ORIGINAL ARTICLES

Large-scale change in the sex ratio of a declining eider *Somateria mollissima* population

Aleksi Lehikoinen, Thomas Kjær Christensen, Markus Öst, Mikael Kilpi, Pertti Saurola & Aarne Vattulainen

The breeding potential of a monogamous animal population should be maximal during equal operational sex ratio, and empirical evidence suggests that the population-wide sex ratio may be linked to population density. We studied the sex ratio of eiders *Somateria mollissima* migrating into the Gulf of Finland, the Baltic Sea, in nine years during 1979-2005 (1979-1980, 1982-1983 and 2001-2005), and the sex ratio of birds collected by Danish hunters during 1982-2004. In two decades, the sex ratio during peak migration has reversed from female bias to male bias, and hunting statistics have shown a significantly increasing adult male bias. Also the proportion of juvenile males has shown a significant increase (Danish hunting statistics 1982-2004), which indicates either that the primary sex ratio of ducklings is exceedingly male biased, or that the mortality of female ducklings has increased. This shift in sex ratio is paralleled by a dramatic decrease in the Baltic eider population which started in the early 1990s. The proportion of juveniles in the hunting bag, an indicator of breeding success in the Baltic, significantly decreased during our study period. The sex ratio of migrating eiders showed seasonal fluctuations, the pattern of which has changed during the study period. Particularly the proportion of late-migrating females has decreased dramatically since the early 1980s, suggesting a declining influx of subadult females. Both the increased male bias and the decreased breeding success are likely to be linked with the population decline. A primary contributor to the shift in sex ratio and the declining trend in breeding success and population size is possibly differential mortality of the sexes during breeding, as the mortality of breeding females has increased sharply in the western Gulf of Finland, mainly due to predation by white-tailed sea eagles *Haliaeetus albicilla* and American minks *Mustela vison*, the former of which has recently increased in numbers. It is unlikely that differential winter mortality of the sexes can explain our results, as the wintering area of eiders from the Gulf of Finland has remained the same, and the Danish hunting bag reflects the existing sex ratio. Our study highlights the need for future empirical and theoretical work on the relationship between population sex ratio and population density.

Key words: Baltic Sea, biased sex ratio, differential mortality, eider, population decline, Somateria mollissima

Aleksi Lehikoinen & Markus Öst*, Bird Ecology Unit, Department of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland - e-mail addresses: aleksi.lehikoinen@helsinki.fi (Aleksi Lehikoinen); markus.ost@novia.fi (Markus Öst)

Thomas Kjær Christensen, National Environmental Research Institute, Department of Wildlife Ecology and Biodiversity, Denmark - e-mail: tk@dmu.dk

Mikael Kilpi, ARONIA Environment, Åbo Akademi University & Novia University of Applied Sciences, Raseborgsvägen 9, FI-10600 Ekenäs, Finland. - e-mail: mikael.kilpi@sydvast.fi

Pertti Saurola, Finnish Museum of Natural History, Finnish Bird Ringing Centre, P.O. Box 17, FI-00014 University of Helsinki, Finland - e-mail: pertti.saurola@helsinki.fi

Aarne Vattulainen, Hanko Bird Observatory, Vapaasataman tulliportti, FI-10900 Hanko, Finland - e-mail: aatu.vattulainen@hotmail.com

*Present address: ARONIA Coastal Zone Research Team, Åbo Akademi University & Novia University of Applied Sciences, Raseborgsvägen 9, FI-10600 Ekenäs, Finland

Corresponding author: Aleksi Lehikoinen

In monogamous animals, the breeding potential of a population is highest when the operational sex ratio is equal (e.g. Fisher 1930, Nunney 1999). An equal sex ratio in the population is usually derived from the Mendelian process of meiosis (Williams 1979) or frequency-dependent selection, since under a biased sex ratio, the production of the less numerous sex increases its fitness (Fisher 1930). Indeed, there are some well documented empirical examples where population decline has been coupled with either male bias (birds: Lens et al. 1998, Afton & Anderson 2001, Ewen et al. 2001; fish: Hanson et al. 2005; invertebrates: Dew & McConnaughey 2005) or female bias (birds: Flint et al. 2000, Alonso et al. 2005; fish: Martin-Smith & Vincent 2005; mammals: Solberg et al. 2002).

