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*Somateria mollissima***

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1 **Consequences of past and present harvest management in a**
2 **declining flyway population of common eiders *Somateria mollissima***

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13 **Abstract**

- 14 1. Harvested species population dynamics are shaped by the relative contribution of
15 natural and harvest mortality. Natural mortality is usually not under management
16 control, so managers must continuously adjust harvest rates to prevent
17 overexploitation. Ideally, this requires regular assessment of the contribution of
18 harvest to total mortality and how this affects population dynamics.
- 19 2. To assess the impact of hunting mortality on the dynamics of the rapidly declining
20 Baltic/Wadden Sea population of common eiders *Somateria mollissima* we first
21 estimated vital rates of ten study colonies over the period 1970–2015. By means of a
22 multi-event capture-recovery model we then used the cause of death of recovered
23 individuals to estimate proportions of adult females that died due to hunting or other
24 causes. Finally, we adopted a stochastic matrix population modelling approach based
25 on simulations to investigate the effect of past and present harvest regulations on
26 changes in flyway population size and composition.
- 27 3. Results showed that even the complete ban on shooting females implemented in 2014
28 in Denmark, where most hunting takes place was not enough to stop the population
29 decline given current levels of natural female mortality. Despite continued hunting of
30 males our predictions suggest that the proportion of females will continue to decline
31 unless natural mortality of the females is reduced.
- 32 4. Although levels of natural mortality must decrease to halt the decline of this
33 population, we advocate that the current hunting ban on females is maintained while
34 further investigations of factors causing increased levels of natural mortality among
35 females are undertaken.

36 5. *Synthesis and applications.* At the flyway scale, continuous and accurate estimates of
37 vital rates and the relative contribution of harvest *versus* other mortality causes are
38 increasingly important as the population effect of adjusting harvest rates is most
39 effectively evaluated within a model-based adaptive management framework.

40

41 Keywords: CMR modelling, demography, hunting bag statistics, multi-event model,
42 population dynamics, prospective population scenarios, sex ratio

43 **Introduction**

44 Management of migratory bird populations requires detailed knowledge about their spatio-
45 temporal dynamics in relation to resource availability and the interplay with human
46 activities and interests affecting these relationships. In theory, flyway populations are
47 spatially well-defined biological units formed by groups of individuals with some degree of
48 similarity in spatio-temporal movements, linked by common population processes through
49 rates of immigration and emigration. As a result, flyways have become the primary unit of
50 focus for conservation and management of migratory birds (Boere, Galbraith & Stroud
51 2006). Effective flyway population management necessitates an understanding of
52 population delineation and knowledge of connectivity, gene flow, location of protected
53 areas and environmental and anthropogenic pressures throughout the annual cycle
54 (Madsen *et al.* 2014). Flyway management also requires good knowledge of total population
55 size and its rate of change over time. Harvest in wintering areas or along migration routes
56 can potentially affect the rate of change of flyway populations through elevated rates of
57 mortality. Within Europe, the high annual kill relative to estimated population size in some
58 populations has led to concern about the contribution of hunting to observed declines
59 (Hirschfeld & Heyd 2005). Recent studies on the effects of hunting of popular quarry species
60 (including waterbirds) on their population trends have assessed the covariance between
61 time series of population trend estimates and various measures of hunting pressure (i.e. the
62 number of animals shot relative to population size), or compared population trends of
63 hunted versus non-hunted species (Jiguet, Godet & Devictor 2012; Pöysä *et al.* 2013).
64 However, the extent to which harvest affects the population dynamics of European
65 waterbirds through elevated mortality remains poorly understood (Devineau *et al.* 2010).

66 Consequently, the need to extend current monitoring through extensive and long-term
67 marking projects of quarry species to facilitate formal estimation of survival and mortality
68 rates due to hunting has recently been highlighted (Elmberg *et al.* 2006). In addition,
69 assessments of a specific management action on the dynamics of a flyway population must
70 consider the possibility of diverging population processes occurring within the same
71 population. Ideally, understanding these processes requires inclusion of data from several
72 representative study sites to effectively scale up and model effects of management at the
73 flyway level (Grosbois *et al.* 2009).

74 The common eider *Somateria mollissima* (hereafter eider) is a large seaduck and a popular
75 quarry species along several of its circumpolar flyways, for instance in Greenland and
76 Canada and in northwest Europe (Gilliland *et al.* 2009; Christensen & Hounisen 2014). In
77 contrast, populations in the UK and Iceland are fully protected (Waltho & Coulson 2015).
78 Several hunted flyway populations of eiders show declining population trends raising the
79 question of how recreational and subsistence harvest contribute to current population
80 declines. For example, Gilliland *et al.* (2009) estimated that harvest rates on Greenlandic
81 wintering quarters were highly unsustainable and advised major harvest reductions which
82 helped the population to recover (Merkel 2010). The Baltic/Wadden Sea flyway population
83 of eiders has also suffered a major decline of an estimated 36% between 1991 and 2000
84 (Desholm *et al.* 2002). The breeding range of this population extends from the northern
85 Baltic Sea, through the coasts of Sweden and Denmark to the Wadden Sea in The
86 Netherlands, whereas the main wintering ground, which is shared among the different
87 population divisions, is located in the Wadden Sea and in inner Danish waters. Among the
88 countries sharing this population eider hunting is most extensive in Denmark. Under the

89 provisions of the EU Bird Directive, Habitat Directive and Ramsar, Bern and Bonn
90 conventions, all member states have a special responsibility to ensure that Eider hunting
91 within their jurisdiction is sustainable. In the light of recent flyway population declines,
92 there is thus an urgent need to assess the population consequences of current levels of
93 hunting. After more than a decade of declines, multiple adjustments to sex-specific hunting
94 season lengths were implemented in Denmark to counteract this negative population trend
95 (Christensen & Hounisen 2014). This resulted in a drop of 82% in the **bag** of adult females
96 and 31% and 58% in first-winter females and males, respectively. Despite this large
97 reduction of the harvest in Denmark a complete ban on hunting females was implemented
98 in 2014 to be evaluated in 2018 (Asferg *et al.* 2016). Using baseline demographic data from
99 a single Danish eider colony, Christensen and Hounisen (2014) predicted that a ban on
100 hunting female eiders would ultimately result in an annual population growth of 0.7%.
101 However, to thoroughly evaluate the effect of hunting regulations on flyway survival rates, it
102 is essential to capture potential differences in the contributions of hunting and natural
103 mortality affecting different divisions of the same flyway population.

104 In this analysis, we attempt to advance our knowledge of the Baltic/Wadden Sea eider
105 population in order to support sustainable harvest management. As a basis for our
106 investigation, we used vital rates estimated from modelling of capture-recapture-recovery
107 data from several study sites. We then used the reported cause of death associated with an
108 extensive number of recoveries to estimate proportions of birds dying due to hunting and
109 other causes. By allowing for adjustments in survival rates depending on hunting intensity,
110 we explored the flyway population consequences of past and present harvest management

111 using a demographic model. We hypothesize that the efficacy of using hunting regulations
112 to increase flyway population size largely depends on current levels of natural mortality.

