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Effects of mate removal on the fecundity of common eider *Somateria mollissima* females

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Behavioural observations, measurements of male and female reproductive success, and DNA microsatellite loci were used to investigate parentage of common eider *Somateria mollissima* clutches and productivity of widowed females in Finland. In an experimental study simulating spring harvest of male eiders, a total of 20 males were shot while attending 16 females (four males after rematings, 16 initial males) during the pre-laying and laying period in 1994. Of the 16 widowed females, 11 nested and five did not. Mean clutch size of breeding widows (4.55) did not differ from that of control females in the same year (4.47; $N = 32$). However, the hatching success of widows was significantly lower than that of control females (53 vs 81%) because of a greater proportion of addled eggs and dead embryos (38% vs 11%). Male removal also appeared to change male and female behaviours resulting in higher incidence of intra-specific brood parasitism and mate replacement. Occurrence of foreign eggs averaged 9.5% during the treatment year but was not observed during a year without disturbance during mating and egg laying (1997). Behaviours of widowed females related to remating attempts varied from active seeking of new mates to total rejection of courting males. Rematings did not lead to full clutch fertilisation among widowed females. Neither did we observe evidence of immigration of new males into the hunting area to court the widows. Male removal clearly lowered the fecundity of eider females, reducing nesting success by 35% of long-term averages. The potential for remating appears to be reduced by the female-biased sex ratio caused by simulated male-only harvest.

Key words: DNA microsatellite markers, eider, nesting success, paternity, *Somateria mollissima*, spring harvest

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In the Baltic Sea, northwestern Europe, the common eider *Somateria mollissima* is an important game species. Wildfowling in Denmark harvest 130,000–140,000 eiders annually (Noer, Clausager & Asferg 1995). In Finland and Sweden the species is considered the most important huntable seaduck, though harvest is only one tenth of that in Denmark (Hario 2001). Because the northern coasts of the Baltic Sea freeze over every winter, Finnish eiders are strictly migratory and winter in the southwest Baltic in the coastal waters of Denmark (Bauer & Glutz von Blotzheim 1969, detailed in Noer 1991). Pair formation occurs on the wintering grounds, and the male follows the homing female to her breeding grounds in spring. Thus, Baltic eiders show the pronounced female-biased natal philopatry typical for most Anatinae (Anderson, Rhymer & Rohwer 1992), and female-choice is prevalent, leading to what is believed to be predominantly monogamous pair bonds (reviewed in Bluhm 1988, Rohwer & Anderson 1988).

Apart from fertilisation, mate guarding is believed to be the only benefit that female eiders receive from males during the reproductive period. The male is thought to provide physical defence from harassment by other males during the period of hyperphagia before laying (Ashcroft 1976, Milne 1976, Spurr & Milne 1976). Because males provide no care for young and leave their incubating mates upon clutch completion (leading to a temporary male-biased sex ratio in habitats surrounding the nesting area), they have traditionally been regarded as a suitable target for spring subsistence harvest. There is a common consensus among Finnish wildfowling that due to perceived male-biased sex ratio and the early pairing (inferentially believed to lead to early fertilisation), males can be harvested without compromising female reproductive success. In cases of unsuccessful fertilisation, availability of paired or satellite males for widowed females would ensure that all females are inseminated.

In recent times, spring harvest of males (or spring shooting) has been gradually banned in most European countries, whereas it is still a common practice in many parts of the world in form of subsistence harvest. In Russia and North America, subsistence harvests account for a considerable number of birds bagged each year (Kostin 1996, Thompson 1996). Within the European

Union, spring hunting is not considered to be consistent with principles of sustainable exploitation of waterfowl, as it has the potential to decrease adult survival (reviewed in Kokko, Pöysä, Lindström & Ranta 1998). In Finland, spring hunting is still allowed, but it is now strictly licensed and regulated (see Hario 2001).

Increased availability of molecular genetic markers has led to a greater understanding of avian mating systems (Birkhead & Møller 1992), although relatively few studies of waterfowl behavioural ecology have employed such markers (e.g. Quinn, Quinn, Cooke & White 1987, Larsson, Tegelström & Forslund 1995, Dunn, Afton, Gloutney & Alisauskas 1999, Svete 1999). This study aims to assess the fertilisation status and remating of experimentally widowed common eider females in Finland by combining behavioural observations of rematings and intraspecific brood parasitism with parentage analyses of clutches using DNA microsatellite markers (Fields & Scribner 1997). We evaluate the effects of the spring harvest by comparing breeding data from widowed females to data from a control group of non-widowed females from the same year and location. This study extends previous studies (Hario, Hollmén & Selin 1995), by the addition of genetic determination of parentage for widows' clutches and also for clutches from an undisturbed year (1997) when no spring harvest occurred on the same island.

