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

Abstract:	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 (Somateria mollissima) 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.

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19 disappeared during the past 15 years, highlighting the non-linear nature of climate change responses.

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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

Introduction

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

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

88

89   **Materials and methods**

90   *Study area*

91   The main study area of ca 100 km^2 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.

100

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.

108

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).

123

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 ± SD = 287 ± 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 ± SD = 144 ± 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 ($r_{nest-adult\ index}$ = 0.85; $r_{nest-eagle\ index}$ =

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 ± SD = 54.8 ± 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 ±

173   SD = 18.7 ± 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).

184

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 ΔAIC (AIC$_i$ – AIC$_{best\ model}$) and AIC weights (weight of evidence for

225   model) for highly supported models with ΔAIC $\leq$ 2 compared to the top model. All models with ΔAIC $\leq$

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 ± SD = 0.46 ± 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

260   *Determinants of breeding parameters*

261   The best-performing model explaining the variation in annual mean body condition was unsurprisingly

262   the null model (see 'Statistical methods' section and Table 2). The most parsimonious model including

263   explanatory terms included a period-specific year trend (Table 2). Female annual mean body condition

264   decreased over time in the first period, while it increased during the second (Fig. 1a, Table 3). A single

265   best-performing model explained the variability in annual body condition, including an interaction

266   between adult predation risk and period, and a main effect of median timing of spring migration (Table

267   3). Increasing adult predation risk during the latter period was associated with less spread in body

268   condition, whereas the annual spread in body condition showed, if anything, a positive relationship with

269   adult predation risk in the first period characterized by very low predation risk (Fig. 1b). Furthermore, the

270   annual variability in female body condition was larger in years with a delayed spring migration

271   phenology (Fig. 1c).

272

273   The abundance of eagles and the first arrival date (FAD) best explained the annual median laying date

274   (Table 3). A later breeding phenology was associated with both increasing abundance of eagles (Fig. 2a)

275   and delayed spring arrival (Fig. 2b). A model containing only island predation risk was the top model

276   explaining breeding synchrony (Table 3). Higher island nest predation risk was associated with less

277   synchronous breeding (Fig. 2c). The most parsimonious and parameter-poor model explaining the interval

278   between spring arrival and timing of breeding was the eagle index (Table 3). Higher eagle abundance was

279   linked to a longer time between spring arrival and onset of breeding (Fig. 2d).

280

281   FAD most parsimoniously explained annual mean clutch size (Table 3). Clutches were larger in years

282   with an advanced spring migration phenology (Fig. 3). A single top-ranked model best explained

283   productivity, including interactive effects between period and Baltic Sea maximum ice cover and year,

284   respectively, as well as a main effect of adult predation risk (Table 3). Increasing ice cover was associated

285   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).

289

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 ± 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).

348

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 (Ejsmond et al. 2021). As formalized in a life-

386 history model by Ejsmond 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 (Ejsmond 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 Dingemanse 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 Dingemanse

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).

423

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.

470

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.

486

487   **Conflict of interest**

488   The authors declare no conflict of interest.

489

490   **Data availability statement**

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

492

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634

Figure captions

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

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

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

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

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

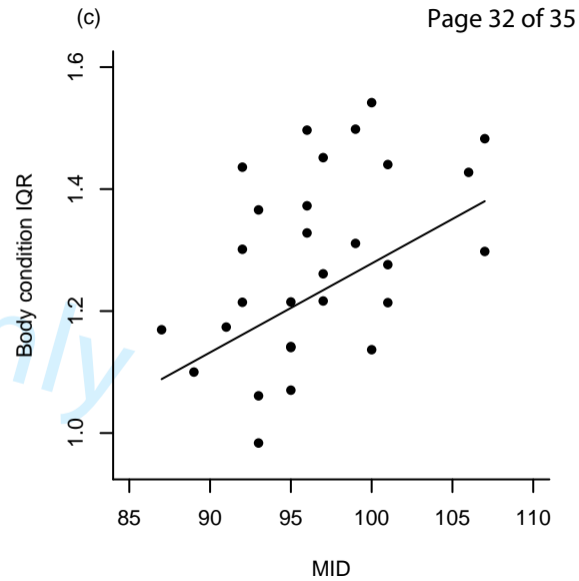| Variable	Mean ± SD	Range	Trend	Period-specific trend
Winter NAO	0.46 ± 1.12	-2.55 to +1.91	None	Decrease in P1, increase in P2*
Ice cover	136 ± 68	37–309	None	Increase in P1, decrease in P2*
FAD	24 Apr ± 7	14 Mar–9 Apr	None	None
MID	6 Apr ± 5	28 Mar–17 Apr	None	None
FAD-MID	13 ± 5	3–23	None	None
Adult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