113

114 **Materials & Methods**

115 *Species and study area*

116 The eider is a colonially breeding sea duck, with a circumpolar distribution comprising
117 several discrete flyway populations (Goudie, Robertson & Reed 2000). One such population
118 extends from the upper Baltic Sea to the Dutch Wadden Sea, involving both fully and
119 partially migrant subpopulations (Ekroos *et al.* 2012a). More than half of the total flyway
120 population overwinters in Danish waters (Ekroos *et al.* 2012a). Between the early 1960s and
121 mid-1990s the annual Danish bag ranged 100,000 – 200,000 individuals corresponding to
122 6.5-9.5% of the flyway population (Noer, Clausager & Asferg 1995). Over the same period of
123 time annual **bags** in Finland and Sweden ranged 25,000 – 27,000 and 3,000 – 5,000 birds,
124 respectively (Desholm *et al.* 2002).

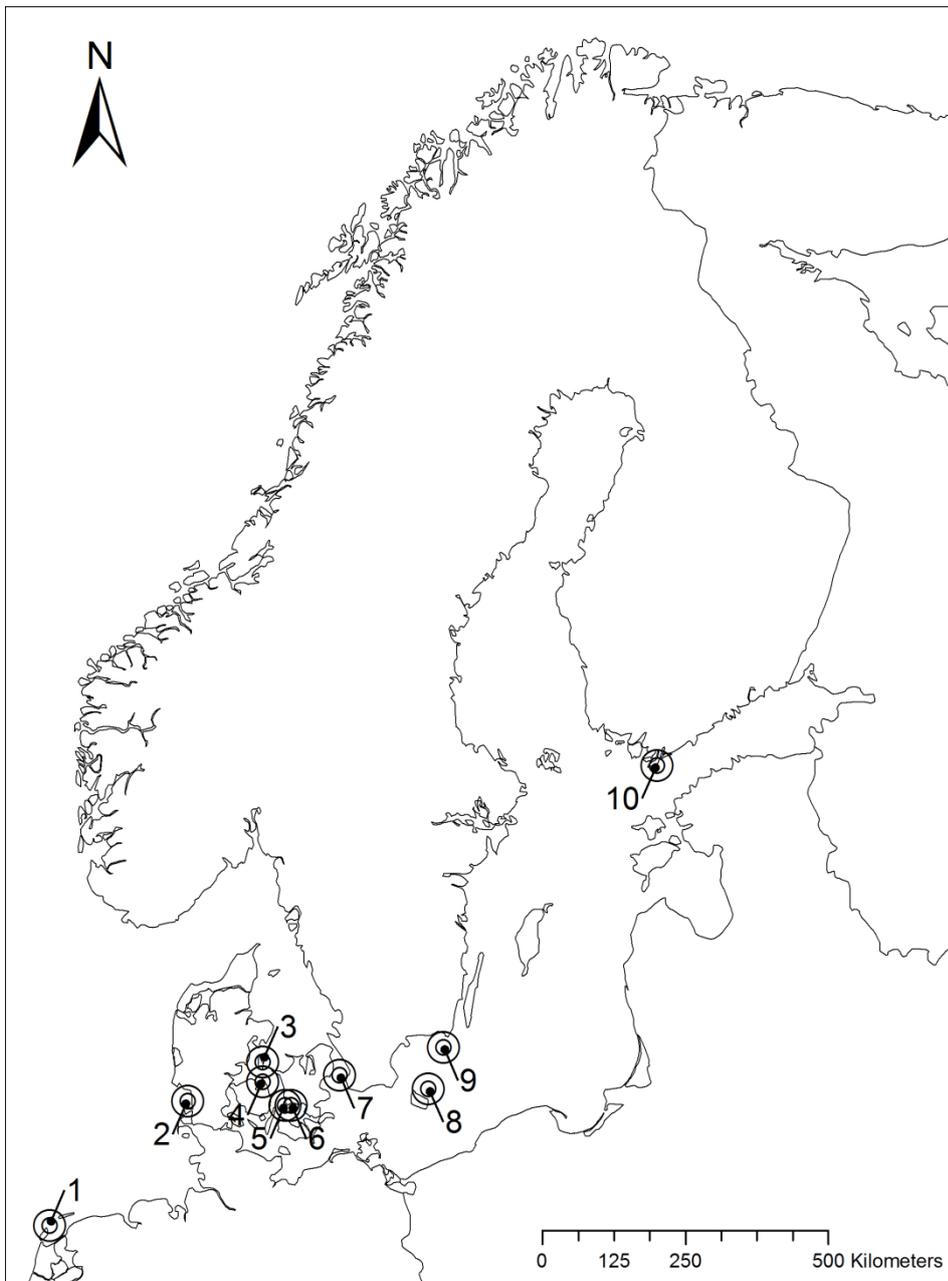
125 Recently, annual **bag** sizes have fallen to 40,000 – 60,000, 4,000 – 6,000 and 5,000 birds in
126 Denmark, Finland and Sweden, respectively (Christensen & Hounisen 2014). The reduction
127 in Denmark was partly due to falling popularity of seaduck hunting (Christensen 2005), and
128 partly to multiple sex-specific reductions in the length of the hunting season of males and
129 females by one and three months, respectively, followed by a complete female hunting ban
130 from the hunting season 2014/2015 (Christensen & Hounisen 2014).

131 *Data*

132 In total, we used encounter histories of some 18,000 adult females ringed at ten study sites
133 (Fig. 1) and 1,300 adult males ringed at Vlieland in the Dutch Wadden Sea which was the
134 only colony with data available on males (for more details of the data, see appendix).

135 *Data accessibility*

136 When/if accepted for publication data will be archived in DRYAD Digital repository.



137

138 **Fig. 1** Sites with available long-term CMR data, 1: Vlieland (NL), 2: Mandø (DK), 3: Stavns Fjord (DK),
139 4: Hindsholm (DK), 5: Helleholm, Agersø (DK), 6: Næbbet, Stignæs (DK), 7: Saltholm (DK), 8:
140 Christiansø (DK), 9: Utklippan (S), 10: Tvärminne (FIN).

141

142 *Statistical analysis*

143 *Step 1 – Flyway vital rates*

144 Grouped by site, 46 years (1970-2015) of ten colony-specific mark-recapture-recovery datasets of
145 breeding females were arranged in one encounter history file. We used the Burnham model
146 (Burnham 1993) for mixtures of live-and-dead encounter data implemented in program MARK
147 (White & Burnham 1999). The Burnham model estimates survival (S) unbiased by permanent
148 emigration, recapture probability (p), recovery probability (r) and site fidelity (F) (Burnham 1993).
149 We specified models with time-dependent and site-specific survival and recapture probabilities,
150 while using Akaike's Information Criterion adjusted for small sample sizes AIC_c to select between
151 candidate models varying with respect to recovery and site fidelity (Burnham & Anderson 2002).

