96]), or phenotype in general [32]. Our  
333 results are more consistent with the personality-matching hypothesis. We conclude this because  
334 female eiders did not plastically adjust their antipredator behaviour to their level of nest concealment  
335 over years (no within-individual effect), while there was a predominance of risk-taking females in  
336 concealed nests (significant among-individual effect). Our findings parallel those of D'Alba et al.

337 [97]: female eiders varying in their physiological stress-coping phenotypes preferred nests with  
338 different shelter, rather than nest shelter directly affecting maternal stress levels. However, because  
339 the low within-individual variation in nest cover (table S2) may prevent the detection of a significant  
340 within-individual effect of variation in nest cover on FID, our findings of support for the personality-  
341 matching hypothesis should be interpreted with some caution.

342 We provide, to our knowledge, the first demonstration that the target of predation determines  
343 the mechanisms adapting risk-taking propensity to the perceived level of threat. Thus, females  
344 plastically adjusted their escape responses to the perceived predation risk on themselves but not on  
345 their nests, whereas nest predation risk affected the relative distribution of risk-taking phenotypes in  
346 the population. Fundamental life-history trade-offs may explain these seemingly counterintuitive  
347 findings. Adult survival in long-lived iteroparous animals is typically high and canalized against  
348 environmental perturbations, and thus species should prioritize their own survival at the expense of  
349 current reproductive success (e.g. [98,99]). Higher individual risk should therefore advance escape  
350 responses, as indeed found here (figure 2D). However, the low average individual variance in island-  
351 specific nest predation risk (see electronic supplementary material S5) may limit the detection of  
352 within-individual effects, and so we encourage research aimed at further disentangling plastic effects  
353 of predation risk on offspring or adults, respectively. Our results also highlight a predominance of  
354 risk-avoiding females (longer FIDs) on islands with high nest predation risk. We hypothesise that the  
355 observed non-random distribution of risk-taking phenotypes may be linked with habitat-specific  
356 directional selection. Open treeless islands have previously been shown to suffer from higher nest  
357 predation risk [34], and to offer less concealed nest sites, in which females display longer FIDs ([94];  
358 this study). Importantly, in open nest-sites, higher stress-sensitivity (commonly associated with risk-  
359 avoidance) has been shown to be associated with lower nest depredation under high predation threat  
360 [56]. Consequently, one may expect reproductive selection for risk-avoiding phenotypes on sparsely

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

## 365 **6 Conclusions**

366 Our long-term study showed that risk-taking propensity can increase at the population level despite  
367 increasing predation pressure, likely due to compensatory changes in nest-site selection and breeder  
368 quality overcoming the direct effects of predation threat on prey behaviour. Nevertheless, at the  
369 individual level, female eiders did show the expected increase in FID with increasing predation risk.  
370 Importantly, our results suggest that the underlying mechanism – behavioural plasticity or selective  
371 (dis)appearance – may differ depending on the target of predation (adults or offspring), in line with  
372 the theoretically predicted reluctance of parents in long-lived species to trade their own survival for  
373 that of their offspring. In addition, greater propensity for risk-taking in concealed nests was likely a  
374 consequence of personality-matching [96], rather than mirroring individual plasticity. We also  
375 highlighted that older and better-condition females engaged in greater risk-taking. An important  
376 insight arises from the current backdrop of unprecedented increase in predation risk. Selective  
377 (dis)appearance effects are typically underestimated in captive populations or in species experiencing  
378 low extrinsic mortality [35]. In contrast, our results suggest that individual quality-dependent  
379 mortality and reproductive output may be important drivers of individual plasticity in antipredator  
380 responses in natural populations experiencing high predation risk and the strength of predator-  
381 induced selection may even affect the direction of selection [100]. Important next steps will be to  
382 elucidate the lifetime fitness consequences of differential risk-taking strategies under variable  
383 predation risk and, as highlighted by our study, such endeavours should strive to isolate the effects of  
384 adult and nest predation in wild animals.