Material and methods

Field work procedures

The study was conducted at the Söderskär Game Research Station, Gulf of Finland (60°07'N, 25°25'E), during the 1994 and 1997 breeding seasons on a population of common eiders individually marked with colour rings. Females nesting around Söderskär station have been studied in detail since 1982 (e.g. Hario & Selin 1988, Laurila & Hario 1988, Hollmén, Lehtonen, Sankari, Soveri & Hario 1999, Franson, Hollmén, Poppenga, Hario & Kilpi 2000) and the entire breeding history of 48 females that were nesting in the study area in 1994 is known.

During the spring of 1994, 20 males were removed by shooting from 16 females from this population (four males

after rematings, 16 initial males) under the license from the State Provincial Office of Southern Finland (no. LUO 62/1994). The remaining members of the study population (32 breeding females) were used as controls. Widowed females were identified by colour rings, and were selected to represent the current age distribution of the study population and the current range of the relative timing of breeding. These parameters are known to have a significant effect on clutch size and female body weight during breeding (Laurila & Hario 1988). The relative timing of breeding was defined as the female's median timing from her previous breeding career (classified as early, median or late). Using females of known age, enabled us to sort data into three age classes (>8 year, 5-8 year and 3-4 year olds). Females were selected to be widowed so that there was no significant difference in the relative timing between experimental widows and controls ($G_5 = 2.571$, $P > 0.1$), nor were differences observed in the proportions of different age classes among groups ($G_5 = 3.346$, $P > 0.1$). This made a direct comparison between the groups feasible.

Due to the severe ice conditions in the winter of 1994, the removal of males began on 25 April (the annual open season of spring shooting is from 10 April to 21 May), upon the first exodus of laying females onto the nesting islands. The last (20th) targeted male was shot on 17 May when laying was completed and incubation was underway for most of the population. Males were shot with a small-game rifle from a blind on the shore, thereby simulating the conventional shooting practice prevailing during spring harvest in Finland (shooting from motorised boats is not allowed). Although the age and timing of previous breedings for each female were known, their current breeding stage at the time of male removal was not known, as is the case during spring hunting.

After the males had been shot, the females were observed closely until the onset of incubation to document possible reparings. The median time interval between mate loss and laying was six days (range: 0-26 days). The median number of days during which a widow was located before she started incubating was three days (range: 1-10 days). During this period, female observations varied from 30 minutes to several hours. Males and females were observed daily from the Söderskär lighthouse from which the entire study area (a 2.5-ha island) can be surveyed. Sex ratios of swimming eiders were determined on a daily basis (weather permitting), for both the study island and the surrounding archipelago. Due to the elevated lighthouse position in close proximity to the eiders, we were able to identify colour ring combinations of all females using a 40x

telescope. The putative mate paired with each female was identified during an observation period of several hours before removal. In all cases, the putative male was the only male escorting the female constantly during one-hour long foraging cycles and intermittent resting hours, and his presence did not provoke threatening behaviour from her. The distance between the male and the female varied from close contact to several tens of metres, depending on the activities of the birds. Pair bonds could also be verified during aggressive encounters following female threat displays against approaching males, as the attending male would immediately chase off intruders.

Measurements of reproductive performance (i.e. laying dates, clutch size, hatching date and hatching result) were obtained by direct observation at each nest on the study island. All nesting females on the study island were captured on day 20 of incubation, weighed, and measurements of their clutches were conducted according to the procedures described in Laurila & Hario (1988). In the surrounding archipelago, another 521 females were captured at the nest (52% of the Söderskär population) during late incubation. On the remaining nests, the presence or absence of colour rings could be verified when the birds were flushed from the nest. The bright colour rings are readily discernable even in flying birds.

Collection of DNA samples

Blood samples collected from the ulnar or jugular vein of captured females were stored in a transport buffer (100mM Tris, 100 mM EDTA, 10 mM NaCl, 0.5% SDS) at -20°C .