152 Annual survival of pre-breeders and adult males was estimated for colonies with suitable data. For
153 pre-breeders, we structured these models with three age-classes for survival, four age-classes for
154 recapture and two age-classes for recovery and site fidelity.

155 *Step 2 – Hunting mortality of adult females*

156 For this step, we used only dead recoveries and pooled data from all colonies. Following Schaub and
157 Pradel (2004) and Souchay and Schaub (2016), we used the known cause of death reported by the
158 public to tease apart mortality due to hunting ($_h$) *versus* other ($_o$) causes. We used program E-SURGE
159 (Choquet 2009) to develop a multi-event ring-recovery model that simultaneously estimated survival
160 (S), proportions of birds dying due to either cause (α_h, α_o), cause-specific recovery probabilities (r_h, r_o)
161 and probabilities that dead individuals were assigned to the correct cause (δ_h, δ_o). We specified a

162 model with four biological states: alive, newly dead due to hunting, newly dead due to other causes
 163 and old dead. The newly dead states ensured that encounters of dead birds were assigned to only
 164 one recovery period, whereas the old dead state was absorbing and unobservable (Gauthier &
 165 Lebreton 2008). Conditional on the states we specified an observation process with four events; not
 166 seen, recovered dead due to hunting, recovered dead due to other causes and recovered dead with
 167 no information of the cause (see appendix for state and event matrices and more details of the
 168 model). We assumed equal mortality rates due to hunting across colonies because birds within the
 169 flyway mix during the hunting season. As we experienced that not all parameters of the global model
 170 (time dependence for all parameters) were separately identifiable, we specified simpler candidate
 171 models. We first specified models with one or both of the cause-specific recovery probabilities (r_h, r_o)
 172 held constant over time. Next, we constrained the recovery probability due to other causes with a
 173 linear trend because evidence suggests it may have declined over time in north-west Europe
 174 (Frederiksen & Bregnballe 2000; Robinson, Grantham & Clark 2009). For a more robust likelihood
 175 optimization procedure, we used the option ‘multiple random initial values’ over successive runs.
 176 To validate the results of the multi-event model, we computed the annual killrate, i.e. the probability
 177 that an adult female eider alive at occasion i dies due to hunting between occasion i and occasion
 178 $i+1$:

$$179 \quad \text{killrate}_{h,ad\ female,i} = \alpha_{h,ad\ female,i} * [1 - S_{ad\ female,i}] \quad \text{eq. 1}$$

180 and compared this to a similar probability i.e. a hunting pressure (HP) calculated based on The
 181 Danish Hunting Bag Record (Strandgaard & Asferg 1980) and The Danish Wing Survey (see Clausager
 182 (2004) and references therein, www.bios.au.dk/vinger):

$$183 \quad \text{HP}_{age-sex,i} = \text{no. bagged}_i * \frac{\text{no.wings}_{age-sex,i}^{\text{shot}}}{\sum \text{no.wings}_i^{\text{shot}}} / N_{age-sex,i}^{\text{postbreed}} \quad \text{eq. 2}$$

184 Where no. bagged_i is the total number of birds bagged in year i , $\text{no. wings}_{age-sex,i}$ is the number of
 185 collected wings of shot birds in each age-sex class in year i , $\sum \text{no. wings}_i$ is the sum of all wings

186 collected in year i and $N_{age/sex,i}^{postbreeding}$ is the number of birds in each age-sex class present in the
187 population immediately following the breeding season (from a post-breeding version of the
188 population model described below). Because of data limitations proportions of immatures and
189 males that died due to hunting could not be directly estimated within the multi-event model as for
190 the adult females. Because the $killrate_h$ (eq. 1) and the HP (eq. 2) both express the probability that
191 an Eider died due to hunting between year i and year $i+1$ we substituted $killrate_{h,immatures-males,i}$ with
192 $HP_{immatures-males,i}$ (eq. 1) and calculated the lacking proportions of immatures and males that died due
193 to hunting.

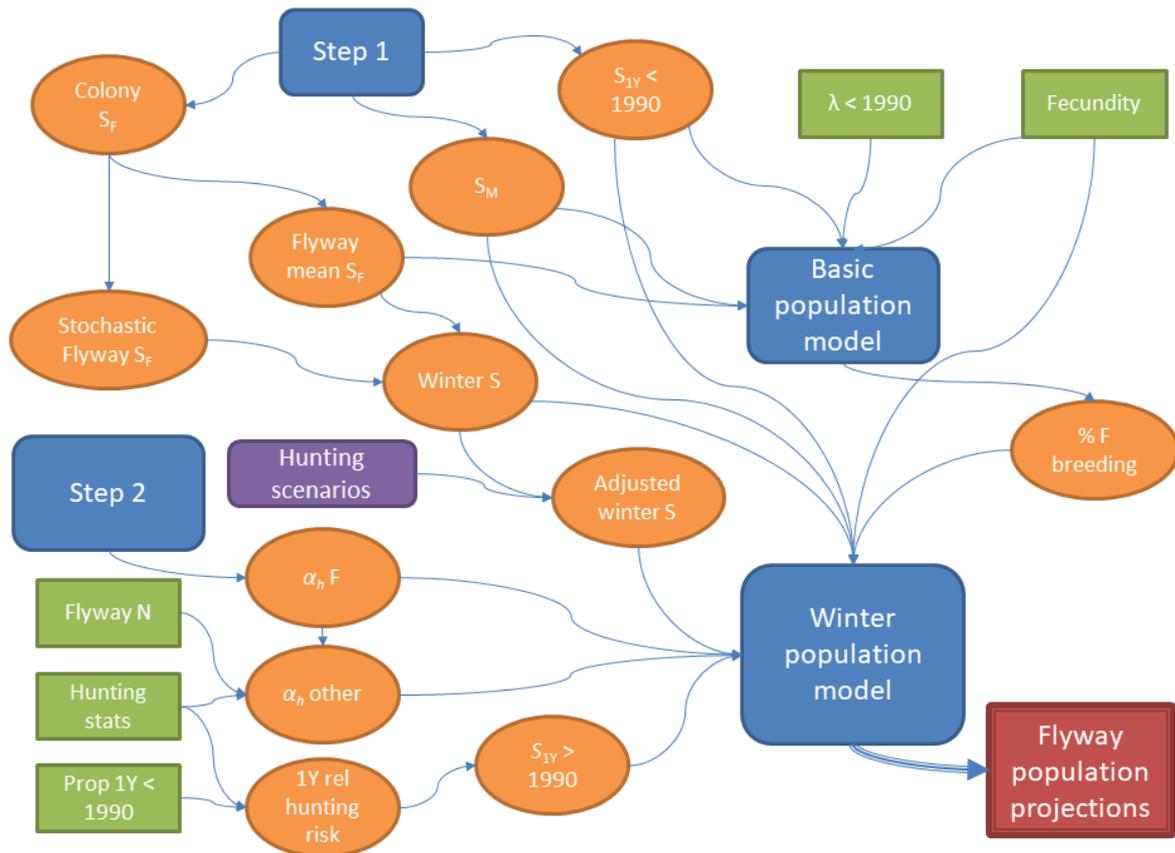
194

195 *Goodness-of-fit-testing*

196 Prior to model fitting we assessed the degree of overdispersion. Because the currently available
197 goodness-of-fit test for multistate models (Pradel, Wintrebert & Gimenez 2003) does not allow for
198 unobservable states, this method was considered inappropriate. We therefore computed the
199 Median-c-hat in program MARK for an analogous capture-recovery model which did not consider
200 separate causes of death. The resulting Median-c-hat value can thus be considered conservative in
201 relation to both step 1 and 2 because these models decrease heterogeneity by splitting data by
202 colony (step 1) or mortality into two components (step 2).

