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## Top-down effects override climate forcing on reproductive success in a declining sea duck

Öst, Markus; Lehikoinen, Aleks; Jaatinen, Kim

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## Top-down effects override climate forcing on reproductive success in a declining sea duck

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Keywords:	Antipredator behaviour, anthropogenic predation facilitation, biotic interaction strength, climate forcing, reproductive success, predator-prey
Abstract:	<p>Population performance is predicted to be more strongly influenced by detrimental species interactions such as predation under benign climatic conditions, and by climate forcing under harsh conditions, reflected in geographical gradients in biotic interaction strength. Less appreciated is the potential for site-specific changes in drivers with the advent of anthropogenic alteration of predator-prey relationships, including apex predator restoration and spread of invasive predators. Particularly interesting is the relative impact of climate and biotic interactions on population performance when these conflict. In this 31-year study (1990-2020), we revisit a common eider (<i>Somateria mollissima</i>) population from SW Finland, Baltic Sea, fifteen years on from an earlier study showing that climate warming positively affected reproductive parameters and performance. However, the population is simultaneously exposed to increasing predation by the rapidly recovering native apex predator and invasive mammals. Based on the current population trend, we predicted (i) a weakening of the previously documented positive effects of a warming climate on vital rates, (ii) intensified predation, and (iii) increasing top-down control of vital rates and accompanying population decline. Five out of seven breeding parameters (annual spread in female body condition, breeding phenology and synchrony, interval between arrival and breeding, fledgling production) were best explained by predation indices, whereas climate signals (winter NAO, Baltic Sea maximum ice cover) on breeding parameters have weakened. Particularly intriguing is that the previous positive association between mild ice winters and subsequent reproductive output has disappeared during the past 15 years, highlighting the non-linear nature of climate change responses. Indirect predation effects (selective disappearance, changed reproductive strategies, nest-site selection and population age distribution) can potentially explain also the remaining breeding parameters (annual mean body condition and clutch size). The observed regime shift in predation risk appears to prevent this now endangered population from reaping the potential benefits of a warming climate.</p>



## 1 **Abstract**

2 Population performance is predicted to be more strongly influenced by detrimental species interactions  
3 such as predation under benign climatic conditions, and by climate forcing under harsh conditions,  
4 reflected in geographical gradients in biotic interaction strength. Less appreciated is the potential for site-  
5 specific changes in drivers with the advent of anthropogenic alteration of predator-prey relationships,  
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7 impact of climate and biotic interactions on population performance when these conflict. In this 31-year  
8 study (1990-2020), we revisit a common eider (*Somateria mollissima*) population from SW Finland,  
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19 disappeared during the past 15 years, highlighting the non-linear nature of climate change responses.  
20 Indirect predation effects (selective disappearance, changed reproductive strategies, nest-site selection  
21 and population age distribution) can potentially explain also the remaining breeding parameters (annual  
22 mean body condition and clutch size). The observed regime shift in predation risk appears to prevent this  
23 now endangered population from reaping the potential benefits of a warming climate.

24 **Keywords:** Antipredator behaviour, anthropogenic predation facilitation, biotic interaction strength,  
25 climate forcing, reproductive success, predator-prey

26

## 27 **Introduction**

28 Climate change and biotic interactions are two key drivers causing changes in species' phenology,  
29 distribution, abundance and reproductive success (Pearson and Dawson 2003, Chen et al. 2011, Stephens  
30 et al. 2016). A long-standing hypothesis (Darwin 1859) holds that climate is the main determinant of  
31 population growth and vital rates in harsh environments, whereas antagonistic species interactions such as  
32 predation emerge as the main driver of change where more benign conditions prevail (Louthan et al.  
33 2015). This hypothesis has received empirical support in explaining spatial variation in vital rates. Thus,  
34 populations residing on the harsh, cold part of the species range, at high latitudes or elevations, appear to  
35 be more directly controlled by climatic conditions (e.g. cold-limited adult survival or reproductive  
36 success), whereas abundance changes on the warm side of the range are more often driven by changes in  
37 biotic interactions (Pearce-Higgins and Green 2014). Predator-prey interactions are especially interesting  
38 in this regard: prey tend to encounter higher predation risk at low latitudes and elevations (McKinnon et  
39 al. 2010, Roslin et al. 2017).

40  
41 The strong focus on changes in the drivers of vital rates and population performance along latitudinal and  
42 elevational gradients has diverted attention from possible changes in these drivers occurring within single  
43 populations. In tandem with climate change, anthropogenic alteration of predator-prey relationships is  
44 increasingly affecting food web dynamics worldwide (Doherty et al. 2016). This human interference  
45 plays a crucial role in not only the spread of invasive predators; it may also involve actively facilitating  
46 unprecedented levels of population recovery of native apex predators following human persecution and/or  
47 use of contaminants (Hipfner et al 2012). An important unresolved question pertains to the relative roles  
48 of climate and biotic interactions as drivers of population performance, when these conflict with each  
49 other. Of particular interest is the situation in which climatically benign environments face increasing  
50 predation threats due to direct and indirect human-induced interference. Will such changes modify the  
51 relative strength of these drivers, result in one of them becoming partly or entirely overridden by the  
52 other, and what may be the repercussions on population productivity?

53 An excellent framework for addressing these questions is the population of common eider ducks  
54 (*Somateria mollissima*; hereafter, eiders) breeding in the Baltic Sea. On the one hand, the focal study site  
55 has experienced especially rapid changes in climate. For instance, mean winter temperatures have  
56 increased over 3 degrees since the 1980s (Lehikoinen et al. 2013). Eiders are likely to benefit from a  
57 warming climate; mild winter conditions are associated with advanced spring migration and breeding  
58 phenology, more synchronous breeding, good body condition of breeding females, large clutch sizes and  
59 higher fledging success (Lehikoinen et al. 2006). On the other hand, the population is exposed to rapidly  
60 increasing predation pressure by the main native predator, the white-tailed eagle (*Haliaeetus albicilla*),  
61 helped from the brink of extinction through diligent conservation efforts, and by invasive mammalian  
62 predators (Öst et al. 2018). Preliminary evidence suggests that at least eagles may also benefit from  
63 warming winters and springs (Penttinen 2017). As the brackish Baltic Sea is species poor, the effects of  
64 predation on prey abundance and productivity may become further exacerbated (Parker et al. 1999), e.g.,  
65 due to low availability of alternative prey sources to predators (e.g., Nordberg and Schwarzkopf 2019).  
66  
67 Here, we revisit the breeding population of eiders from SW Finland, the Baltic Sea, fifteen years on from  
68 the earlier study on the role of climatic variables in influencing breeding parameters (Lehikoinen et al.  
69 2006). Given the recent precipitous population decline (Ekroos et al. 2012), we predicted (i) a weakening  
70 of the previously documented positive responses to a warming climate, i.e., a weaker connection between  
71 climate and phenology and/or body condition, (ii) intensified predation on all life-stages of eiders, and  
72 (iii) a corresponding strengthening of top-down control by predators with negative repercussions on  
73 individual fitness and population productivity. We also examined the drivers of intra-annual variability in  
74 breeding phenology and body condition, allowing us to evaluate the relative importance of climate  
75 forcing and predation-driven control on breeding decisions and performance. Current literature is divided  
76 as to whether reproductive synchrony is, first and foremost, an antipredator strategy (Ims 1990, Abbey-  
77 Lee and Dingemanse 2019, Descamps 2019), or linked to climate forcing (Lehikoinen et al. 2006,  
78 Halupka and Halupka 2017, Hällfors et al. 2020, Ejsmond et al. 2021). The severity of predation or

79 climate effects is also intricately linked to the distribution of individual body conditions within the  
80 population. In long-lived species exhibiting intermittent breeding, the opportunities to commence  
81 breeding may be related to both climatic changes (Love et al. 2010), and/or to predation risk (Öst et al.  
82 2018). The reigning conditions may thereby dictate intra-annual variation in breeder body condition when  
83 e.g. harsh conditions thwart the breeding of low-quality individuals and only allow high-quality  
84 individuals to breed, hence reducing intra-annual variation in body condition. Shedding light on how this  
85 particular population of eiders is able to cope with the large-scale changes in its environment is  
86 particularly important due to its current high conservation concern (Ekroos et al. 2012, BirdLife  
87 International 2015, Lehikoinen et al. 2019).