Significance: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.
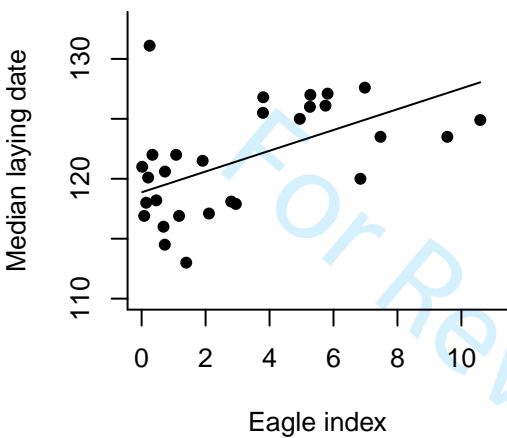
668 **Table 2.** Top models (ΔAICc ≤ 2) assessing the role of climate and predation variables, their potential
669 interactions with period (1990-2005; 2006-2020) (Supporting information), and any period-specific time
670 trends (Table 1), in predicting breeding parameters of female eiders. The null 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	ΔAICc	w_i	R^2
Mean condition	Null	2	26.0	0	0.23	0
	Year + period + year × period	**5**	**26.3**	**0.31**	**0.20**	**0.23**
	Period + island predation + period × island predation	5	27.4	1.42	0.16	0.20
Condition IQR	**Adult predation + period + MID + adult predation × period**	**6**	**-41.2**	**0**	**0.21**	**0.63**
Median laying	Eagle index + FAD + ice cover	5	152.3	0	0.12	0.63
	Eagle index + FAD	**4**	**1537**	**1.42**	**0.06**	**0.58**
Laying IQR	**Island predation**	**3**	**120.8**	**0**	**0.35**	**0.27**
	Adult predation	3	121.3	0.5	0.27	0.26
Laying-MID	Eagle index + adult predation	4	174.7	0	0.10	0.50
	Eagle index	**3**	**174.7**	**0.02**	**0.10**	**0.45**
	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 × period	5	176.1	1.43	0.05	0.52
Mean clutch	**FAD**	**3**	**-24.6**	**0**	**0.35**	**0.32**
	FAD + FAD-MID	4	-23.0	1.55	0.16	0.34
	FAD + ice cover	4	-22.8	1.74	0.15	0.34
Productivity	**Adult predation + ice cover + year + period + ice cover × period + year × period**	**8**	**27.6**	**0**	**0.68**	**0.71**

673

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
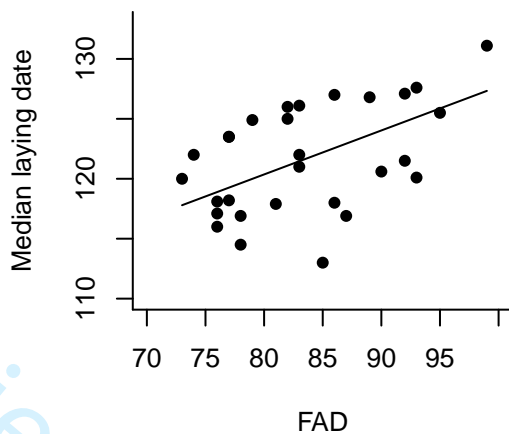677

Response	Explanatory variables	Estimate ± SE	t	*P*
Mean condition	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
Condition IQR	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
Median laying	Eagle index	0.86 ± 0.19	4.54	< 0.001
	FAD	0.37 ± 0.08	4.42	< 0.001
Laying IQR	Island predation	9.38 ± 2.90	3.24	0.003
Laying-MID	Eagle index	1.31 ± 0.28	4.70	< 0.001
Mean clutch	FAD	-0.014 ± 0.004	-3.54	0.001
Productivity	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

678

(a)

Eagle index

Median laying date

(b)

FAD

Median laying date

(c)

Island predation risk

Laying date IQR

(d)