A sample of liver tissue was collected from the males shot ($N = 16$; four males were lost in ice), and was stored in a transport buffer (10% DMSO and saturated NaCl_2) at -20°C .

After hatching, egg shell membranes ($N = 25$) and dead embryos ($N = 9$) from the nests of 11 breeding widowed females in 1994 were collected, and vascular areas of membranes were dissected and stored in a transport buffer. An additional 14 eggs remained unhatched. In gross examination, eggs showed no signs of embryonic development, but were classified as 'addled' because of difficulties in distinguishing between infertile bird eggs and those in which embryo mortality had occurred at a very early stage (e.g. Birkhead, Veiga & Fletcher 1995). An additional two eggs/hatchlings were lost (disappeared) before sampling.

In 1997 (when no spring shooting experiment was performed), reproductive data, blood samples and egg shell membranes ($N = 67$) were collected from females at 14 nests, to measure fecundity and intraspecific

brood parasitism under natural conditions. These data included only one female that was widowed in 1994. Breeding studies were conducted at Söderskär also during the intermittent years 1995 and 1996, and the return rate and breeding success of the 1994 widows were monitored.

Assignment of individual genotypes

DNA was extracted from blood and tissues in 1994 using standard proteinase-K and phenol-chloroform methods (Sambrook, Fritsch & Maniatus 1989), and from blood in 1997 with the Puregene (Gentra, Inc.) isolation kit. DNA concentrations were determined by fluorimetry, and samples were aliquoted to stocks of 20 ng/ml. Three bi-parentally inherited microsatellite loci (Ala1, Sfi4 and Sfi5; Fields & Scribner 1997) were used for parentage analyses in 1994, and four loci (Ala1, Sfi5, Sfi10 and Sfi11; Fields & Scribner 1997; K.T. Scribner, unpubl. data) were used in 1997. In 1994, DNA samples were screened for variation using primers end-labelled with gamma-³²P using T4 polynucleotide kinase according to the manufacturer's specifications (Pharmacia). Polymerase chain reactions (PCR) were conducted in 25 µl volumes using approximately 100 ng of DNA, buffer (10 mM Tris-HCl, pH 8.3, 1.5 mM MgCl₂, 50 mM KCl, 0.01% gelatin, 0.01% NP-40), 0.01% Triton-X 100, and 0.25 units of Taq polymerase (Perkin-Elmer). Primer and dNTP concentrations were 400 nM and 200 µM, respectively. PCR consisted of 35 cycles (denaturation at 94°C for one minute, annealing for two minutes). Annealing temperatures were 47°C for Ala1, 50°C for Sfi4, 48°C for Sfi5, 52°C for Sfi10, and 50°C

for Sfi11. PCR products were separated on 6% denaturing polyacrylamide gels. In 1994, gels were dried and autoradiographed for 12-36 hours using intensifying screens. In 1997, gels were visualised by scanning with a Hitachi FM BIO II scanner. An M13 control sequencing reaction (USB) and individuals with a known genotype were run adjacent to the samples to provide unambiguous size standards.

Putative female and male parents (i.e. incubating females and males known to be in association with the females at various times during the courtship and egg laying) were run side-by-side with their putative offspring to allow identification of maternal and paternal alleles and parental assignment or exclusion. For each offspring, females and males were either excluded as possible parents based on comparisons of offspring and parental alleles across the loci, or were designated as possible parents based on co-occurrence of alleles in putative parents and offspring. When both alleles at each locus in the offspring were present in corresponding loci of the putative parents, they were considered the likely parents of the offspring. When the offspring possessed an allele that was alien to putative parents, the offspring was considered an extra-pair progeny, or alien (i.e. result of parasitic laying). When no DNA was available from the putative father but the entire clutch possessed only two alleles per locus that were not found in the putative mother, the offspring were considered likely to have been sired by one male only.

The similarity of variances was tested using the F-test. When variances were found homoscedastic across samples, a parametric test was applied; otherwise differences

Table 1. Breeding data and distribution of intra-pair and alien progeny in the families of the widowed common eider females at Söderskär in 1994.