385 7 **References**

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- 622

623 **8 Tables**

624 **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

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626

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

<b>Fixed effect</b>	<b>Estimate <math>\pm</math> standard error</b>	<b>z</b>	<b>p</b>
Intercept	0.63 $\pm$ 0.09	6.713	<0.001
<b>Female minimum age</b>	<b>-0.46 <math>\pm</math> 0.04</b>	<b>-11.736</b>	<b>&lt;0.001</b>
<b>Body condition index</b>	<b>-0.08 <math>\pm</math> 0.03</b>	<b>-2.599</b>	<b>0.009</b>
<b>Nest cover</b>	<b>-0.13 <math>\pm</math> 0.04</b>	<b>-3.220</b>	<b>0.001</b>
Clutch size	-0.00 $\pm$ 0.3	-0.069	0.943
<b>Island-specific adult predation risk</b>	<b>0.07 <math>\pm</math> 0.03</b>	<b>2.104</b>	<b>0.035</b>
Island-specific nest predation risk	-0.00 $\pm$ 0.3	-0.071	0.945

631

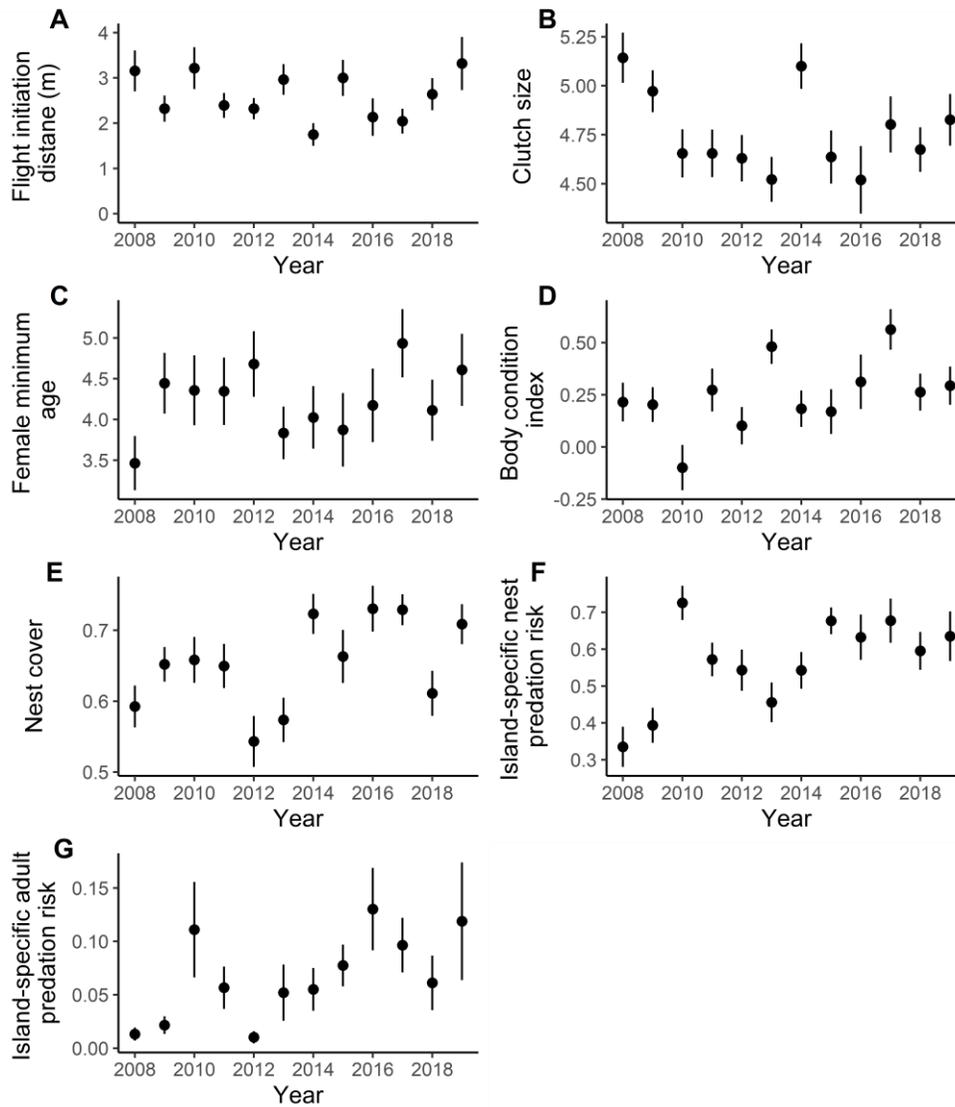
632 **Table 3:** GLMM explaining variation in FID in relation to within- and among-individual changes in  
633 explanatory variables (minimum age, body condition, nest cover, clutch size and island-specific adult  
634 and nest predation risk). Female and island identity were included as random effects.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