## 89 **Materials and methods**

### 90 *Study area*

91 The main study area of ca 100 km<sup>2</sup> is located close to Tvärminne, southwestern Finland (59°50'N,  
92 23°15'E), in the hemiboreal zone (Lehikoinen et al. 2006). The breeding area is situated on the southern  
93 portion of the species' European distribution (Keller et al. 2020). The 35 study islands represent both  
94 open islets and forested islands. We also utilized data on eider migration and white-tailed eagle  
95 (*Haliaeetus albicilla*) abundance from the Hanko Bird Observatory situated 20 km west of Tvärminne  
96 (59°49'N, 22°54'E). The white-tailed eagle is the most important predator of adult eiders in our study area  
97 (Öst et al. 2018). The 31-year data set covers 1990-2020. However, data on eider breeding parameters  
98 were unavailable from Tvärminne in 1992, a final brood count (see below) was not conducted in 1993,  
99 and migration data from the Hanko Bird Observatory was lacking from 1990.

### 101 *Climate indices*

102 Following previous work (Lehikoinen et al. 2006), we used two climate indices at a geographic scale  
103 appropriate for capturing the annual cycle of this short-distance migratory population: the extended  
104 annual PC-based winter NAO (December–March) as a large-scale index of winter severity in the northern

105 Europe (Hurrell 1995), and the maximum ice extent of the Baltic Sea (Seinä and Palosuo 1996). The  
106 latter index more conveniently lends itself to statistical analysis than dates of ice break-up at the breeding  
107 grounds, due to an increasing incidence of ice-free winters at Tvärminne.

#### 109 *Eider migration phenology*

110 Hanko Bird Observatory, located at the entrance of the Gulf of Finland, acts as a major migration corridor  
111 for eiders returning from Danish waters to their breeding grounds in the Gulf. Eiders leave their wintering  
112 areas en masse resulting in relatively synchronous arrival across the Finnish breeding areas (Lehikoinen  
113 et al. 2008), wherefore the annual migration phenology determined at the Hanko Bird Observatory is  
114 representative for the bulk of the Finnish eider population. Visual counts of spring-migrating eiders were  
115 conducted daily at the Hanko Bird Observatory by 1–6 observers using a 4-hour standardized census  
116 beginning at sunrise (Lehikoinen et al. 2008). Observation activity during the spring migration period of  
117 eiders does not show any temporal trend nor relationship with sea ice phenology (Lehikoinen et al. 2006),  
118 and since 2002 the observatory has been occupied year-around. We determined the early (first arrival date  
119 (FAD)) and the median (MID) phase of migration as the day of the year when the season's cumulative  
120 sum of migrating eiders reached 5% and 50%, respectively (Lehikoinen et al. 2006). In addition, the time  
121 lapse between FID and MID was determined (Lehikoinen et al. 2006), because the synchrony of  
122 migration may affect density-dependent processes such as predator-prey interactions (Bauer et al. 2016).

#### 124 *Eider breeding parameters*

125 In part as a consequence of synchronous spring arrival, geographic variation in mean annual breeding  
126 phenology across the Finnish breeding range is limited (Hario and Öst 2002). The incubation stage of  
127 each clutch in Tvärminne was estimated annually using egg flotation, allowing us to determine the annual  
128 median laying date ( $n = 8600$  nests; annual mean  $\pm$  SD =  $287 \pm 113$  nests, range 53–500 nests). We used  
129 annual median laying dates to reduce the effect of outliers. We also calculated the time difference  
130 between annual median laying dates at Tvärminne and the MID recorded at the Hanko Bird Observatory.



131 Annual reproductive success at Tvärminne was determined during large-scale brood counts ca 6 weeks  
132 after peak hatching, from fixed vantage points distributed evenly across the entire study area (Lehikoinen  
133 et al. 2006). The ratio of nearly fledged ducklings per adult female (sum of brood-caring and solitary  
134 adult females) was used as an annual index of duckling production.

135

136 Annual mean clutch sizes were calculated from clutches known to be completed (incubated at least 5  
137 days) and not exceeding seven eggs (total  $n = 7445$  clutches), as seven eggs is the maximum number of  
138 eggs laid by one female (Waldeck et al. 2004). Although also smaller clutches may contain parasitic eggs,  
139 this proportion is only ca 6 % in this population (Waldeck et al. 2004) and thus unlikely to bias the  
140 results. We aimed at trapping all incubating females with hand nets towards the end of the incubation  
141 period. Females were weighed to the nearest 10 g and the length of the radius-ulna was measured to the  
142 nearest 1 mm. This allowed us to obtain a size-corrected body condition index at hatching. Females in  
143 their first week of incubation were omitted to avoid including birds still in the process of laying additional  
144 eggs (Öst et al. 2008a), leaving us with a sample of 4305 females (annual mean  $\pm$  SD =  $144 \pm 55$ , range  
145 42–248). As eiders fast during incubation, it is crucial to take into account the incubation stage to  
146 compare individual differences in energy reserves rather than variation in size. To this end, we used the  
147 standardized residuals of a linear regression of log-transformed estimated weight at hatching on log-  
148 transformed radius-ulna length (Öst et al. 2008a). Weight at hatching was estimated as the weight of the  
149 female at trapping subtracted by the estimated weight loss during the remaining course of incubation.  
150 This estimate of mean weight loss rate during incubation was derived as the slope of the linear regression  
151 of log-transformed body mass on log-transformed incubation time and projected hatching date (Öst and  
152 Steele 2010).

153

#### 154 *Quantifying predation*

155 We calculated three predation risk indices: annual nest predation risk, annual adult predation risk and  
156 white-tailed eagle abundance. Although these indices are correlated ( $r_{\text{nest-adult index}} = 0.85$ ;  $r_{\text{nest-eagle index}} =$

157 0.77;  $r_{\text{adult-eagle index}} = 0.70$ ; all  $p$ -values  $< 0.001$ ,  $n = 30$ ), they are likely to capture partially  
158 complementary aspects of prevailing risk. Thus, exclusive egg predators (corvids, gulls) do not pose a  
159 threat to adult female eiders, wherefore the optimal antipredator responses to adult and egg predators may  
160 differ. Likewise, indices based on actual instances of predation (adult predation risk index), as opposed to  
161 those based on the mere presence of predators (eagle index), may not convey identical information to  
162 prey, or such cues may differ in perceptibility. Annual nest predation risk ('island predation risk') was  
163 estimated as the number of depredated nests at first encounter divided by the total number of nesting  
164 attempts (including depredated nests at first encounter and nests in which the ducklings had already  
165 hatched) on each island (Jaatinen et al. 2014). To obtain a spatially representative annual index giving  
166 equal weight to each breeding island, we calculated the average of all island-specific proportions of  
167 depredated nests in each respective year. Only depredated nests encountered during our first visit to each  
168 part of the islands were considered, because additional visits may induce nest depredation and  
169 abandonment, and because nests are revisited only on the core study islands. The annual nest censuses  
170 were done at a phenologically equivalent time: the time interval between the annual median nest census  
171 date at Tvärminne and FID at the Hanko Bird Observatory (mean  $\pm$  SD =  $54.8 \pm 6.2$  days) showed no  
172 time trend ( $r = 0.25$ ,  $n = 29$ ,  $p = 0.18$ ). Likewise, the total length of the annual nest census period (mean  $\pm$   
173 SD =  $18.7 \pm 7.2$  days) showed no temporal trend ( $r = 0.25$ ,  $n = 30$ ,  $p = 0.18$ ). The second predation index  
174 quantified annual adult predation risk; the total number of incubating females killed at their nests during  
175 nest censuses at Tvärminne divided by the total number of nesting attempts in each year (Jaatinen et al.  
176 2011, Öst et al. 2018). In total, the remains of 677 predator-killed incubating female eiders were  
177 encountered. This number included both cases with an identified and unidentified predator; the two most  
178 important predators were the white-tailed eagle (64.8 % of identified kills,  $n = 228$ ) and the American  
179 mink (*Neovison vison*) (23.0% of identified kills,  $n = 81$ ). The third index characterized annual abundance  
180 of white-tailed eagles in the study area. This index was calculated by dividing the total sum of daily  
181 numbers of resident white-tailed eagles observed at the Hanko Bird Observatory during 1 April–15 June