203 *Overview of the population model*

204 Fig. 2 provides an overview of the complex process involved in modelling of the flyway population of
205 eiders and population consequences of prevailing hunting restrictions.



206
 207 **Fig. 2** Conceptual diagram showing the flow of data, analyses and modelling involved in projections
 208 of flyway population change. Blue elements indicate the main steps of the analysis, green elements
 209 indicate external information (literature values and hunting stats), orange elements indicate
 210 estimated quantities, purple elements indicate hypothetical scenarios, and dark red indicates the
 211 main aim of the analysis: projections of flyway population size and composition.

212 Not all demographic quantities necessary to model the population were directly available and some
 213 parameters had to be approximated while making assumptions and by including other data sources.

214 By assuming a population growth rate of 3.46% prior to 1991 as indicated by aerial surveys (Joensen
 215 1974) we parameterized a basic population projection model with survival rates from step 1 and
 216 age-specific fecundity (clutch size x hatching success) of 4.1 (Christensen & Hounisen 2014) in order
 217 to approximate the probability of breeding after the second year of life, i.e. for adults (b_3). Initial
 218 population sizes (i.e. in 1970) were back-calculated based on the assumed population growth rate
 219 prior to 1991 and a flyway population size in 1991 of 1.7 million birds (Rose & Scott 1997):

220
$$pop_{1970\ n1-6} = \left(\frac{pop_{1991}}{\lambda^{21}} \right) * age_{dist\ n1-6} \quad \text{eq. 3}$$

221 Where $pop_{1970\ n1-6}$ is the population size in 1970 of the six age and sex-classes, pop_{1991} is the flyway
 222 population size in 1991, λ is the population growth prior to 1991 and $age_{dist\ n1-6}$ is the stable age
 223 distribution originating from the basic population model. Given the assumption that no breeding
 224 occurs before the third year of age ($b2 = 0$) we then estimated the probability of breeding among
 225 third-year or older individuals ($b3$) by adjusting this parameter to match the assumed population
 226 growth of 3.46%.

227 An estimate of first-year survival was only available for the initial period of population increase, up
 228 to 1981. To approximate survival from the subsequent period, we used data from The Danish
 229 Hunting Bag Record and The Danish Wing Survey, which annually since 1982 has assigned age and
 230 sex of 1.3–4.0% of all eiders shot in Danish waters. Assuming that first-year birds constituted c. 28%
 231 of the total population at the start of the open season in the early 1990s (Noer, Clausager & Asferg
 232 1995), and that the relative hunting risk of first-year individuals was the same before and after the
 233 decline (but prior to the first sex-differentiated hunting regulation), we calculated the proportion of
 234 first-year 1Y birds for the phase of decline:

235
$$\widehat{prop1Y_{decline}^{pop}} = \frac{\widehat{prop1Y_{decline}^{bag}}}{\widehat{Relrisk}} \quad \text{eq. 4}$$

236
$$\widehat{Relrisk} = \text{logit} \left(\widehat{prop1Y_{increase}^{bag}} \right) - \text{logit} \left(\widehat{prop1Y_{increase}^{pop}} \right)$$

237 Where $\widehat{Relrisk}$ is the estimated relative hunting risk of first-winter birds and $\text{logit}(p) = \ln \left(\frac{p}{1-p} \right)$.

238 By trial and error, we then used a population projection model (presented in detail below) to adjust
 239 first-year survival in order to match the decline in percentage among first-winter birds at the start of
 240 the hunting season.

241

242 *A population model with a mid-winter census*

243 Waterbirds are usually counted during winter (Scott & Rose 1996), when birds from multiple
 244 colonies assemble in large flocks which makes them easier to count. To be able to compare empirical
 245 monitoring data i.e. population counts with our model predictions, we constructed a Lefkovich
 246 transition matrix that tracks the population at mid-winter. Our age-specific estimates of survival
 247 (breeding-to-breeding) therefore had to be adjusted to fit with a mid-winter population census. We
 248 assumed that the elevated mortality during the first year of life was restricted to the period from
 249 hatching to mid-winter, and that survival during the second half of the first year of life was
 250 comparable to the second year of life. Denoting our mean estimates of survival S_0^{step1} , S_1^{step1} ,
 251 $S_{ad\ female}^{step1}$ and $S_{ad\ male}^{step1}$, we computed the relevant parameters for the matrix model as:

$$252 \quad SW_0 = \frac{S_0^{step1}}{\sqrt{S_1^{step1}}} \quad \text{eq. 5}$$

$$253 \quad SW_1 = S_1^{step1} \quad \text{eq. 6}$$

$$254 \quad SW_2 = \sqrt{S_1^{step1}} * \sqrt{S_{ad\ female}^{step1}} \quad \text{eq. 7}$$

$$255 \quad SW_{adF} = S_{ad\ female}^{step1} \quad \text{eq. 8}$$

$$256 \quad SW_{adM} = S_{ad\ male}^{step1} \quad \text{eq. 9}$$

257

258 *The midwinter-midwinter matrix model*

$$\begin{bmatrix} 0 & f_{2F} & f_{adF} & 0 & 0 & 0 \\ SW_1F & 0 & 0 & 0 & 0 & 0 \\ 0 & SW_2F & SW_{adF} & 0 & 0 & 0 \\ 0 & f_{2M} & f_{adM} & 0 & 0 & 0 \\ 0 & 0 & 0 & SW_1M & 0 & 0 \\ 0 & 0 & 0 & 0 & SW_2M & SW_{adM} \end{bmatrix} \begin{bmatrix} n_{1F} \\ n_{2F} \\ n_{adF} \\ n_{1M} \\ n_{2M} \\ n_{adM} \end{bmatrix}$$

261

262

263 The mid-winter matrix population model had three age-classes; first-winter ($_1$), second-winter ($_2$) and
264 adult ($_{ad}$) and two sex classes; females (F) and males (M) allowing simultaneous monitoring of the
265 dynamics of the population sex ratio. Fertility rates (f) expressed as the number of first-winter
266 females ($f_2F + f_{ad}F$) and males ($f_2M + f_{ad}M$) produced per second-winter ($_2F$) and adult winter female
267 ($_{ad}F$), were approximated as:

$$268 \quad f_2F = f_2M = \sigma * z * \sqrt{S_1F} * b2 * SW_0 \quad \text{eq. 10}$$

$$269 \quad f_{ad}F = f_{ad}M = \sigma * z * \sqrt{S_{ad}F} * b3 * SW_0 \quad \text{eq. 11}$$

270 where σ denotes the primary sex ratio i.e. the sex distribution at birth (assumed to be 0.5), z is the
271 fecundity i.e. the number of hatchlings per breeding female, and $b2$ and $b3$ are age-specific breeding
272 probabilities. Values of fecundity were derived from the literature (Bregnballe 1991).