While there is broad consensus about the expected relationship between sex ratio and optimal breeding performance in monogamous animals, the relationship between population density and sex ratio is poorly understood. Evidence from polygynous, sexually dimorphic species indicates that high population density can result in increased mortality of males relative to females, with a concomitant female bias in the population (reviewed by Clutton-Brock et al. 1997). Helle et al. (1999) found that an increased male bias in the Finnish population of the polygynous capercaillie *Tetrao urogallus* was con-

nected with population decline, i.e. declining population density (see also Wegge 1980). Interestingly, analogous albeit inverse results were obtained in a rapidly expanding population of the socially monogamous snow goose *Anser caerulescens caerulescens*, in which a slight male bias shifted into a slight female bias, probably due to increased mortality of male goslings between hatching and fledging (Cooch et al. 1997).

In waterfowl, primary sex ratios at hatching seem close to unity (Swennen et al. 1979, Blums & Mednis 1996), but secondary sex ratios in Anatidae are often male biased (Blums & Mednis 1996). This may be linked to selective hunting of one sex or different mortality rates during the breeding season, as females may experience higher mortality than males in consequence of their larger breeding effort. In the eider *Somateria mollissima*, which is a socially monogamous duck, Kilpi et al. (2003) presented evidence for a significant male bias (56.6% males) in a large population segment breeding in the Gulf of Finland. Wintering eider populations are also male biased based on birds sampled through hunting (58-64% males; Noer et al. 1995). Since earlier assessments of adult sex ratios in the Baltic eiders seem to agree on a sex ratio close to unity (Almkvist et al. 1975, Hario et al. 2002), Kilpi et al. (2003) suggested that a substantial change in the overall sex ratio has occurred

during the 1990s. This hypothesised change in sex ratio coincides with a substantial decrease in the Baltic eider population (Desholm et al. 2002).

Eiders are also heavily hunted in their wintering areas in Denmark. In 2000, the total wintering population including the Baltic population (400,000 birds) was estimated to have halved since 1990 (Desholm et al. 2002), but the total bag in Denmark was still around 80,000 birds (Christensen 2005). The Finnish breeding population dropped by 46% during 1997-2006, and in the Gulf of Finland the population has declined by about 30% since the late 1980s (Hario & Rintala 2007). In face of a large population decline, all mortality components affecting the adult population are important, and the suggested increase in male sex-bias (Kilpi et al. 2003) may reflect large-scale changes in mortality patterns of eiders from the Gulf of Finland.

The first aim of our study was to investigate whether the sex ratio has really been biased towards males over a longer time period. If such a shift has occurred, we hypothesise, based on the general scheme of biased sex ratio by Blums & Mednis (1996), that an increased male bias may arise from 1) reduced female winter survival, 2) reduced female breeding survival, 3) differential hunting mortality or 4) an increasingly male biased primary sex ratio. In order to evaluate these alternatives, it is important to define the wintering area of focal birds through ringing recoveries, to assess whether some general conditions have changed over the last decades that could potentially cause differential winter mortality of the sexes, and to analyse whether the female mortality rate has increased on the breeding grounds.

Our second aim was to evaluate if the potential increase in male bias is negatively linked with breeding success, which was done by assessing long-term changes in the proportion of juveniles in the Danish hunting bag, an indicator of breeding success in the Baltic (cf. Noer et al. 1995, Lehikoinen et al. 2006b).

Assessing the sex ratio of potential breeders from a large population segment is laborious. Eiders are sexually dimorphic as to plumage characters, and migrate in small flocks, which are easily counted. The eastern-central part of the Gulf of Finland represents the edge of the breeding range of eiders, and thus birds passing into the Gulf are presumably associated with the breeding population. The sex ratio can be assessed by observing passing birds at the entrance of the Gulf, which acts as a major migration funnel (Kilpi et al. 2003).

Methods

Population trend of eiders in the Gulf of Finland

Hario & Selin (1986) and Hario & Rintala (2004, 2007) identify two contrasting phases of eider population dynamics in the Gulf of Finland. The first period (1969-1985) is a period of continuous increase, ending in a peak phase (late 1980s), followed by a second phase (1989-2004) of continuous decline.

Migration data

We counted migrating eiders within identification distance at Hanko Bird Observatory (HALIAS; 59°49'N, 22°54'E; Fig. 1) by means of spotting scopes (20-60x) every spring during 1979-2004 (excluding 1990). Birds in migratory flight were counted at the Observatory by 1-6 observers using standardised routines including a 4-hour standardised count beginning at sunrise (Lehikoinen & Vähätalo 2000).