182 in each year (i.e., the breeding season of eiders) with the number of annual observation days during the  
183 same period (Jaatinen et al. 2011).

#### 185 *Statistical methods*

186 All statistical analyses were performed in R (version 3.5.3, R Core Team 2019). We first assessed  
187 temporal trends in all variables based on their linear trend (slope of linear change with time), also testing  
188 for period-specific trends using analysis of covariance (lm function) (Table 1). Accordingly, we divided  
189 that data in two periods of similar length (1990–2005 and 2006–2020, respectively). This division  
190 represents a natural dividing line because the previous analysis of climate effects on eider breeding  
191 performance (Lehikoinen et al. 2006) was exclusively conducted during the first period. Our continuous  
192 long-term observations from this population led us to expect poor agreement between previous  
193 predictions and current reproductive performance, for unknown reasons. Admittedly, this division is  
194 unlikely to capture the exact tipping point of any potential regime shift. However, our purpose here was  
195 rather to retrospectively analyse how well the predictions regarding climate impacts on reproductive  
196 performance, based on the data then at hand, hold true under the current conditions. With respect to  
197 describing the variability in breeding phenology and body condition, interquartile range was preferred  
198 over standard deviation to limit the influence of outliers. For example, the right-hand tail of the annual  
199 breeding phenology distribution (i.e., the late breeders) depends on the length of our annual monitoring  
200 scheme.

201  
202 In the main statistical analysis, we explored how climate variables, migration metrics and predation  
203 indices (explanatory variables) affected breeding parameters of female eiders (response variables) using  
204 analysis of covariance. Migration metrics were regarded as explanatory rather than response variables,  
205 because spring migration phenology is likely affected by local conditions at the Danish wintering  
206 grounds, the predation risks of which remain undocumented. Furthermore, as our main focus is on time  
207 and period-specific trends in breeding parameters, year and two-way interactions between period and the

208 explanatory variables (climate, migration, predation and year) were included as candidate explanatory  
209 variables. Inclusion of year in the model selection process is also important to avoid bias in our parameter  
210 estimates due to time trends and to account for any time trends not fully captured by the other variables.  
211 The large number of potential explanatory terms (10 main effects and a pre-selected set of interactions)  
212 compared to the sample size necessitated pre-screening of candidate explanatory variables. This was  
213 followed by model selection to identify the most parsimonious model explaining the variation in focal  
214 breeding parameters. Thus, to facilitate effective model selection, candidate explanatory terms proceeding  
215 to the final model selection stage had either a significant (1) univariate association with the focal response  
216 variable or (2) interaction with time period (Supporting information). We excluded median spring arrival  
217 (MID) as a candidate explanatory variable of the interval between median arrival and median onset of  
218 breeding (laying-MID), as this explanatory variable is a constituent part of the response variable.

219  
220 We used an information-theoretic approach to model selection. For each response variable, we used the  
221 'dredge' function from the MuMIn package (Barton 2019) to create model sets from the respective global  
222 models (Supporting information). We used Akaike Information Criterion corrected for small sample size  
223 (AICc) for model comparisons because our sample size to model parameter ratio was under 40 (Burnham  
224 and Anderson 2002), and we present  $\Delta\text{AIC}$  ( $\text{AIC}_i - \text{AIC}_{\text{best model}}$ ) and AIC weights (weight of evidence for  
225 model) for highly supported models with  $\Delta\text{AIC} \leq 2$  compared to the top model. All models with  $\Delta\text{AIC} \leq$   
226 2 were considered equally fit (Burnham and Anderson 2002). When this occurred, we retained the top  
227 models with the fewest number of parameters, and among these, the model with the lowest AICc value  
228 was chosen as the final model (Table 2). This approach was adopted given the potential leniency of the  
229 AIC based approach in retaining model terms (Aho et al. 2014), and to minimize the risk of overfitting.  
230 One screening step to this end included examination of 'pretender' variables (Anderson 2008), i.e.,  
231 related candidate top models differing in their number of parameters but having similar log-likelihoods.  
232 One exception to the above model selection process was the analysis of annual mean body condition,  
233 scaled to have a mean of zero for the entire (pooled) sample of females. The null model containing an

234 overall mean only was therefore the a priori expected best-performing model, and so we focused here on  
235 identifying the best-performing non-null model. The final models were then subjected to diagnostic tests  
236 for potential multicollinearity and influential outliers. All final models had variance inflation factors  
237 (VIFs) below 3, suggesting no multicollinearity (Zuur et al. 2010). Likewise, we found no evidence of  
238 influential outliers in any final model (all Cook's distances  $< 1$ ; all standardized residuals  $< 3$ ).

239

## 240 **Results**

### 241 *Temporal and period-specific trends in variables*

242 Seven out of 15 variables showed a significant time trend (Table 1). In terms of climatic variables, there  
243 were no overall differences in winter NAO or Baltic Sea maximum ice cover between the study periods  
244 (two sample t-tests:  $t_{29} = 0.63$ ,  $p = 0.53$  and  $t_{29} = -0.11$ ,  $p = 0.92$ , respectively). However, both climate  
245 indices exhibited mutually consistent period-specific trends: NAO decreased over time in period 1 but  
246 increased in period 2, and, conversely, the Baltic Sea maximum ice cover increased over time in period 1  
247 and then decreased in period 2. Furthermore, the winter NAO-index (mean  $\pm$  SD =  $0.46 \pm 1.12$ ) was  
248 significantly above zero during the entire study (one-sample t-test:  $t_{30} = 2.27$ ,  $p = 0.03$ ).

249

250 All three predation indices increased over time, with the increase in eagle abundance being steeper during  
251 period 2 (Table 1). Among the eider breeding parameters, variability (i.e., IQR) in female body condition  
252 decreased over time, median laying occurred later and breeding synchrony decreased over time. The  
253 interval between median arrival and breeding and the annual spread in female body condition increased  
254 over time in the first period, while it decreased over time in period 2 (Table 1). The time between median  
255 arrival and median onset of breeding increased over time during latter period, while being relatively  
256 stable during the first period (Table 1). Finally, there were significant period-specific time trends in  
257 female mean body condition and production of nearly fledged young (see the respective top models  
258 below).

259

### *Determinants of breeding parameters*

The best-performing model explaining the variation in annual mean body condition was unsurprisingly the null model (see ‘Statistical methods’ section and Table 2). The most parsimonious model including explanatory terms included a period-specific year trend (Table 2). Female annual mean body condition decreased over time in the first period, while it increased during the second (Fig. 1a, Table 3). A single best-performing model explained the variability in annual body condition, including an interaction between adult predation risk and period, and a main effect of median timing of spring migration (Table 3). Increasing adult predation risk during the latter period was associated with less spread in body condition, whereas the annual spread in body condition showed, if anything, a positive relationship with adult predation risk in the first period characterized by very low predation risk (Fig. 1b). Furthermore, the annual variability in female body condition was larger in years with a delayed spring migration phenology (Fig. 1c).