273 Based on these demographic quantities (see appendix for an overview) we constructed a mid-winter
274 to mid-winter, time-dependent matrix population model. We then included among-colony variation
275 and stochasticity in adult female survival ($S_{ad}F$) and clutch size by means of simulations that for every
276 iteration ($n=10,000$) and every year ($n=45$) randomly drew a new estimate from a density
277 distribution function given by the mean and standard error of the estimates while the population
278 was projected over time. Likewise, stochasticity was also included for the other survival parameters.

279 Scenarios reflecting changes in hunting intensity were generated by adjusting reference survival
280 rates ultimately resulting in changes of the matrix elements in the population model. We used the
281 time frame of prevailing hunting regulations to extract mean survival rates and adjusted these
282 according to changes in hunting intensity (corrected from (Schaub & Pradel 2004)):

$$283 \quad S_{adj,i} = 1 - (1 - S_{base}) * (1 - \alpha_{h,base}) - (1 - c * x_i) * (1 - S_{base}) * \alpha_{h,base} \quad \text{eq. 12}$$

284 Where S_{base} and $\alpha_{h,base}$ are mean survival and proportion of birds dying due to hunting during the
285 reference period, c is the degree of compensation (fully additive effect = 1, fully compensatory effect
286 = 0), x_i is the % change in α_h relative to the reference and S_{adj} is then the adjusted survival rate given
287 the change in hunting intensity. Given the long life expectancy of the eider and because we track the
288 population from the time of mid-winter where natural mortality is no longer high for first-year birds
289 we assumed a fully additive effect of hunting ($c = 1$).

290 Given the estimated and approximated demographic rates, we projected the Baltic/Wadden Sea
291 eider population between 1970 and 2014. Subsequently, we used survival rates adjusted for changes
292 in hunting intensity following the most recent hunting regulations to predict the prospective
293 population trajectory between 2014 and 2025. In addition, we modelled the population
294 consequences that hunting regulations would have entailed if levels of natural mortality had
295 remained unchanged since 1998.

296

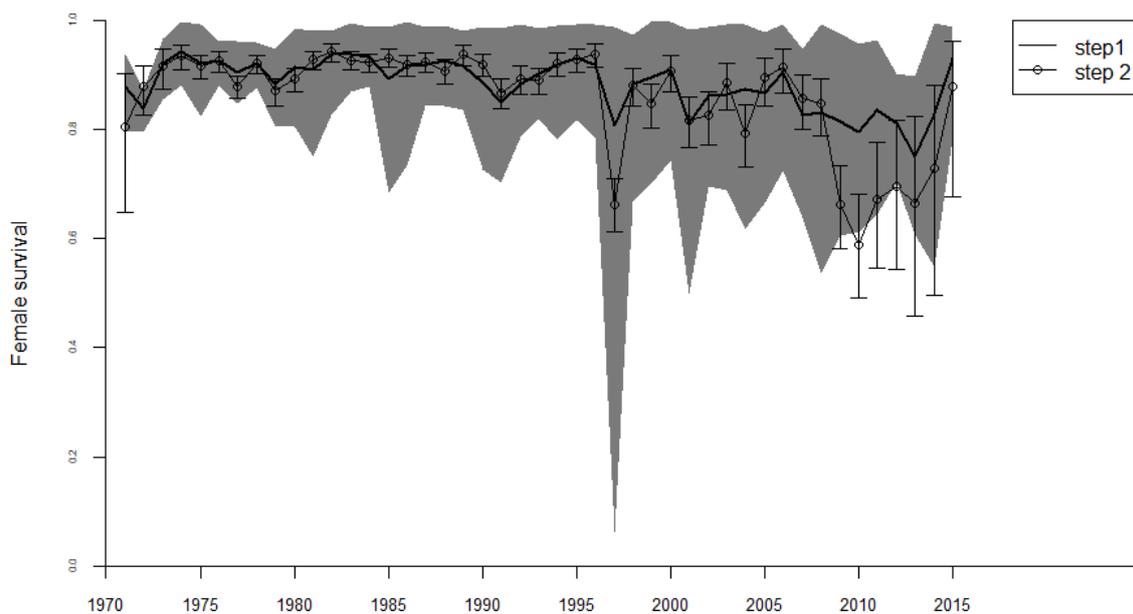
297 **Results**

298 Goodness of fit of a capture-recovery model with no stratification of mortality, time-dependent
299 survival and a trend on the recovery rate indicated a slight lack of fit (median $\hat{c} \pm 95\% \text{ CI} = 1.60 \pm$
300 0.17). Therefore, we did not expect bias in parameter estimates of neither the colony-specific
301 survival analysis (step 1) nor the cause-specific mortality analysis (step 2) that stratifies mortality
302 based on the known cause of death.

303 Assuming common recovery rates (r), a subset of candidate models estimated time-series of colony-
304 specific adult female survival (step 1, estimates presented in appendix) over 45 years (1971-2015).
305 QAIC model selection identified a model with a common and linear trend over time (T) on recovery
306 rates (except Vlieland) as the most parsimonious; $S(g*t) p(g*t) r(T, VL) F(g)$. In addition, separate
307 single-site capture-recapture-models also estimated first-year survival of hatchlings $S_0^{step1} = 0.12$,
308 second-year survival $S_1^{step1} = 0.83$ and adult male survival $S_{adM}^{step1} = 0.92$.

309 Among the set of candidate models some of the cause-specific (multi-event) mortality models (step
 310 2) were over-parameterized and generated unreliable parameter estimates with large standard
 311 errors. However, a constraint on recovery rates from causes other than hunting (representing a
 312 decline over time as in step 1) facilitated identifiability of all parameters. In step 2, model
 313 $S(t), \alpha_h(t), r_h, r_o(T), \delta_h, \delta_o$ was selected as the best (Deviance: 34049, no. of parameters: 95), clearly
 314 better than the second best model candidate $S(t), \alpha_h(t), r_h, r_o, \delta_h, \delta_o$ (Deviance: 34144, no. of
 315 parameters: 94, delta-AIC: 93). According to the best model, the probability for hunters to recover
 316 rings of shot birds was estimated as 0.36 (95% CI, 0.25-0.49), whereas the recovery probability of
 317 birds dead due to other causes fell linearly from 0.32 to 0.04 between 1970 and 2015; similar
 318 declines have been reported for other species (Robinson, Grantham & Clark 2009; Frederiksen *et al.*
 319 2018). Furthermore, the probability that recoveries were correctly assigned to hunting (δ_h) and other
 320 causes (δ_o) were estimated as 0.94 and 0.95, respectively.