At HALIAS, eiders pass close to the coastline during the spring, primarily in small flocks of maximum a few tens of birds that allow accurate recording of the sex ratio in the group based on plumage characteristics (Mullarney et al. 2001), separating adult males, subadult males and females. Migrating flocks were sexed in 1979-1980, 1982-1983 and 2001-2005. Subadult males constituted a very small proportion (< 2% of all sexed birds) and were not included in the analyses of population sex ratios.

All data are presented as sums for 5-day periods from 5 March onwards. Since the sex ratio is subject to seasonal changes during the migration period (Kilpi et al. 2003), we present the sex ratio for two different periods: 1) during the entire migration season and 2) during a 15-day period around peak migration. Because the timing of peak migration shows annual variation depending on the severity of the preceding winter, and the timing of the peak has advanced (Vähätalo et al. 2004, Lehikoinen et al. 2006b), we selected the peak period separately for each year. We selected the first clear 5-day migration peak and added 5 days before and after. This 15-day period thus formed our peak migration period. During 1979-1999, the median spring migration of eiders at HALIAS took place between 27 March and 19 April (Lehikoinen & Vähätalo 2000). Since the onset of egg laying and incubation may affect the movements of males in the local breeding population, which in turn can potentially bias our estimate of the sex ratio of migrating eiders, we
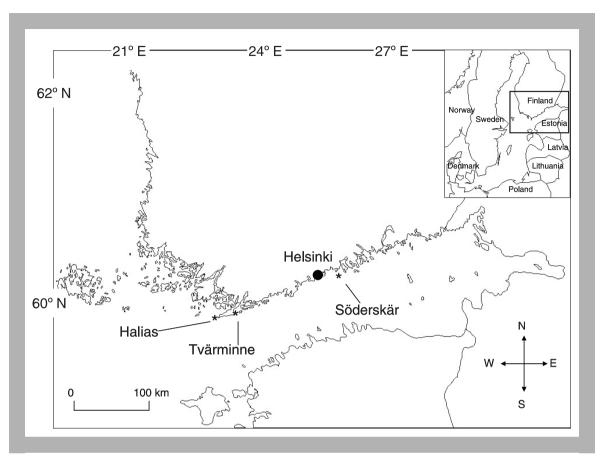
Figure 1. The northern Baltic Sea, including the Gulf of Finland and the study sites Hanko Bird Observatory (Halias) and Tvärminne. The easternmost large occurrence of eiders in the Baltic Sea (Söderskär) is shown on the map.

documented the phenology of egg laying in a population breeding nearby (see 'Female mortality and egg-laying phenology on the breeding grounds' below).

The sex ratio of migrating eiders in relation to time period (1980s vs 2000s) and season (see below) was analysed with logistic regression, and deviations from a 1:1 ratio were tested with two-way binomial proportion tests for multiple samples (Crawley 2002). The sampling unit in these analyses was the 5-day observation period. The dependent variable used in logistic regression was the proportion of males (logit link function), and the time period (categorical), season (prior to peak migration, peak migration, after peak migration; categorical), and their interaction were independent variables in the analysis. Significance testing was based on analysis of deviance, and to compensate for overdispersion as evidenced by the larger residual deviance as compared to the residual degrees of freedom, F-tests

rather than χ^2-tests were applied (Crawley 2002). In the binomial proportion tests, 5-day observation periods with expected cell frequencies of <5 were excluded from the analysis, as χ^2 approximation may not be appropriate for such small samples (Sokal & Rohlf 1995).

Ringing recoveries

We assessed the wintering area used by eiders marked in Finland east of $22°E$ (mainly on the northern coast of Gulf of Finland). In total, we used 853 recoveries of birds ringed during the increase phase in 1960-1985, and 262 recoveries of birds ringed after 1985. We compared the central points of the recoveries by using the two-sample randomisation test method of Lokki & Saurola (1987); this bootstrap method is based on Monte Carlo simulation, and it does not require any assumptions of the underlying distribution of the observations. We performed 2,000 bootstrap simulations in this study.