Female code	Clutch size	Paternity resolved ¹		Paternity not resolved ²		Eggs hatched	%	Sperm duration (days)
		Intra-pair	Alien/EPP ³	Viable	Added			
12036	5	1	0	2	2	3	60	..
12063	5	1	1	2	1	4	80	..
5559	5	4	0	1	0	5	100	..
35166	3	0	0	3	0	3	100	..
3241	5	1	2	2	0	1	20	≥20
4333	5	1	0	1	3	2	40	1
35013	4	4	0	0	0	0	0	≥2
7428	5	3	1	1	0	3	60	≥5
12218	4	2	1	1	0	4	100	≥7
12015	4	0	0	1	3	1	25	17
3607	5	0	0	0	5	0	0	..
Total	50	17	5	14	14	26		
Mean	4.55						53.2	
SD	0.69						38.9	
N	11						11	

¹ Based on viable eggs with embryonic development.

² For viable eggs, progeny could not be resolved.

³ Extra-pair progeny.

were tested with non-parametric tests. Means quoted are arithmetic means, given ± 1 standard deviation; tests are two-tailed. To illustrate the sex ratio distribution in relation to the breeding schedule on the study island and in the surrounding archipelago we added a LOWESS smoother (locally weighted scatterplot smoother) to the graphical data (Wilkinson, Hill, Miceli, Birkenbeuel & Vang 1992). Smoothing does not presuppose the shape of the function (only that it has a unique Y value for every X). Computations were achieved using the SYSTAT 5.0 software package.

Results

Clutch size and hatching rates

Of the 16 widows, 11 were found incubating a clutch (Table 1); the other five were not associated with any nest site, neither on the study island nor in the surrounding archipelago, and were considered non-breeders.

The clutch size of widowed breeders ($4.55 \text{ eggs} \pm 0.69$; see Table 1) was similar to that of controls ($4.47 \text{ eggs} \pm 0.76$; one-way ANOVA: $F = 0.087$, $df = 1, 41$; $P > 0.1$) whereas the hatching rate ($53.2\% \pm 38.9$) was significantly lower than that of controls in 1994 ($81.1\% \pm 31.3$; $F = 5.767$, $df = 1, 41$, $P = 0.042$). Similarly, when the current hatching rate was compared to the mean hatching rate of a female's previous breeding history during 1982–1993, the emerging difference was significantly greater in widows' clutches ($-34.5\% \pm 46.6$) than in controls' clutches ($+6.6\% \pm 40.1$; $F = 6.465$, $df = 1, 28$, $P = 0.034$).

Viability of eggs and sperm duration

The low hatching success of widows as compared to controls was primarily due to a combined effect of added eggs and embryonic deaths, which was higher in widows' clutches ($37.7\% \pm 36.8$) than in those of controls' ($11.4\% \pm 22.9$; $F = 7.314$, $df = 1, 37$, $P = 0.020$). Thus, the lowered fecundity of breeders was primarily due to lowered viability of eggs and not to lowered clutch size.

The remating response of the widows varied greatly. Behavioural observations revealed six cases of rapid mate replacement (involving four females) after mate loss. In two of these cases (females 12036 and 12063; see Table 1), the males were shot in succession after the loss of the initial male. In both cases, the male was shot immediately after copulation. However, in the broods none of the resulting progeny was found to be sired by the last male. Accordingly, females were either unaware of their own fertilisation status or they were seeking bet-

ter-quality males (see e.g. Birkhead & Møller 1992). On the other hand, the fact that the last male was observed copulating with female 12036 on the day before clutch initiation, but did not sire the last progeny, suggests that he had not taken over in time to fertilise the egg, or that any last male advantage, if occurring in common eider, is not 100%. The remaining two females (females 5559 and 35166 in Table 1) repaired only once each, but their progeny either was not resolved (female 35166), or no male sample could be obtained (female 5559).

The paternity was established for most of the seven widows that did not remate. The viability of their males' sperm varied greatly (see Table 1): from at least 20 days to only one day (one male shot after copulation at the initiation of egg laying; the first egg was then fathered by him, but the rest of the clutch remained unfertilised). In contrast to females 12036 and 12063 that were actively seeking copulations, most widows were always seen alone. As males were not readily available, few males seemed attracted to widowed females. Only one of these females (female 3241) was once seen soliciting copulations, but without response. Either these widows were not appealing to males, or they chose to stay unpaired. Of the five non-breeding widows, one was seen being courted on several occasions, but apparently she did not respond. The other four were always seen alone.