Fixed effect	Estimate $\pm$ standard error	z	p
Intercept	0.49 $\pm$ 0.12	4.266	<0.001
<b>Age<sub>Within</sub></b>	<b>-0.26 <math>\pm</math> 0.03</b>	<b>-9.062</b>	<b>&lt;0.001</b>
<b>Age<sub>Among</sub></b>	<b>-0.34 <math>\pm</math> 0.07</b>	<b>-4.810</b>	<b>&lt;0.001</b>
Body condition <sub>Within</sub>	-0.04 $\pm$ 0.03	-1.340	0.180
<b>Body condition<sub>Among</sub></b>	<b>-0.13 <math>\pm</math> 0.06</b>	<b>-2.185</b>	<b>0.029</b>
Nest cover <sub>Within</sub>	-0.03 $\pm$ 0.02	-1.277	0.202
<b>Nest cover<sub>Among</sub></b>	<b>-0.25 <math>\pm</math> 0.07</b>	<b>-3.306</b>	<b>&lt;0.001</b>
Clutch size <sub>Within</sub>	0.03 $\pm$ 0.03	1.233	0.217
Clutch size <sub>Among</sub>	-0.01 $\pm$ 0.06	-0.247	0.805
<b>Island-specific adult predation risk<sub>Within</sub></b>	<b>0.10 <math>\pm</math> 0.03</b>	<b>3.445</b>	<b>&lt;0.001</b>
Island-specific adult predation risk <sub>Among</sub>	0.02 $\pm$ 0.07	0.288	0.77
Island-specific nest predation risk <sub>Within</sub>	-0.02 $\pm$ 0.03	-0.641	0.521
<b>Island-specific nest predation risk<sub>Among</sub></b>	<b>0.15 <math>\pm</math> 0.03</b>	<b>2.404</b>	<b>0.016</b>