Sex and age ratio of hunted eiders

Data on the long-term dynamics of the sex-ratio and the ratio of juveniles to adults in the Baltic-Wadden Sea eider population was obtained from the Danish wing survey, in which ca 500-4,000 wings from hunter-shot eiders have been aged and sexed each year since 1982 (annual reports published by Danish Environmental Research Institute on http://www.dmu.dk). When calculating these ratios, we corrected the data for differences in hunting practices, e.g. a reduction in the length of the open hunting season in 2004/05. According to previous analyses, data from the Danish wing survey are unbiased with respect to the temporal and spatial occurrence of the wintering population of eiders in Danish waters (Noer et al. 1995, Christensen 2005).

Female mortality and egg-laying phenology on the breeding grounds

The number of breeding eiders has been monitored in the Tvärminne archipelago, Hanko, southwest Finland ($59°50'N$, $23°15'E$), during 1990-2006 (study site described in detail by Öst & Kilpi (2000) and Kilpi et al. (2001)). During monitoring, we noted all fresh carcasses of eider females (excluding the years 1992-1993, 1995 and 2000). To correct for annual variation in the size of the breeding population and our monitoring effort, the mortality rate of females was calculated by dividing the total number of dead females by the total number of counted nests (all nests, including destroyed or abandoned nests and nests in which the ducklings had already hatched were included), and we analysed temporal trends in mortality rate using Spearman rank correlation.

Timing of egg laying was measured to an accuracy of ± 1 day by egg floatation (Kilpi & Lindström 1997, Lehikoinen et al. 2006b).

Modelling of sex ratio

Using modelling, we investigated how big the differential mortality of the sexes should be to cause the observed adult sex ratio. We used the population development of white-tailed eagles *Haliaeetus albicilla* (number of breeding pairs in the Finnish archipelago; Stjernberg et al. 2005) as an estimate of increasing mortality (no monitoring data of American minks *Mustela vison* were available). The male model was:

$$NM_t = NM_{t-1}(a + b_1 E_{t-1}/(NM_{t-1} + NF_{t-1}) + \varepsilon_{t,1}) + Rm_t \quad (1),$$

in which the amount of male recruits was

$$RM_t = 0.2 \times NF_{t-2}R_{t-2}RS_{t-2} + 0.8 \times NF_{t-3}R_{t-3}RS_{t-3} \quad (2).$$

The corresponding female model was

$$NF_t = NF_{t-1}(a + b_2 E_{t-1}/(NM_{t-1} + NF_{t-1}) + \varepsilon_{t,2}) + RF_t \quad (3),$$

in which the amount of female recruits was

$$RF_t = 0.2 \times NF_{t-2}R_{t-2}(1\text{-}RS_{t-2}) + 0.8 \times NF_{t-3}R_{t-3}(1\text{-}RS_{t-3}) \quad (4).$$

NM and NF are the population sizes for males and females, respectively, with years indicated with subscripts (based on Figure 6A), a denotes the background adult survival similar for males and females, while b_1 and b_2 represent the increased mortality rate of adults due to eagles. The number of breeding eagle pairs in the Finnish archipelago, E, in year t, is indexed in proportion to the Finnish eider population size (eagles/eider population; Hario & Rintala 2007), and normalised so that the eagle situation in 2004 has value 1. Based on simplification of Cramp & Simmons (1977), 20% of the individuals recruit at the age of two and the rest at the age of three years. The recruitment rate, R, based on recruitment values from Hario & Rintala (2006), is assumed to steadily decline from 30% to 16% because the proportion of juveniles in the hunting bag has decreased by 47% in 1982-2004 (see Fig. 6C). RS is the proportion of male recruits based on Danish hunting bag statistics (see Fig. 6B), and ε_t is unknown noise in the model. Based on the above models, we can construct linear regression models:

$$Y_{t,1} = a + b_1 x_t + \varepsilon_{t,1} \quad (5)$$

$$Y_{t,2} = a + b_2 x_t + \varepsilon_{t,2} \quad (6),$$

where ε_t is proposed to be binormally distributed. The explanatory variable is

$$x_t = E_{t-1}/(NM_{t-1} + NF_{t-1}) \quad (7),$$

and the response of the regressions is survival (growth rate without recruitment):