Occurrence of parasitic laying in 1994 and 1997

The parentage of added eggs cannot be resolved. However, of the viable offspring of known origin in 1994 ($N = 22$; see 'Paternity resolved' in Table 1), 23% ($N = 5$) were not consistent with the female and/or the male associated with the nest, thus being either parasitic or extra-pair progeny ('Alien/EPP' in Table 1). In none of the five cases where DNA analyses suggested a progeny unrelated to the social parents did we calculate the likelihood of: 1) quasi-parasitism (in which the male fertilises a non-attending female which then lays in the pair's nest), and 2) dump nesting or parasitic laying (in which both parents are outsiders), nor did we have behavioural observations to allow further classifications.

During 1997 when no disturbance occurred, we failed to detect evidence of parasitic laying and EPP based on DNA analyses, significantly differing from the frequency of Alien/EPP in Table 1 ($9.5\% \pm 14.2$; $U = 105.0$, $N_1 = 11$, $N_2 = 14$, $P = 0.032$). This finding was also in accordance with our behavioural observations and nest checks. In 1997 the prevalence of added eggs in the entire study colony was 12.3% (± 25.0), which is similar to the prevalence in controls in 1994 (11.4%; $U = 560.5$, $N_1 = 41$, $N_2 = 28$, $P > 1.0$).

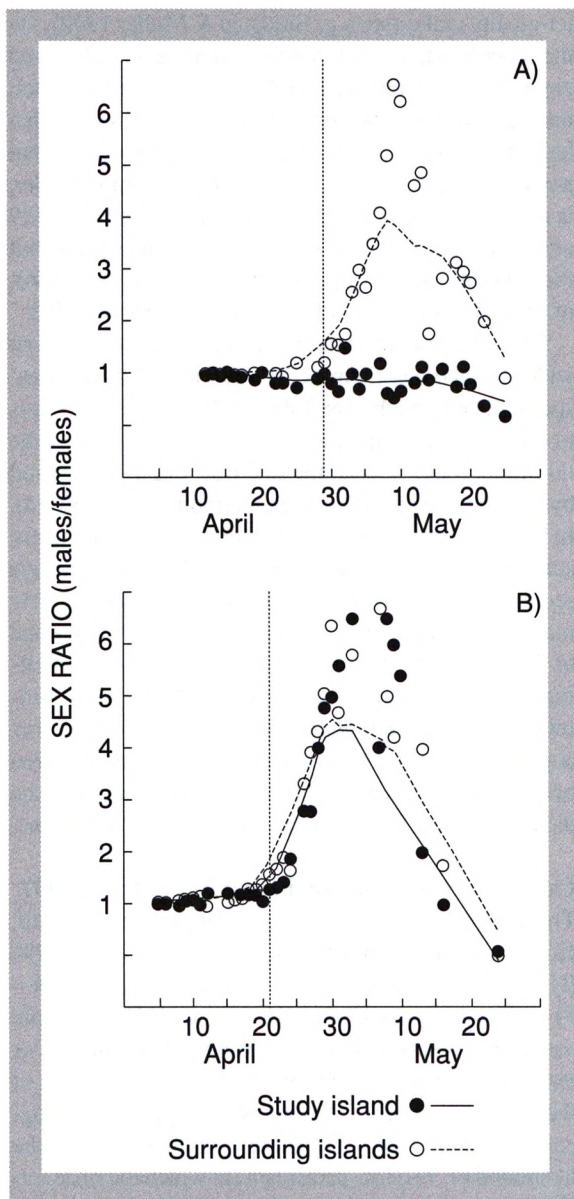


Figure 1. Seasonal development of the sex ratio (males:females) of eiders around the island where spring shooting was conducted in 1994 ('Study island') and in the surrounding archipelago of the study area ('Surrounding islands') during April-May 1994 (A) and 1997 (B). The vertical punctuated lines indicate start of laying (Date 0 = 1 April), and the lines give the smoothed (LOWESS) curves of the sex ratios in the respective years. Ratios remaining below 1 indicate a female bias.

Sex ratio changes in a spring-harvested population

The sex ratio became female-biased around the study islands when males had been removed, but became increasingly male-biased on the surrounding islands as the laying season progressed (Fig. 1). A male bias is nor-

mal after egg-laying begins, whereas the sex ratio at arrival on the nesting grounds in spring is 1:1 (see Fig. 1). Every year, there is a short-term male peak in abundance during peak initiation of incubation when 4-10 times more males are counted than females. Normally, as in 1997 (see Fig. 1), there are no differences in sex ratio between the study island and the rest of the Söderskär archipelago. However, in 1994, as males were being removed from the breeding stock of the study island, the sex ratio there became female-biased, thereby clearly deviating from that of the surrounding archipelago. Despite the close proximity of the two areas (approximately 50-700 m) and frequent interactions between birds at the feeding sites, there was no apparent immigration of males towards the waters immediately surrounding the study island and frequented by the widows.