321 Estimates of adult female survival from step 1 and 2 were high and stable as the population grew
 322 until the early 1990s, but declined markedly hereafter, in particular after the mid-1990s (Fig. 3).

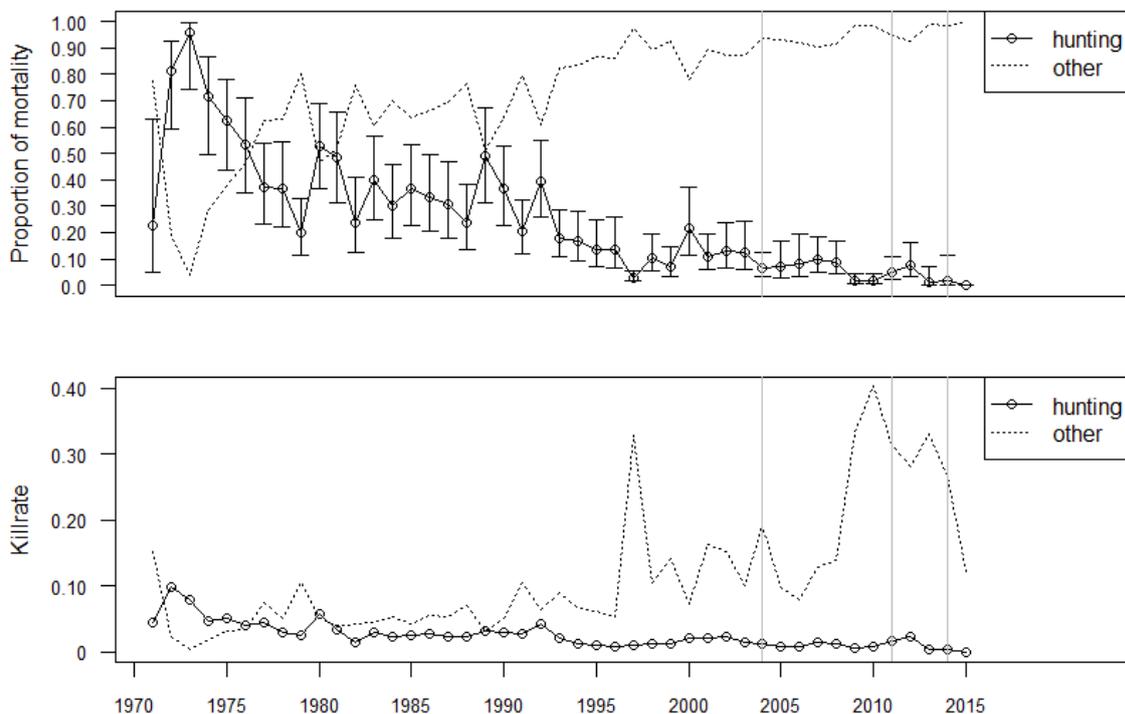


323

324 **Fig. 3** Estimates of adult female survival at the flyway level from a colony-specific capture-recapture-
 325 recovery analysis (step 1), and a multi-event model with two causes of death i.e. hunting and other
 326 causes (step 2). The black solid line and grey scaled areas represent mean estimates of simulations
 327 based on step 1 and 95% confidence intervals, respectively. Connected open circles and error bars
 328 represent estimates and 95% confidence intervals from step 2.

329 It is evident that the cause-specific multi-event model applied in step 2 tended to underestimate
 330 survival relative to step 1, especially over the most recent period. Because live recaptures were
 331 included in step 1 and not in step 2 we considered survival estimates from step 1 more accurate and
 332 used these to model the flyway population of eiders. Mean adult female survival in the non-hunted
 333 colony of Vlieland was 0.90, only 1%-point higher than in the other study colonies without incidence
 334 of epidemic disease.

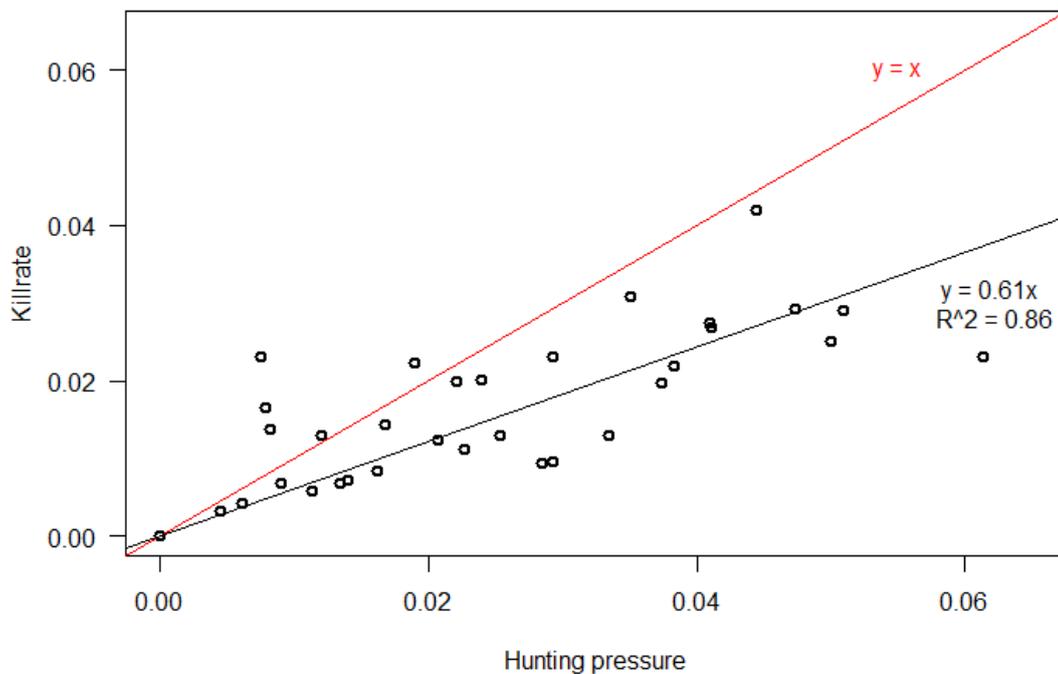
335 Significant declines in both α_h ($r = -0.83$, $n = 45$, $p < 0.01$) and $killrate_h$ ($r = -0.77$, $n = 45$, $p < 0.01$)
 336 indicated major reductions in the hunting pressure over time (Fig. 4).