The abundance of eagles and the first arrival date (FAD) best explained the annual median laying date (Table 3). A later breeding phenology was associated with both increasing abundance of eagles (Fig. 2a) and delayed spring arrival (Fig. 2b). A model containing only island predation risk was the top model explaining breeding synchrony (Table 3). Higher island nest predation risk was associated with less synchronous breeding (Fig. 2c). The most parsimonious and parameter-poor model explaining the interval between spring arrival and timing of breeding was the eagle index (Table 3). Higher eagle abundance was linked to a longer time between spring arrival and onset of breeding (Fig. 2d).

FAD most parsimoniously explained annual mean clutch size (Table 3). Clutches were larger in years with an advanced spring migration phenology (Fig. 3). A single top-ranked model best explained productivity, including interactive effects between period and Baltic Sea maximum ice cover and year, respectively, as well as a main effect of adult predation risk (Table 3). Increasing ice cover was associated with lower offspring production during the first period, while this relationship disappeared in the latter

286 period (Fig. 4a). Offspring production also increased over time during the first period, while productivity  
287 was progressively declining in the latter period (Fig. 4b). Increasing adult predation risk was also  
288 associated with reduced productivity (Fig. 4c).

## 290 Discussion

291 We find that the impact of climate signals on reproductive parameters of eiders has been reduced and that  
292 this change may be associated with a predation risk regime shift, with profound repercussions on  
293 reproductive performance (Tables 2-3). Our findings demonstrate that a shift from climate- to biotic  
294 interaction-driven control of vital rates can occur at a single study site in the absence of latitudinal  
295 differences. We believe that these processes also affect female survival. Thus, a recent multi-colony study  
296 from the Baltic/Wadden Sea population (Tjørnløv et al. 2020) showed no universal effects of winter  
297 climate (NAO index, winter water temperatures in Denmark) on survival of adult female eiders, despite a  
298 shared wintering ground in Danish waters. Consequently, factors operating at the level of individual  
299 breeding colonies, such as predation risk during nesting, explain the bulk of the variation in adult female  
300 survival (Tjørnløv et al. 2020) and also local population dynamics (Jónsson et al. 2013). This re-analysis  
301 paints a dramatically different picture of the drivers of breeding parameters of female eiders, as we find a  
302 decoupling of the previously identified positive relationship between mild winters and subsequent  
303 breeding success (Lehikoinen et al. 2006). Based on our results we conclude that the ongoing predation  
304 risk regime shift will suppress the reproductive potential of this population, driving population growth  
305 towards steep declines, rather than increases, in the future. This prediction agrees well with current  
306 assessments of the population trend, characterized by a precipitous decline (Ekroos et al. 2012, Tjørnløv  
307 et al. 2020), substantiating the recent assessment of increased extinction risk posed to this species in  
308 Europe (BirdLife International 2015).

309  
310 *Annual variation in body condition and clutch size*

311 Annual mean body condition and clutch size seemingly stand out as exceptions to the rule of predator  
312 control on reproductive parameters (Tables 2-3). However, the effects of predation may operate more  
313 subtly in these cases, through selective disappearance and changes in reproductive strategies, nest-site  
314 selection and the population age distribution. Female annual mean body condition has increased over the  
315 past 15 years (Fig. 1a, Öst et al. 2018), concomitant with a sharp increase in the incidence of intermittent  
316 breeding (Öst et al. 2018). We identify two plausible, non-exclusive explanations. First, only good-  
317 condition individuals may opt to breed under the current severe predation threat (Öst et al. 2018),  
318 consistent with the 'reproductive suppression hypothesis' (Wasser and Barash 1983). Second, poor-  
319 condition females may more likely experience early nest depredation prior to our monitoring (Mohring et  
320 al. 2021), because good body condition is linked to higher nest success (Lehikoinen et al. 2010). The  
321 recent increase in mean body condition may also partly reflect an aging population. This is because body  
322 condition increases slightly but significantly with age in eiders (Jaatinen and Öst 2011) as well as in other  
323 waterfowl (Clark et al. 2014), and the predation-induced decline in productivity (Fig. 4c) may  
324 increasingly affect recruitment into the breeding population. Indeed, ancillary analysis shows that the  
325 annual proportion of first-time breeders significantly declined over time, controlling for variable trapping  
326 efficiency (proportion of trapped females of all nests) in the preceding year (logistic regression on data  
327 from 1996-2020:  $b = -0.037 \pm 0.0064$  SE,  $z_{22} = -5.70$ ,  $p < 0.001$ ). Thus, the predicted probability of  
328 encountering a first-time breeder, with trapping efficiency held constant at its mean, decreased from 0.61  
329 in 1996 to 0.39 in 2020.

330  
331 Clutch size decreased with later first arrival (Fig. 3), a result qualitatively similar to that of previous work,  
332 showing that clutch sizes tended to decrease with later ice breakup (Lehikoinen et al. 2006). A legitimate  
333 question, therefore, is why the rapidly increasing predation pressure (Table 1) is not reflected in an  
334 accompanying decrease in clutch size, either because elevated perceived predation risk should reduce  
335 investment in egg production (Zanette et al. 2011), or simply because of undetected partial clutch  
336 depredation (Öst et al. 2008a). Furthermore, the time trend towards later breeding (Table 1) should



337 negatively affect clutch size (Lehikoinen et al. 2006, Öst et al. 2008a). However, there are several  
338 compensatory mechanisms that could mask such effects on clutch size. First, the recent increase in mean  
339 body condition (Fig. 1a) and the increasing proportion of older, experienced breeders (see preceding  
340 paragraph) should, all else being equal, translate into larger clutch sizes (Öst and Steele 2010, Clark et al.  
341 2014). Also the proportion of females nesting on forested islands has gradually increased over time due to  
342 selection imposed by eagle predation (Ekroos et al. 2012), which may further offset any predation-  
343 induced reductions in clutch size as clutches are larger on forested islands (Öst et al. 2008a) and in more  
344 concealed nests (Öst and Steele 2010). Furthermore, the main mesopredators preying on eider eggs,  
345 hooded crows *Corvus cornix* and large gulls *Larus* spp., have declined over the course of the study  
346 (EIONET 2020), which may further relax partial clutch depredation, and thus affect the observed clutch  
347 sizes (Öst et al. 2008a).

#### 349 *Annual variation in breeding phenology and synchrony*

350 Winter climate indices did not explain the variation in annual median laying dates (Tables 2-3), and  
351 neither the winter NAO index nor the timing of ice break significantly correlated with the timing of  
352 breeding in our earlier analysis (Lehikoinen et al. 2006). Instead, the median laying date showed the  
353 strongest association with eagle abundance (Fig. 2a) and first arrival dates (Fig. 2b). In combination, the  
354 strong temporal increase in eagle abundance and the absence of a time trend in first arrival dates caused a  
355 significant delay in the timing of breeding over time (Table 1). This result is noteworthy against the  
356 backdrop of increasing winter NAO and decreasing maximum ice cover in the latter period (Table 1),  
357 begging the question of whether eiders may show limited temperature-mediated plasticity of reproductive  
358 timing in response to climate warming, like some other seabirds (Keogan et al. 2018, Descamps et al.  
359 2019). However, we find this explanation unlikely. Thus, we analysed the supplementary data of Hällfors  
360 et al. (2020), which included the ringing dates of newly-hatched eider ducklings in Finland during 1977-  
361 2005, a period of mild predation pressure and a significantly decreasing maximum ice-covered area in the  
362 Baltic Sea ( $r = -0.42$ ,  $p = 0.02$ ). In eiders, these ringing dates equal hatching dates, because duckling leave

363 the nest within 24 h of hatching. These data revealed that eiders indeed advanced their breeding schedule  
364 both with increasing winter NAO and with decreasing maximum ice cover, regardless of whether annual  
365 mean or median hatch dates were considered, and these correlations also held significant after controlling  
366 for year in partial correlation analyses (all absolute  $r > 0.5$ , all  $p < 0.01$ ). We conclude that the breeding  
367 phenology of eiders is not fundamentally insensitive to climatic cues, consistent with recent work  
368 suggesting that early-breeding duck species (such as eiders) may actually show higher plasticity to spring  
369 temperatures than late-breeding ones (Messmer et al. 2021). Nevertheless, the marked increase in  
370 predation pressure imposed by eagles has halted, and eventually reversed, the expected advance in  
371 breeding phenology associated with mild winters during the study period.