Eagle index

Median laying–MID

(a) (b) Oikos (c)
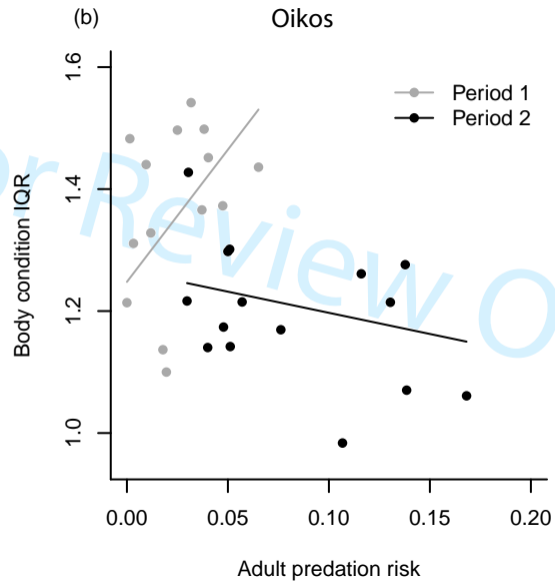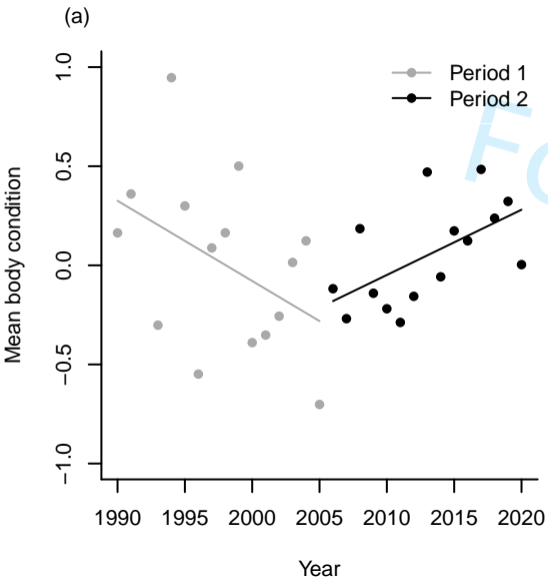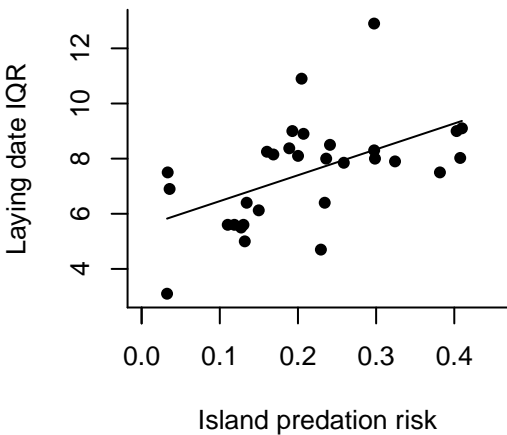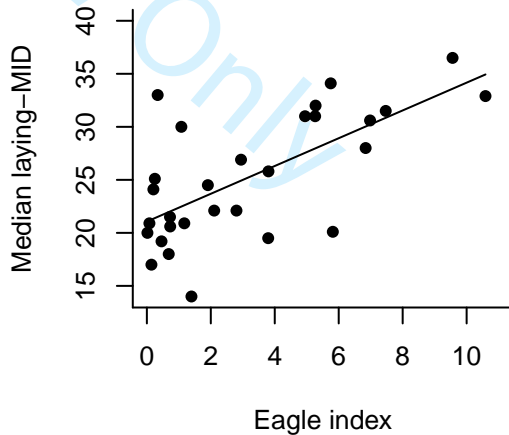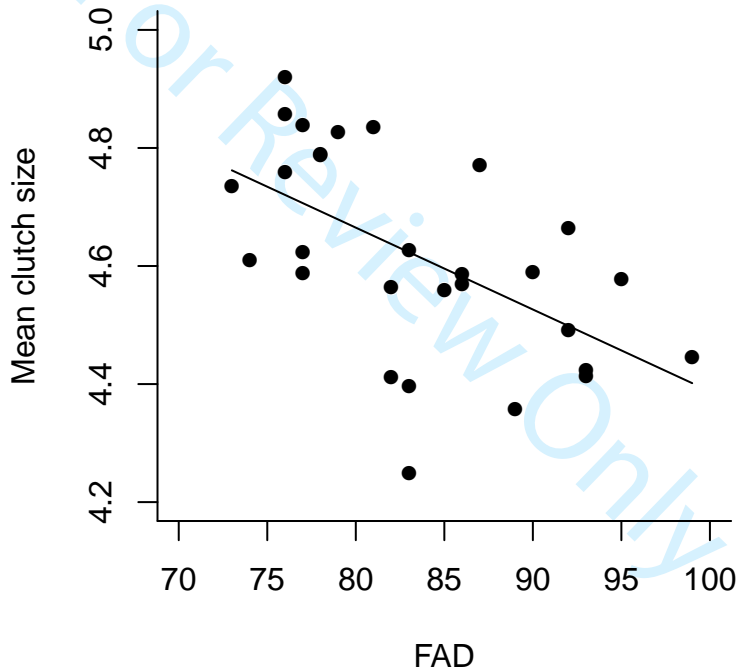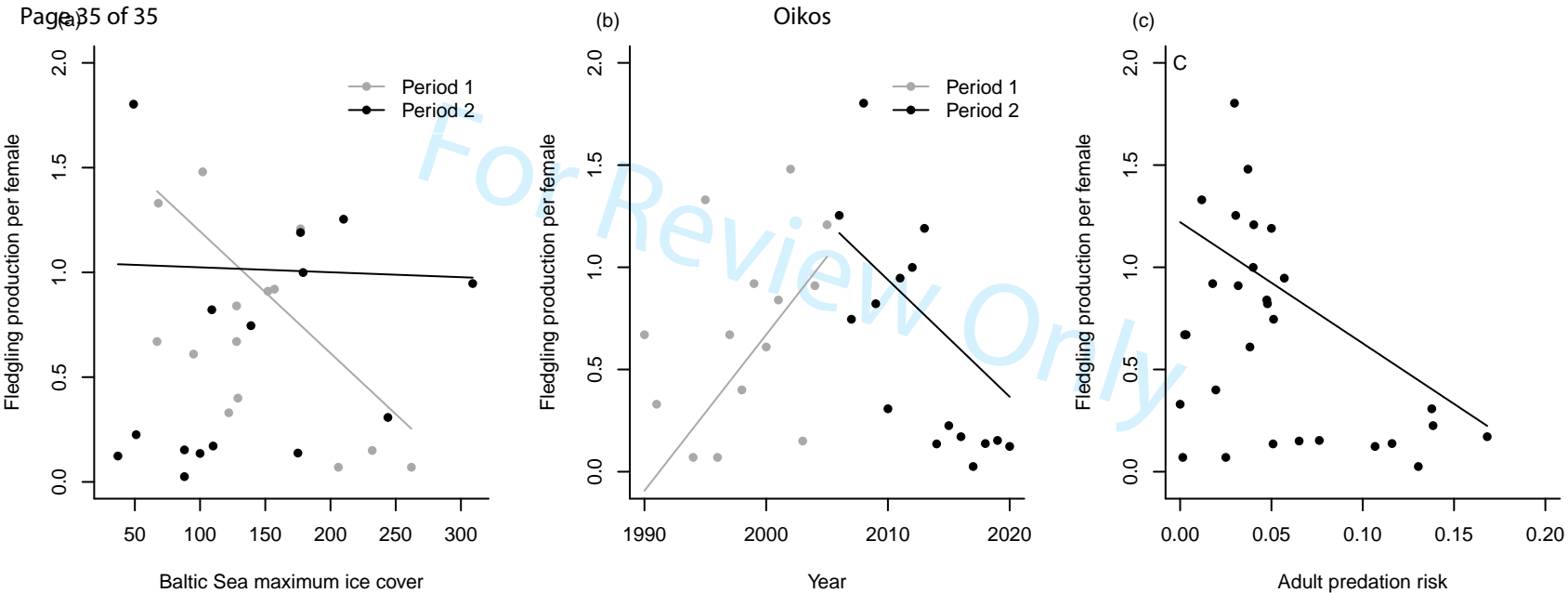
1   **Supporting information**

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

Response	Main effects	Interactions
Mean condition	Y, P, Island predation	P × Y, P × Island predation
Condition IQR	Y, P, Ice cover, Adult predation, Island predation, Eagle index, FAD, MID	P × Y, P × Adult predation
Median laying	NAO, Ice cover, Adult predation, Island predation, Eagle index, FAD, FAD-MID	P × Ice cover
Laying IQR	Y, Adult predation, Island Predation	None
Laying-MID	Y, P, Adult predation, Island predation, Eagle index, NAO	P × Y, P × NAO
Mean clutch	Ice cover, FAD, FAD-MID	None
Productivity	Y, P, Adult predation, Island predation, Ice cover	P × Y, P × Ice cover, P × 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