337

338 **Fig. 4** Upper panel shows estimates from step 2; The proportion of mortality of adult females caused
 339 by hunting (open connected circles) and other causes (dotted line) between 1971 and 2015. Error
 340 bars on the proportion dying due to hunting indicate 95% confidence intervals. Lower panel shows
 341 the resulting killrate which is the probability of dying due to hunting or other causes (lower panel).
 342 Grey, vertical lines indicate the implementation of past hunting regulations.

343 The two independent measures of hunting intensity were highly correlated, but the $killrate_h$ from the
 344 analysis in step 2 was consistently lower than the analogous hunting pressure calculated from bag
 345 statistics ($Killrate_{adult\ female} = 0.61 \times HP_{adult\ female}$, $R^2 = 0.86$, Fig. 5).

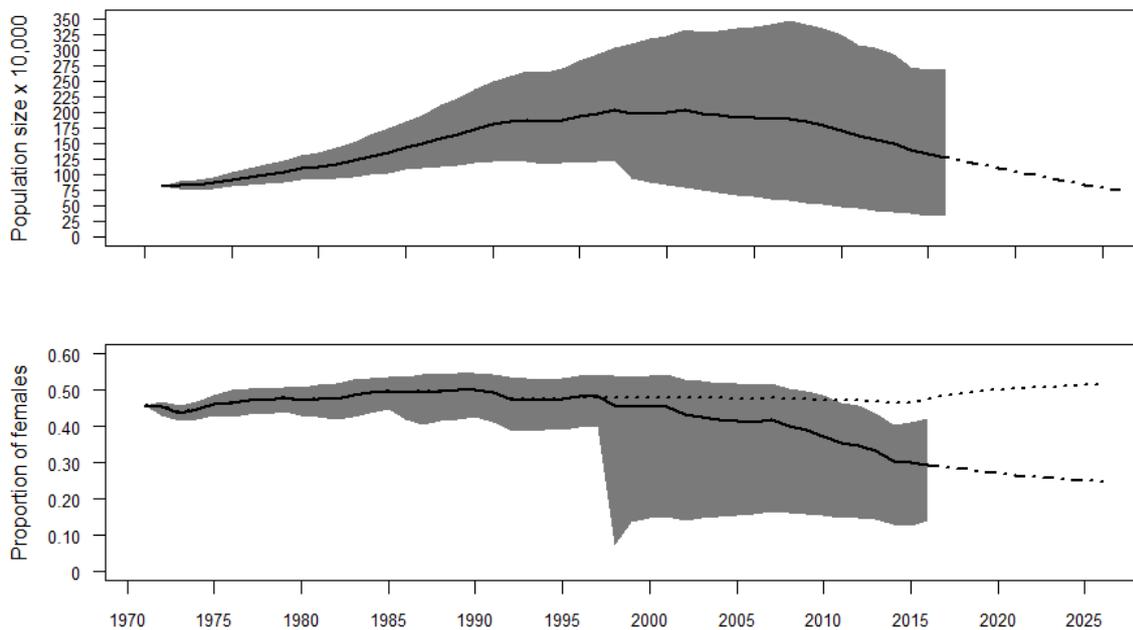


346
 347 **Fig. 5** Relationship between the hunting pressure based on bag statistics and the killrate from
 348 hunting derived from results of a multi-event model with two causes of death i.e. hunting and other
 349 causes (step 2). The red line indicates a 1:1 relationship.

350 By means of a basic population model and a target population growth rate, the probability of
 351 breeding among adults (b_3) was by trial and error estimated as 0.70. The proportion of first-year

352 individuals in the hunting record and their relative hunting risk indicated that survival of hatchlings
 353 had declined to 0.09 (0.12 prior to the early 1990s).

354 The reconstructed population trajectory suggested a relatively weak population increase of 8%
 355 throughout the 1990s, followed by a considerable decline in population size of 35% between year
 356 2000 and 2014 (Fig. 6, upper panel). Given high rates of natural mortality the recently implemented
 357 hunting ban on females appears insufficient to fully counteract the observed decline. The scenario
 358 with stable survival of adult males resulted in annual growth of 0.95 for the interval 2014-2025,
 359 hence natural mortality must decrease in order to revert this negative population trend (Fig. 6,
 360 upper panel). We further predict that despite the current hunting ban on females the proportion of
 361 females in the population will continue to decrease from 30% in 2014 (among adults) to 25% in 2025
 362 (Fig. 6, lower panel).



363

364 **Fig. 6** Population trajectory of the mid-wintering Baltic/Wadden Sea flyway population of eiders
 365 between 1971 and 2025 (upper panel). The black solid and dot-dashed lines represent mean
 366 retrospective and prospective population trajectories, respectively. The lower panel shows the
 367 population sex ratio as the proportion of females among adult birds. Black solid and dot-dashed lines

368 *is under the assumption of constant male survival, whereas the black dotted line assumes a similar*
369 *absolute change in adult male survival since 1991 (on the logit scale) as observed for the females.*
370 *Grey scaled areas indicate 95% confidence intervals, which originate from simulations based on*
371 *variation between study colonies.*

372

373

374

375 **Discussion**

376

377 *Population trends and processes*

378 Despite multiple restrictive hunting regulations, our reconstructed population trajectories
379 indicate that the wintering Baltic/Wadden Sea flyway population of eiders was reduced
380 considerably since year 2000. Moreover, model predictions indicate that levels of natural
381 mortality among adult females have recently increased to an extent that cannot be
382 counteracted through hunting regulations. Population trends of the Baltic/Wadden Sea
383 flyway population differ according to source (Ekroos *et al.* 2012a). While mid-winter counts
384 suggest a significant population reduction throughout the 1990s (followed by a slight
385 increase), nest counts indicate a considerable population decline between 2000 and 2009. It
386 has been suggested that this discrepancy arises from a delay in age of first breeding, an
387 increase in non-breeding frequency, changes in census methods or combinations of these
388 factors (Ekroos *et al.* 2012a). Based on demographic data from multiple colonies we present
389 a reconstructed population trajectory that seems to confirm the trend inferred from nest
390 counts, i.e. that the largest population reduction occurred after year 2000. It is important to
391 note that our results rely on the assumption that our study colonies are representative of
392 the overall population.

393 Factors causing increased natural mortality rates among breeding females likely differ
394 between population divisions. For example, in the Western Gulf of Finland incubating

395 females suffer from predation by a rapidly growing population of white-tailed sea eagles
396 *Haliaeetus albicilla* and non-native American mink *Neovison vison* (Ekroos *et al.* 2012b).
397 Outbreaks of avian cholera have struck several eider colonies in The Netherlands, Denmark
398 and Sweden, in some cases wiping out 90% of the females nesting there (Swennen & Smit
399 1991; Christensen *et al.* 1997; Tjørnløv, Humaidan & Frederiksen 2013). Moreover, an
400 unusually large number of eiders have been found dead at Christiansø in the Baltic Sea,
401 presumably due to starvation at the end of the breeding season (Garbus *et al.* 2018). Food
402 deficiency, associated with lower nutrient levels in the marine environment (Laursen &
403 Møller 2014) and overharvest of shellfish (Camphuysen *et al.* 2002) may also affect body
404 condition as pre-breeding females rely on body reserves to complete migration and
405 breeding.