$$Y_{t,1} = (NM_t\text{-}RM_t)/NM_{t-1} \quad (8)$$

$$Y_{t,2} = (NF_t\text{-}RF_t)/NF_{t-1} \quad (9)$$

Using multivariate regression, we modelled how strong the eagle predation would have to be to cause the observed bias in sex ratio. The survival of males
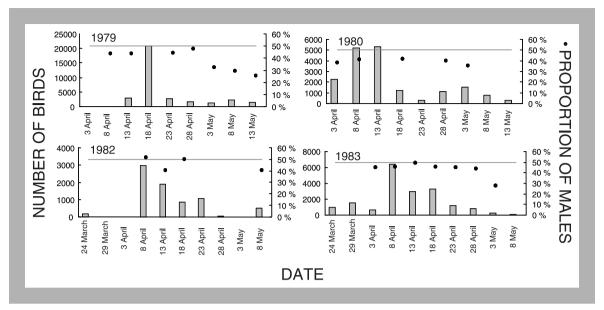
Figure 2. Number of spring migrating eiders (bars) and the proportion of males (●) in 5-day periods at HALIAS in 1979, 1980, 1982 and 1983. An equal 1:1 sex-ratio is indicated by the horizontal line. Dots are shown if the number of sexed individuals exceeded 20 individuals.

and females was assumed to be linearly related to the amount of white-tailed sea eagles (x_t = eagle pairs/eider index) with independent effects, while the background survival without eagles (intercept) was assumed to be similar in both sexes. The model was fitted using maximum likelihood, assuming a bivariate normal error distribution, and allowing for unknown covariation in the survival of both sexes (for more details about multinormal likelihood functions, see Dennis et al. (1998)). We calculated 95% confidence intervals for the parameters from the likelihood profiles (Hilborn & Mangel 1997). The modelling concerned years 1986-2004 when the population development of Finnish eiders is known (Hario & Rintala 2007).

Results

Sex ratio of eiders migrating into the Gulf of Finland

In 1979-1983, the overall sex ratio of migrants was female biased, significantly deviating from unity (Proportion test: $\chi^2_{26} = 429.8$, P < 0.001; Fig. 2, Table 1). During 2001-2005, however, the sex ratio was skewed towards males, again significantly deviating from an even sex ratio (Proportion test: $\chi^2_{64} = 2506.9$, P < 0.001; Fig. 3, see Table 1). Consequently, the sex ratio differed significantly between time periods, males comprising 42.2% (N = 16,830) and 58.7% (N = 202,200) of the total number of sexed birds in 1979-1983 and 2001-2005, respectively (Logistic re-

Table 1. Sex ratios of migrating eiders at the Hanko Bird Observatory during the whole migration period and during the peak migration period during 1979-1980, 1982-1983 and 2001-2005.

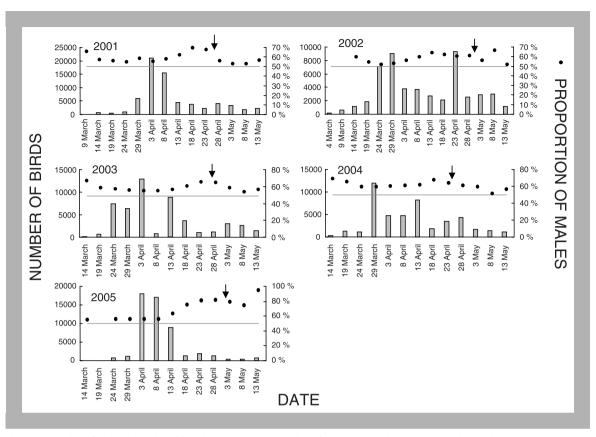| Year | During the whole migration season | | During the peak migration period | | |
	% males	N	% males	N	Period
1979	32.3	4372	44.2	955	11-25 April
1980	36.0	479	41.6	123	6-20 April
1982	48.1	1263	50.4	546	1-15 April
1983	45.8	10716	46.3	7484	1-15 April
2001	57.7	55090	56.6	32550	27 March-10 April
2002	57.5	43214	53.1	16071	22 March-5 April
2003	56.8	33838	55.2	12171	27 March-10 April
2004	60.6	35718	59.3	14296	27 March-10 April
2005	61.7	34340	55.9	20107	27 March-10 April

Figure 3. Number of spring migrating eiders (bars) and the proportion of males (●) in 5-day periods at HALIAS in 2001-2005. An equal 1:1 sex-ratio is indicated by the horizontal line. Dots are shown if the number of sexed individuals exceeded 20 individuals. Arrows show annual mean laying dates at Tvärminne, situated close to HALIAS, during 2001-2005.