372  
373 Both laying asynchrony and the interval between arrival and laying has increased over time (Table 1), due  
374 to increasing island nest predation risk (Fig. 2b) and eagle abundance (Fig. 2c), respectively. These  
375 results not only contradict a previous report indicating that breeding synchrony increased with an  
376 increasing winter NAO-index (Lehikoinen et al. 2006), but also challenge prevailing views of climate  
377 change impacts on breeding synchrony. Thus, a contracted, rather than expanded, breeding period is the  
378 expected response to climate warming in early-breeding, single-brooded short-distance migrants such as  
379 the eider, potentially reflecting a shrinking temporal window of resource availability (Halupka and  
380 Halupka 2017, Hällfors et al. 2020). This view draws primarily on ‘classic’ model systems involving a  
381 warming-induced phenological mismatch between food requirements and resource availability (e.g.,  
382 Visser et al. 1998). In contrast, the staple food of eiders, the blue mussel *Mytilus trossulus*, is abundant  
383 and available all year round during the ice-free season (e.g., Westerbom et al. 2019). This  
384 notwithstanding, one could envision also global warming-induced breeding desynchronization,  
385 particularly in capital breeders relying on stored reserves (Ejmsmond et al. 2021). As formalized in a life-  
386 history model by Ejmsmond et al. (2021), late-arriving and/or poor-condition individuals may be unable to  
387 accumulate sufficient body reserves in time to allow prompt breeding initiation during early spring  
388 conditions, translating into increased population-level breeding asynchrony. Conversely, late annual

389 breeding phenology in capital breeders is expected to increase breeding synchrony (Ejmsmond et al. 2021).  
390 Clearly, these predictions do not match well with our findings, as median laying occurred later concurrent  
391 with decreased breeding synchrony over time. Alternatively, more low-quality individuals (e.g., those in  
392 poor body condition) may be able to accumulate the prerequisite breeding resources when benign pre-  
393 breeding conditions prevail in winter and early spring (e.g., Love et al. 2010), and such individuals  
394 typically breed later (Jaatinen and Öst 2016). However, also this scenario is unlikely, considering that  
395 progressively milder winter conditions in the latter period (Table 1) were associated with less annual  
396 variation in body condition (Fig. 1b), and because the blue mussel stocks at Tvärminne are likely to  
397 suffer, rather than benefit, from a warming climate (Jaatinen et al. 2021). Instead, the predation risk-  
398 induced selective disappearance of poor-quality individuals from the active breeding pool (see above)  
399 may be associated with both the increasing mean body condition (Fig. 1a), and its reduced variability  
400 (Fig. 1b) during the latter period of elevated predation threat.

401  
402 Our findings suggest that predator-prey interactions primarily shape the degree of reproductive  
403 synchrony. In an antipredator context, a common premise is that synchronous reproduction should be  
404 adaptive when facing specialist predators, while asynchrony should be favoured where generalists abound  
405 (Ims 1990, Descamps 2019). The main predators of adult eiders, eggs and offspring are all characterized  
406 by a broad diet, including the white-tailed eagle (Ekblad et al. 2016). However, recent experimental work  
407 indicates that the adaptive value of breeding synchrony may be independent of predator functional  
408 responses (Abbey-Lee and Dingemans 2019). Thus, asynchronous breeding may represent a general  
409 adaptive response of prey to elevated predation risk regardless of predator functional responses,  
410 inherently generated by personality-dependent antipredator responses (Abbey-Lee and Dingemans  
411 2019). Indeed, female eiders are characterized by strong and consistent individual differences in  
412 antipredator boldness, indexed by human-induced flight initiation distance (Seltmann et al. 2012, Öst et  
413 al. 2015). We now turn to the proximate mechanisms linking increased predation risk to increased  
414 breeding asynchrony. A plausible mechanism is re-nesting following early nest depredation that may

415 prolong the breeding season. For example, half of the eider females subject to experimental removal of  
416 their first-laid eggs prior to clutch completion initiated a second clutch in Norway, on average 11 days  
417 after being experimentally depredated (Hanssen and Erikstad 2013). On top of this mechanism, there may  
418 be carry-over effects of past nest depredation events. Predator-induced breeding failure increases  
419 breeding dispersal in the subsequent season (Dow and Fredga 1983; Switzer 1993, Öst et al. 2011).  
420 Breeding dispersal, in turn, delays breeding in eiders (Öst et al. 2011, Jaatinen and Öst 2016), likely  
421 because dispersal to unfamiliar and potentially dangerous nesting areas requires more careful nest  
422 prospecting (Jaatinen and Öst 2016).

#### 424 *Annual variation in productivity*

425 Perhaps our most intriguing finding was that the negative effect of increasing Baltic Sea maximum ice  
426 cover on subsequent duckling production disappeared between the study periods (Fig. 4a). The increase in  
427 productivity following mild ice winters observed during the first period corroborates previous findings  
428 (Lehikoinen et al. 2006) and is the expected response. Thus, female eiders produce larger clutches with  
429 earlier ice break-up (Lehikoinen et al. 2006), which also survive better after hatching (Öst et al. 2008b).  
430 Furthermore, disease prevalence is typically positively related to population density (e.g., Morand and  
431 Poulin 1988). It is noteworthy that a reovirus-associated duckling mass mortality in 1996 (Hollmén et al.  
432 2002) – when the study population reached its maximum density – was preceded by the harshest ice  
433 winter during the first study period. In contrast, mild ice conditions were unrelated to subsequent  
434 offspring production during the second period. This intriguing finding clearly warrants further  
435 investigation. We can speculate that with the advance of increasingly ice-free winters, we may have  
436 reached the point where any additional positive effects of ice-free conditions become marginal or even  
437 non-existent. This finding could also arise as a ‘by-product’ of variable predation risk imposed by white-  
438 tailed eagles, but also American minks, increasingly affecting not only the survival of adult females (Öst  
439 et al. 2018), but also that of ducklings. Preliminary evidence suggests that the reproductive success of  
440 white-tailed eagles may be negatively affected by harsh conditions in winter and early spring (Penttinen

441 2017). Winter severity may also affect the availability of alternative prey available to these generalist  
442 predators, with potential spin-off effects on predation pressure on eiders.

443

#### 444 *Conclusions*

445 To conclude, our findings suggest a three-decade-long shift from mainly climate-driven to predation-  
446 driven control of reproductive parameters and productivity in eiders, an emblematic Holarctic species.

447 This study demonstrates that the mode of population regulation may change within a single study site due  
448 to human-induced alteration of predation risk. Consequently, non-linear responses to climate change  
449 should be considered when analyzing long-term data on vital rates, particularly when anthropogenic  
450 interventions in predator-prey relationships are present. The predation risk regime shift appears to prevent  
451 this now endangered population from reaping the potential benefits of a warming climate identified  
452 earlier (Lehikoinen et al. 2006). We therefore urge well-directed conservation efforts aimed at mitigating  
453 predation impacts on ground-nesting waterbirds struggling under the current intense predation risk  
454 regime.