406 Over time, the marked difference in mortality between the sexes may have resulted in
407 large-scale changes of the population sex ratio with a gradual increase in the proportion of
408 males from 32.2% in 1979 to 61.7% in 2005 (Lehikoinen *et al.* 2008). Through spring 2013
409 and 2014 counts of eiders migrating into the Baltic Sea suggested an even stronger (67%)
410 male bias (Berg 2014). Lehikoinen *et al.* (2008) suggested that the current decline of the
411 flyway population was intimately linked to large-scale changes in the population sex-ratio,
412 as the two processes occurred in parallel. We found that under the assumption of constant
413 survival of adult males, the skewed adult sex ratio can be explained solely by the increased
414 rate of mortality among nesting females. This is also supported by studies reporting equal
415 proportions of the sexes at hatch (Swennen, Duiven & Reyrink 1979; Blums & Mednis 1996).

416 A highly skewed sex ratio is however, not the only driver of structural change in this
417 population. The declining proportion of first-year birds in The Danish hunting record
418 suggested either a decline in fecundity or first-year survival (Ekroos *et al.* 2012a). Assuming
419 that fecundity has remained stable, our models suggest that first-year survival from
420 hatching has fallen considerably, i.e. from 0.12 to 0.09 between periods of opposing
421 population trends. Observations indicate that an increasing proportion of newly hatched
422 ducklings disappear between the colony at Christiansø in the Baltic Sea and their nursery
423 feeding grounds 18 km away near Bornholm (Kofod & Buchmann 2016). First-year survival
424 probability as low as 0.01 – 0.05 reported from the Gulf of Finland (Hollmen *et al.* 1999)
425 confirms a recent and very dramatic structural change operating at an early life stage. Such

426 a massive die off of ducklings might be caused by starvation or increased predation
427 susceptibility as a potential result of high infection rates with acanthocephalan parasites
428 (Hollmen *et al.* 1999), or by thiamine deficiency (Morner *et al.* 2017) causing a lower weight
429 gain or neurological disorder in ducklings. Although a decline in adult female survival is likely
430 to have the highest negative impact on the population, low duckling survival also
431 contributes to further reductions in flyway population size.

432

433 *Harvest management*

434 Harvest rates assessed from independent data sources, i.e. ring-recoveries and hunting
435 statistics, both indicated a major reduction over time in the contribution of harvest to the
436 mortality of adult females. This is partly due to fewer active, Danish seaduck hunters (Asferg
437 *et al.* 2003; Christensen 2005), but also to a set of restrictions on the length of the hunting
438 season on females (Christensen & Hounisen 2014). The effectiveness of shortening the
439 hunting season depends on both the spatio-temporal distribution of the hunted population
440 and the motivation for hunters to maintain their annual harvest (Sunde & Asferg 2014). In
441 this case hunters did not compensate for the shorter season by intensifying their kill of
442 females, in contrast to males (Christensen & Hounisen 2014). Despite high killrates from
443 hunting throughout the 1970s and 80s, extremely low natural mortality ensured population
444 growth at that time. Although hunting in this period was intense, our results show that
445 survival of adult females that mainly winter in an entirely hunting-free area in the Dutch
446 Wadden Sea was only 1%-point higher compared to birds subject to hunting in Danish
447 waters. In contrast to the period of population increase, the period of decline following year
448 2000 was characterized by high natural mortality and low hunting mortality.

449

450 *Data and knowledge gaps*

451 We found that the estimate of mortality due to hunting was substantially lower when
452 inferred from the ring-recovery model compared to the hunting statistics, although hunting
453 mortality between 2011 and 2014 was so low that the difference was negligible. While this
454 bias highlights the need for caution and for using independent data for validation of model

455 results, it might also have interesting, underlying causes. For instance: a) the size of the
456 flyway population might be larger than current estimates suggest, b) the Danish wing survey
457 might not be representative, c) colonies where birds were ringed might be subject to less
458 hunting than average, d) α_h estimates from the multi-event model might be biased low if the
459 recovery probability from hunting was estimated too high, or e) low temporal variability of
460 α_h towards the end of the time series might constitute a risk of bias in either α_h itself or in
461 the cause-specific recovery probability r_h (Schaub & Lebreton 2004; Schaub & Pradel 2004;
462 Schaub 2009). Clearly, better monitoring (e.g. regular coordinated and standardised mid-
463 winter surveys for more accurate population size estimates and sustained mark-recapture
464 studies involving adult females, ducklings and ideally adult males) would reduce such
465 potential sources of bias. Estimation of demographic parameters could be further improved
466 by also including birds ringed outside the study colonies.

467 *Recommendations*

468 Sustainable harvest management should aim to protect not only adult females but also first-
469 winter birds. In fact, one potentially unintended consequence of the female hunting ban
470 implemented in 2014 was a marked reduction in the bag of first-winter birds, which in the
471 field resemble adult females (Christensen & Hounisen 2014). Within the European Union,
472 the Annex II of the EU Birds Directive (79/409/EEC) aims to control levels of hunting by
473 listing species that can be legitimately hunted in some (Annex II/B) or all member states
474 (Annex II/A), but the Directive does not regulate national harvest rates. Although common
475 in North America (Klimstra & Padding 2012), a coordinated flyway approach to harvest
476 management has so far only been applied to one European quarry species, the pink-footed
477 goose *Anser brachyrhynchus*, where adaptive harvest management has been applied in an
478 attempt to reach a specific target spring flyway population size based on scientific principles
479 (Madsen *et al.* 2016). Given the high, recent rates of natural mortality among females and
480 first-year individuals, our predictive population projections clearly demonstrate the current
481 need to maintain the hunting ban on female eiders. There is also a pressing need to study
482 the underlying causes of high natural mortality, especially among the nesting female eiders,
483 to target conservation efforts. We believe that investigations of important causes of natural
484 mortality should try to assess the impact of avian and mammalian predation, food
485 limitations causing starvation over the breeding season and frequency of epidemic disease.

486 In addition, focus should also be directed towards survival of hatchlings during the first
487 months of life because high mortality among hatchlings may later contribute to further
488 population declines due to the lack of recruits. Finally, we advocate that sustainable harvest
489 management of the Baltic/Wadden Sea flyway population of Common Eiders should be
490 founded on the principles of adaptive management, based on continuous monitoring of
491 reproductive success, vital rates and levels of natural and hunting mortality as crucial
492 components for future evaluations of harvest management.

493

494 Authors' contributions

495 RST and MF conceived the study; RST developed the statistical and population models, with input
496 from RC, RP and MF; RST collated the mark-recapture-recovery data from numerous contributors;
497 TKC provided Danish hunting data. RST analysed the data and led the writing of the manuscript. All
498 authors contributed critically to the drafts and gave final approval for publication.

499

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