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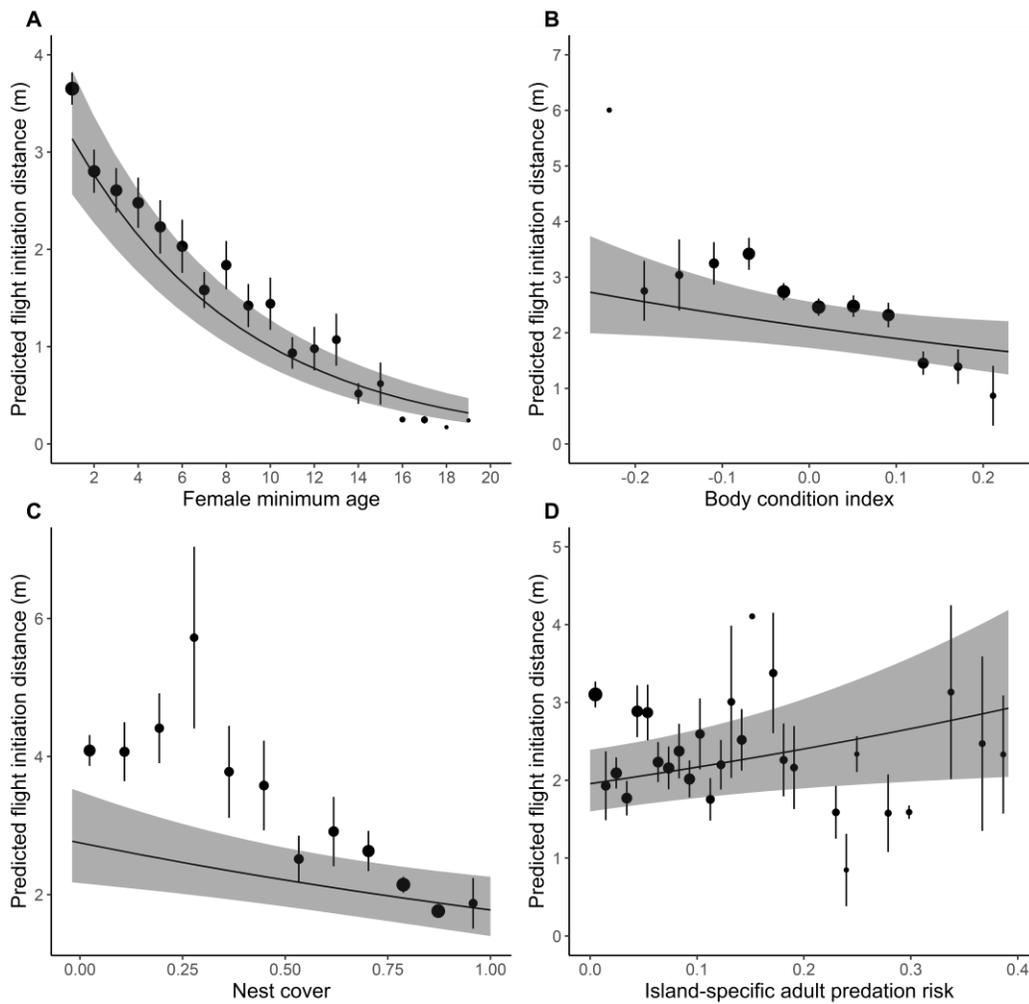
639 **Figure 1.** Yearly fluctuations in female eider (A) flight initiation distance, (B) clutch size, (C)  
 640 minimum age, (D) body condition index, (E) nest cover and island-specific (F) nest and (G) adult  
 641 predation risk over the 12-year study period. Black dots correspond to yearly population-level mean  
 642 values of the focal variables and bars account for yearly population-level standard errors.



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645 **Figure 2.** Relationship between predicted flight initiation distance of incubating female eiders and  
646 (A) female age, (B) body condition, (C) nest concealment, and (D) island-specific adult predation  
647 risk. Black dots correspond to mean values of the explanatory variable over regular intervals with dot  
648 size being proportional to the number of available data points for each interval, and bars account for  
649 standard errors. Regression lines depict the population response without integrating random effects,  
650 while the grey areas account for 95% confidence intervals.



651

652 **Data accessibility.**

653 The data supporting this study are available from the Dryad Digital Repository:

654 <https://doi.org/10.5061/dryad.m37pvmd59> [101]. Electronic supplementary material is available

655 online.

656 **Authors' contributions.**

657 B.M.: conceptualization, data curation, formal analysis, investigation, visualization, writing—

658 original draft, writing—review and editing; F.A.: conceptualization, investigation, writing—review

659 and editing, supervision; K.J.: conceptualization, funding acquisition, investigation, writing—review

660 and editing; B.S.: investigation, writing—review and editing; E.L.: data curation, investigation;

661 M.Ö.: conceptualization, funding acquisition, investigation, project administration, supervision,

662 writing—review and editing. All authors gave final approval for submission.

663 **Competing interests.**

664 The authors declare that there is no conflict of interest.

665 **Funding.**

666 This research was supported by the Swedish Cultural Foundation in Finland [grant numbers 17/3317,

667 16/1476, 15/3296, 14/2657, 13/2654, 138139, 149014, 158026, 168333, and 177733 to MÖ] and the

668 Academy of Finland [grant numbers 266208 to KJ and 128039 to MÖ]. KJ was funded by grants

669 from Sophie von Julins Stiftelse and from the Ministry of Agriculture and Forestry of Finland [grant

670 to the Nature and Game Management Trust Finland].

671 **Acknowledgments.**

672 We thank Tvärminne Zoological Station for providing facilities. We thank all field assistants who

673 helped collecting the data. We thank Coraline Bichet for fruitful discussions on within-subject

674 centring. Handling of animals was reviewed and approved by the National Animal Experiment Board

675 [permit number ESAVI/1697/04.10.03/2012] and complied with the regulations of Tvärminne  
676 Zoological Station.