455

#### 456 **Speculations**

457 It is well known and documented that climate change responses may depend on relative latitudinal  
458 position. Thus, cold-adapted species are typically facilitated by warming at the colder range edges, but  
459 decrease at the warmer edge through detrimental biotic interactions, particularly through increased  
460 predation pressure. Our results are consistent with these broad-scale patterns, as the focal study  
461 population of common eider ducks is situated on the warm side of the species range, and has experienced  
462 rapid warming over the study period. Let us focus solely on the ultimate causes for these patterns and  
463 ignore the proximate mechanisms underlying the rapidly increasing predation risk the population, i.e.,  
464 human alteration of predation risk. If so, our results may also be viewed as an example of a situation in  
465 which the population experiences a shift from climate- to biotic interaction-driven control of vital rates as  
466 local climatic conditions gradually change. This alternative interpretation should be tempered with utmost

467 caution, however, because the proximate mechanisms of the increase in predation risk are not primarily  
468 associated with climate as such, and it is at present unclear whether global warming has beneficial or  
469 harmful effects on the predators involved.

### 471 **Alternative viewpoints**

472 We argue for the far-reaching impact of the main native predator, the white-tailed eagle, on common  
473 eiders. This is because eagles cause high mortality of both breeding females and ducklings and they are  
474 extremely conspicuous, thus inducing fear effects, with potentially long-lasting ramifications on eider  
475 reproductive behaviours and fitness. Convincing as these arguments are, the relative role of invasive  
476 mammalian predators, American minks and raccoon dogs, is likely underestimated. Thus, an invasive  
477 predator control scheme was launched in the study population over a decade ago to curb the increasing  
478 predation pressure by invasives. Thus, in other parts of the Baltic Sea lacking invasive predator control,  
479 the total predation pressure experienced by breeding female eiders is likely to be even higher.  
480 Furthermore, the proportion of depredated female eiders attributed to particularly the raccoon dog is  
481 disproportionately low compared to their actual impact on the population. This is because raccoon dogs  
482 occur erratically and typically settle on the same island for longer periods, leading eiders to abandon their  
483 nesting island in that season, and thus few females will succumb to predation. Determining the relative  
484 importance of native and non-native predators on the common eider population requires further research  
485 conducted in multiple populations.

### 487 **Conflict of interest**

488 The authors declare no conflict of interest.

### 490 **Data availability statement**

491 Data will be available from the Dryad Digital Repository upon acceptance of publication.

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634

For Review Only

635 **Figure captions**

636 **Figure 1.** Annual mean body condition and its variability (interquartile range) of female eiders at  
637 hatching of their clutch as a function of the most-parsimonious explanatory variables. Annual mean body  
638 condition was explained by a period-specific time trend (a), and the variability in body condition by an  
639 interaction between period and adult predation risk (b), as well as the median migration day (MID) at the  
640 Hanko Bird Observatory (c). The study periods refer to years 1990-2005 and 2006-2020, respectively.

641

642 **Figure 2.** Annual median laying date, its variability (interquartile range), and the interval between median  
643 laying and median spring arrival of female eiders as a function of the most-parsimonious explanatory  
644 variables. The annual median laying date was explained by the abundance of white-tailed eagles in spring  
645 (a) and the first arrival date (FAD) (b) at the Hanko Bird Observatory. Annual variability in laying dates  
646 was explained by annual island nest predation risk (c), and the interval between laying and median spring  
647 arrival (MID) at the Hanko Bird Observatory (d) by eagle abundance.

648

649 **Figure 3.** Annual mean clutch size of female eiders as a function of the most parsimonious explanatory  
650 variables. Annual mean clutch was explained by the first arrival date (FAD) at the Hanko Bird  
651 Observatory.

652

653 **Figure 4.** Annual production of nearly fledged young per adult female eider as a function of the most-  
654 parsimonious explanatory variables. Annual productivity was explained by an interaction between period  
655 and the Baltic Sea maximum ice cover (a), a period-specific time trend (b), as well as adult predation risk  
656 (c). The study periods refer to years 1990-2005 and 2006-2020, respectively.

657

658 **Table 1.** Descriptive statistics of climate variables (winter NAO, Baltic Sea maximum ice cover ( $10^3$   
659  $\text{km}^2$ )), migration phenology variables (FAD, MID, FAD-MID (days)), predation variables (adult and  
660 island predation risk, eagle index) and breeding parameters of female eiders (mean body condition and its  
661 spread, median laying date and its spread, interval between median laying and MID (days), mean clutch  
662 size and production of nearly fledged young per adult female). Shown are also significant linear time  
663 trends in 1990-2020 (regression coefficients ( $\pm$  SE)) and period-specific time trends (i.e., significant  
664 interactions period  $\times$  year), with a short verbal description (P1: 1990-2005; P2: 2006-2020)  
665

Variable	Mean $\pm$ SD	Range	Trend	Period-specific trend
Winter NAO	0.46 $\pm$ 1.12	-2.55 to +1.91	None	Decrease in P1, increase in P2*
Ice cover	136 $\pm$ 68	37–309	None	Increase in P1, decrease in P2*
FAD	24 Apr $\pm$ 7	14 Mar–9 Apr	None	None
MID	6 Apr $\pm$ 5	28 Mar–17 Apr	None	None
FAD-MID	13 $\pm$ 5	3–23	None	None
Adult predation	0.056 $\pm$ 0.05	0.00–0.168	0.004 (0.0006)***	None
Island predation	0.22 $\pm$ 0.11	0.033–0.41	0.01 (0.001)***	None
Eagle index	3.01 $\pm$ 3.06	0.00–10.59	0.31 (0.023)***	Steeper increase in P2***
Mean condition	0.03 $\pm$ 0.35	-0.70 to +0.95	None	See Fig. 1a
Condition IQR	1.28 $\pm$ 0.15	0.98–1.54	-0.008 (0.003)**	Increase in P1, decrease in P2*
Median laying	1 May $\pm$ 5	20 Apr–11 May	0.29 (0.09)**	None
Laying IQR	7.51 $\pm$ 1.93	3.11–12.9	0.09 (0.037)*	None
Laying-MID	51 $\pm$ 6	40–62.5	0.46 (0.1)***	Increase in P2, stable in P1*
Mean clutch	4.62 $\pm$ 0.17	4.25–4.92	None	None
Productivity	0.64 $\pm$ 0.50	0.025–1.80	None	See Fig. 4b