Discussion

The lowered hatching success of widowed females in 1994 appears to have been caused by the elevated proportion of addled eggs and embryonic deaths, which was almost three times higher than under undisturbed conditions in 1997 and 2.5 times higher than in control females in 1994. The increase in incidence of addled eggs may be due either to the non-breeding widows choosing to lay parasitic (infertile/fertile) eggs in neighbours' nests and/or to a lower percentage of fertilised eggs in the nests of the widows, following removal of the mate. As the fertilisation status of the addled eggs cannot be resolved this question could not be addressed.

However, we observed no alien eggs in Söderskär nests in the undisturbed year 1997. Neither was there any sign of extra-pair progeny among the 14 clutches studied during 1997, and the proportion of addled eggs observed for control females in the experiment year (1994) did not vary significantly from the proportion in the non-experiment year (1997). Our results suggest that the mean frequency 9.5% of alien/EPP eggs and 37.7% of addled eggs/embryonic deaths found in 1994 do not represent normal proportions in this population. The proportions were significantly higher then, probably due to the disturbance effect of the spring shooting on the behaviour of individual females.

We found no evidence of rematings leading to full clutch fertilisation among widowed females that lost their initial male in the spring shooting. Neither was there any convincing evidence of extra males immigrating to the hunting area and courting the widows during the period of fertility prior to laying. No new permanent pair

bonds with neighbouring or 'free' males could be established. Instead, the rematings seemed to have taken the form of rapid mate replacement prior to egg laying (see Birkhead & Møller 1992). Thus, the possibility of remating seemed to be reduced by the female biased sex ratio caused by the harvesting. Contrary to the common belief (e.g. Kalchreuter & Aebischer 2001), male removal appeared to lower the fecundity of individual females, reducing the hatching success by an average of 40%.

It was noteworthy that clutch size remained 'normal', possibly due to increased dump nesting (non-attending widows laying infertile/fertile eggs in their neighbours' nests), EPP, or numbers of infertile eggs in the colony. There was no practical way to identify males that already had fertilised their female, as sperm viability appeared to vary greatly among individuals. Thus, it was not possible to selectively target males that were already 'freed' from mate guarding duties.

Although the remating potential of widows during 1994 seemed limited, it was only temporary. In 1995, the year after the experiment, all the widowed females that did not repair in 1994 ($N = 12$) returned to the study area. All but one had found a new mate and nine pairs bred. In 1996, 11 females returned of which nine had mated; the other two did not breed that year. These findings suggest that short-term effects (i.e. within the same breeding season) of mate removal may be more significant than long-term effects on eider behaviour and breeding success. The mean 7,000 males shot in Finland each spring represent 8% of the male population (the Åland Islands excluded). With the lowered fecundity of their females, roughly 4% of the offspring are lost due to spring shooting along the entire Finnish coast (Hario et al. 1995).

Evaluation of the potential effects of spring harvest on population trends requires knowledge of a wide range of population parameters, many of which are very difficult to estimate. In their model of possible effects of spring harvesting, Kokko et al. (1998) defined the cost of harvest as a corresponding loss in harvest opportunities in autumn due to lower recruitment. The cost will be sex specific as females and males play different roles in producing the recruitment population in summer. Despite being largely theoretical, their model gives the impression that the simple wisdom of "not to deduct from the capital" does hold (Kokko et al. 1998). In our study, we did not take into account the losses induced by non-breeding due to widowhood, which would further incur costs. The cost of killing a male in spring is highest if the probability that it was paired is high (as it was in our study), and if the breeding success of widows

remains low (below 50%, which is possible). Deduced from the model, it is then possible that spring hunting of males reduces the sustainable autumn bag more than its immediate benefits (by saving females) yield. An apparent conflict of interest in the Baltic Sea is that the harvests in spring and autumn are made by hunters in different countries. Spring hunting of male eiders in Finland affects the population that winters in Denmark where it is harvested in autumn. Accordingly, harvest practices in one country should be of immediate interest to other EU countries and considered, if hunting practices among countries are to be standardised.

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