666 Significance: \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$ .  
667

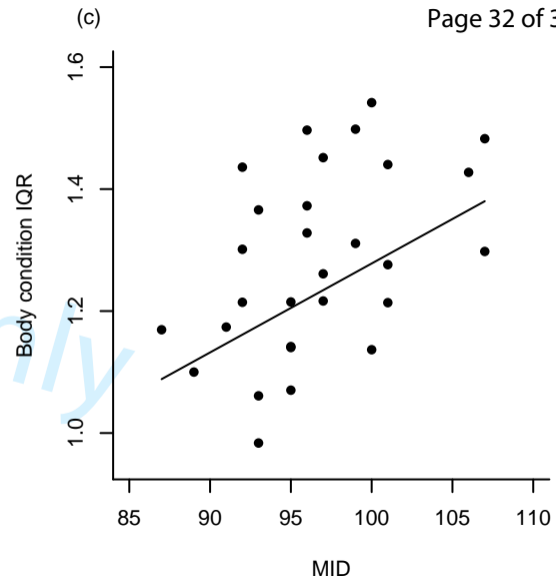
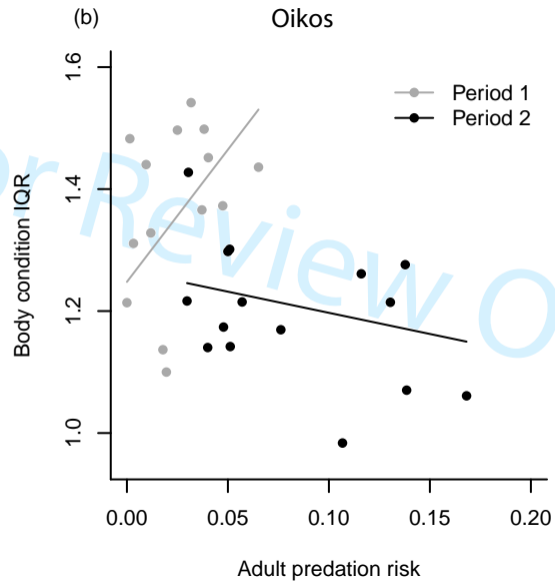
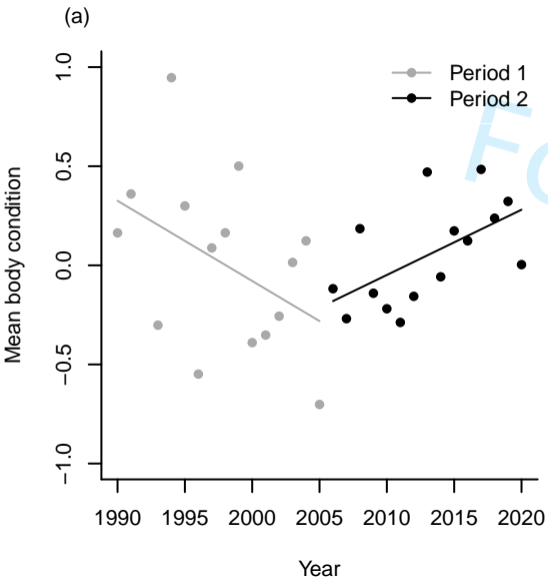
668 **Table 2.** Top models ( $\Delta AIC_c \leq 2$ ) assessing the role of climate and predation variables, their potential  
 669 interactions with period (1990-2005; 2006-2020) (Supporting information), and any period-specific time  
 670 trends (Table 1), in predicting breeding parameters of female eiders. The null model for mean body  
 671 condition was disregarded on a priori grounds (see text). Models highlighted in bold were selected as the  
 672 'best' model. K = # of parameters,  $w_i$  = model weight,  $R^2$  = coefficient of variation

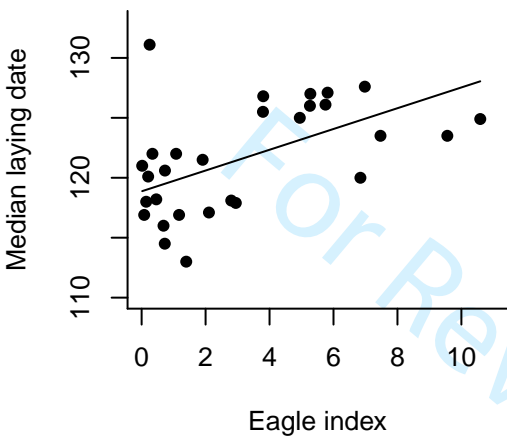
Variable	Model	K	AICc	$\Delta AIC_c$	$w_i$	$R^2$
<b>Mean condition</b>	Null	2	26.0	0	0.23	0
	<b>Year + period + year <math>\times</math> period</b>	<b>5</b>	<b>26.3</b>	<b>0.31</b>	<b>0.20</b>	<b>0.23</b>
	Period + island predation + period $\times$ island predation	5	27.4	1.42	0.16	0.20
<b>Condition IQR</b>	<b>Adult predation + period + MID + adult predation <math>\times</math> period</b>	<b>6</b>	<b>-41.2</b>	<b>0</b>	<b>0.21</b>	<b>0.63</b>
<b>Median laying</b>	Eagle index + FAD + ice cover	5	152.3	0	0.12	0.63
	<b>Eagle index + FAD</b>	<b>4</b>	<b>153.7</b>	<b>1.42</b>	<b>0.06</b>	<b>0.58</b>
<b>Laying IQR</b>	<b>Island predation</b>	<b>3</b>	<b>120.8</b>	<b>0</b>	<b>0.35</b>	<b>0.27</b>
	Adult predation	3	121.3	0.5	0.27	0.26
<b>Laying-MID</b>	Eagle index + adult predation	4	174.7	0	0.10	0.50
	<b>Eagle index</b>	<b>3</b>	<b>174.7</b>	<b>0.02</b>	<b>0.10</b>	<b>0.45</b>
	Year	3	175.7	1.04	0.06	0.43
	Eagle index + island predation	4	175.9	1.23	0.05	0.48
	Year + period + year $\times$ period	5	176.1	1.43	0.05	0.52
<b>Mean clutch</b>	<b>FAD</b>	<b>3</b>	<b>-24.6</b>	<b>0</b>	<b>0.35</b>	<b>0.32</b>
	FAD + FAD-MID	4	-23.0	1.55	0.16	0.34
	FAD + ice cover	4	-22.8	1.74	0.15	0.34
<b>Productivity</b>	<b>Adult predation + ice cover + year + period + ice cover <math>\times</math> period + year <math>\times</math> period</b>	<b>8</b>	<b>27.6</b>	<b>0</b>	<b>0.68</b>	<b>0.71</b>



674 **Table 3.** Final general linear models explaining variation in breeding parameters of female eiders. Period  
 675 (1990-2005; 2006-2020) was treated as a two-level categorical variable with period 1 as the reference  
 676 category; year was entered as a continuous variable throughout the study and starting from 1990  
 677

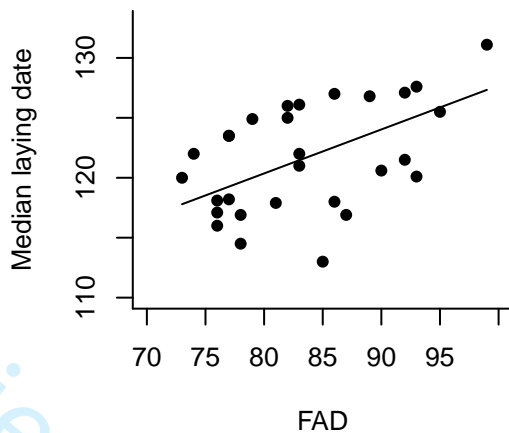
<b>Response</b>	<b>Explanatory variables</b>	<b>Estimate ± SE</b>	<b>t</b>	<b>P</b>
<b>Mean condition</b>	Year	-0.04 ± 0.019	-2.17	0.04
	Period 2	-147 ± 54.22	-2.71	0.01
	Year × period 2	0.073 ± 0.027	2.71	0.01
<b>Condition IQR</b>	Adult predation	4.34 ± 1.52	2.85	0.009
	Period 2	0.019 ± 0.071	0.26	0.79
	MID	0.015 ± 0.0042	3.50	0.002
	Adult predation × period	-5.029 ± 1.60	-3.15	0.004
<b>Median laying</b>	Eagle index	0.86 ± 0.19	4.54	< 0.001
	FAD	0.37 ± 0.08	4.42	< 0.001
<b>Laying IQR</b>	Island predation	9.38 ± 2.90	3.24	0.003
<b>Laying-MID</b>	Eagle index	1.31 ± 0.28	4.70	< 0.001
<b>Mean clutch</b>	FAD	-0.014 ± 0.004	-3.54	0.001
<b>Productivity</b>	Adult predation	-5.93 ± 2.065	-2.87	0.009
	Ice cover	-0.0058 ± 0.001	-3.91	< 0.001
	Year	0.076 ± 0.02	3.86	< 0.001
	Period 2	267.13 ± 55.63	4.80	< 0.001
	Ice cover × period 2	0.0056 ± 0.0019	3.00	0.007
	Year × period 2	-0.13 ± 0.028	-4.82	< 0.001



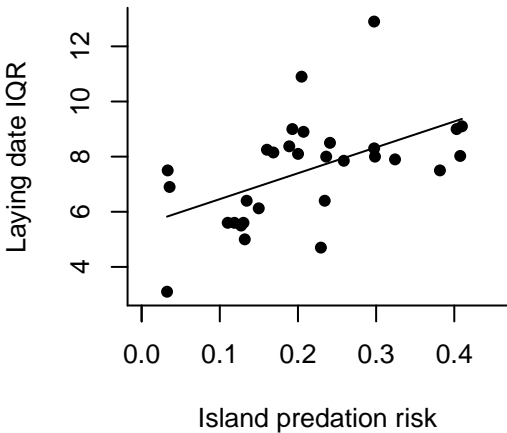


Oikos

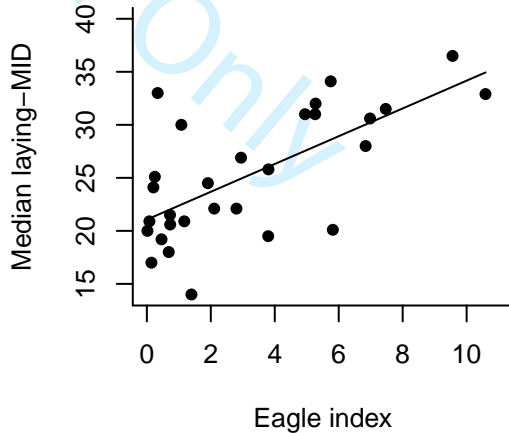
(b)

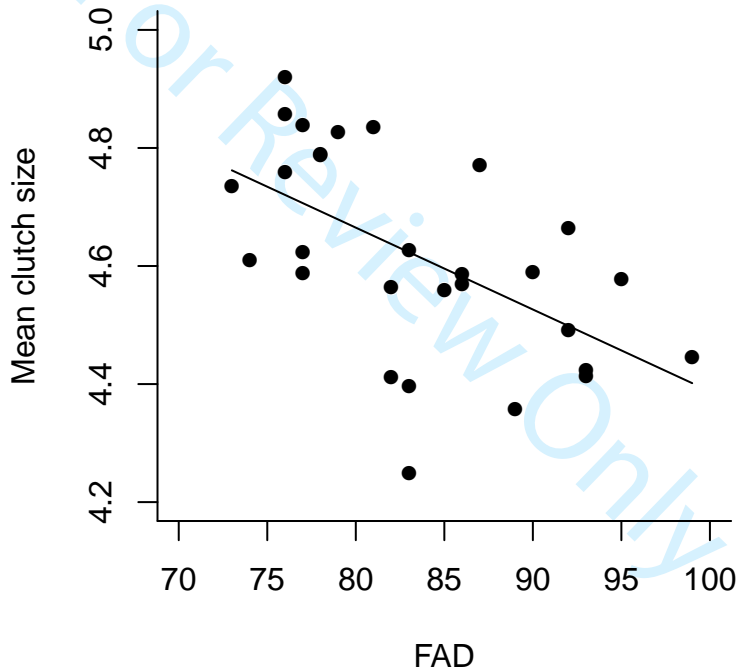


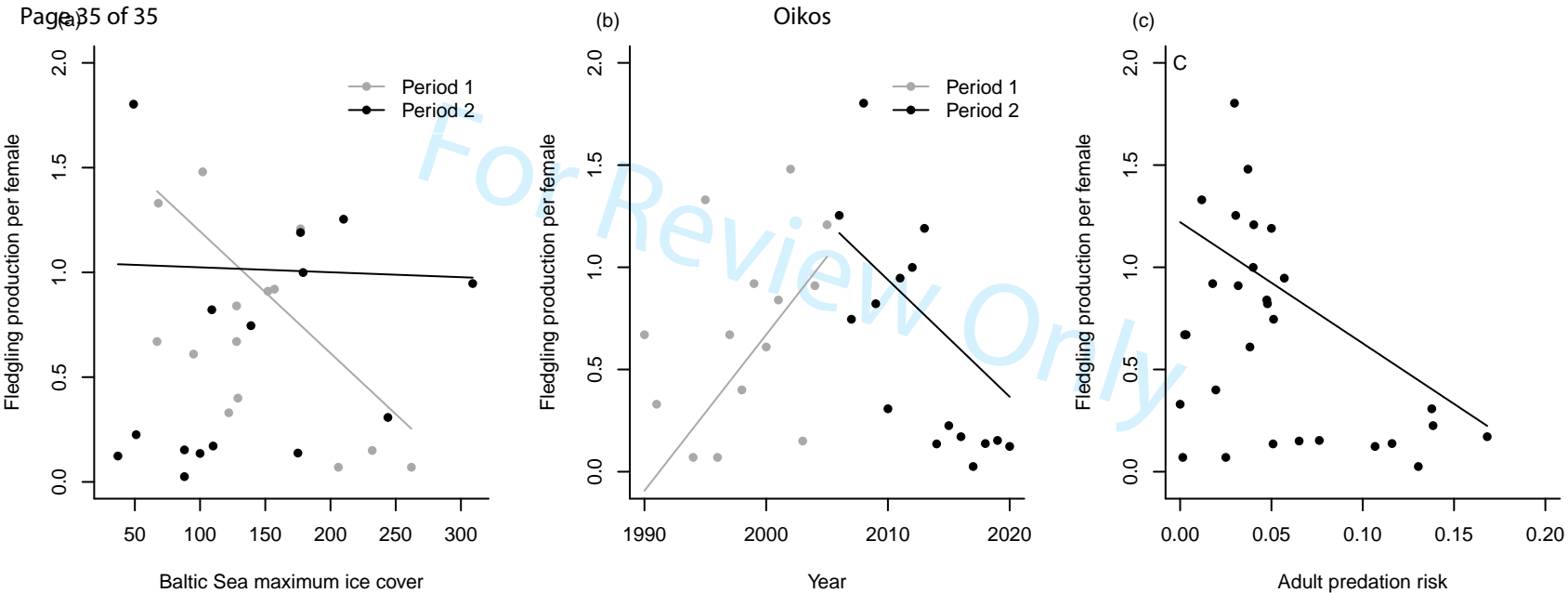
(c)



(d)







1 **Supporting information**2 **Supplementary table:**3 **Table S1:**

4 Initial set of candidate explanatory variables and interactions explaining variation in breeding parameters  
 5 of female eiders. These selected candidate explanatory terms used at the final model selection stage had  
 6 either a significant univariate association with the focal response variable ('Main effects') or significant  
 7 interaction with time period ('Interactions')

8

<b>Response</b>	<b>Main effects</b>	<b>Interactions</b>
Mean condition	Y, P, Island predation	$P \times Y$ , $P \times$ Island predation
Condition IQR	Y, P, Ice cover, Adult predation, Island predation, Eagle index, FAD, MID	$P \times Y$ , $P \times$ Adult predation
Median laying	NAO, Ice cover, Adult predation, Island predation, Eagle index, FAD, FAD-MID	$P \times$ Ice cover
Laying IQR	Y, Adult predation, Island Predation	None
Laying-MID	Y, P, Adult predation, Island predation, Eagle index, NAO	$P \times Y$ , $P \times$ NAO
Mean clutch	Ice cover, FAD, FAD-MID	None
Productivity	Y, P, Adult predation, Island predation, Ice cover	$P \times Y$ , $P \times$ Ice cover, $P \times$ Island predation

9 Abbreviations: Y = year; P = period (1990-2005 and 2006-2020, respectively); IQR = interquartile range,

10 FAD = first arrival date; MID = median arrival date, NAO = extended annual PC-based winter NAO