gression: Δ Deviance = 1735.23, $F_{1,99}$ = 65.68, P < 0.001; see Figs. 2-3). The sex ratio also showed significant seasonal fluctuations during migration (Logistic regression: Δ Deviance = 190.23, $F_{2,97}$ = 3.60, P = 0.03; see Figs. 2-3). During the peak migration period, males comprised 46.3% in 1979-1983 and 55.9% in 2001-2005. Furthermore, the seasonal pattern of sex ratio fluctuation differed significantly between the time periods, as verified by the significant interaction between time period and season (Logistic regression: Δ Deviance = 302.29, $F_{2,95}$ = 5.72, P < 0.01). During 1979-1983, the sex ratio was most strongly female biased in the end of the season (see Fig. 2). This pattern differs from the sex ratio trends of the 2000s. During 2001-2005, the sex ratio was strongly male biased during early migration and male bias decreased during the peak migration. However, the male bias increased again after the peak, but decreased towards the end of the season as in the counts of 1979-1983. Following this drop in the proportion of males, when the sex ratio usually approached unity (except for 2005), the pro-

portion of males increased again, producing an undulating trend curve (see Fig. 3). To illustrate the timing of our sex ratio counts relative to the breeding phenology of the local breeding population, the mean laying dates at Tvärminne during 2001-2005 are also shown in Figure 3.

Wintering area
The wintering area of the eiders from the Gulf of Finland is given by gross recovery distribution maps for the two time intervals 1) prior to 1985 (increasing population; Fig. 4), and 2) since 1989 (decreasing population; Fig. 5). Of all ringing recoveries, 87.0% (N = 969) were hunted birds, 5.7% (N = 65) were killed by oil and 6.3% (N = 70) were caught from fish-nets.

The recovery data from these two periods show a slight but statistically significant difference in the distribution of recoveries (observed distance between means: 24.2 km; mean positions: 55°38'N, 10°65'E in 1969-1984, N = 674, and 55°25'N, 10°34'E in 1989-2004, N = 441; randomisation test for two-sample
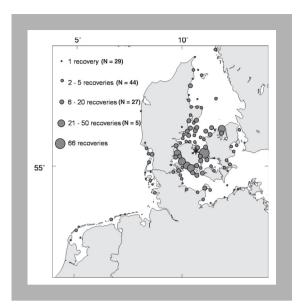
294

Figure 4. Ringing recoveries of eiders ringed in Finland (east of 22°E), found during the winters of 1969/70-1984/85 (December-February; N = 674), with a fuse radius of 10 km. The arithmetic mean coordinate of the recoveries is shown by the asterisk.
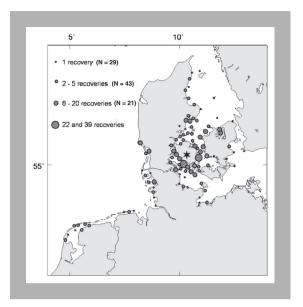

Figure 5. Ringing recoveries of eiders ringed in Finland (east of 22°E), found during the winters of 1989/90-2004/05 (December-February; N = 441), with a fuse radius of 10 km. The arithmetic mean coordinate of the recoveries is shown by the asterisk.

locations: $P < 0.002$). However, there are no indications that there have been marked and general changes in the winter distribution of eiders in the Baltic-Wadden Sea flyway population (*cf*. Desholm et al. 2002; see Figs. 4-5).

Trends in the Danish hunting bag
The proportion of males among eiders bagged in Danish waters during the winter hunting seasons 1982/83-2004/05 showed a significant increase in both adult (linear regression: $F_{1,21} = 33.9$, $r^2 = 0.62$, $P < 0.001$) and juvenile birds (linear regression: $F_{1,21} = 5.36$, $r^2 = 0.20$, $P = 0.03$; Fig. 6A-B). The increase in the proportion of males in the adult age class with time was significantly more pronounced than the corresponding increase in the proportion of males in the first-winter age class, as evidenced by the significant interaction term in an ANCOVA of the proportion of males, with age class (first-winter birds/adults) and time as main effects (ANCOVA: time × age class: $F_{1,42} = 5.20$, $P = 0.03$). Likewise, the proportion of juvenile birds in the bag significantly decreased during the same time period (Linear regression, $F_{1,21} = 11.4$, $r^2 = 0.35$, $P = 0.002$; see Fig. 6C).

Female breeding mortality
On average, 515 ± 114 (SD; range 377-711, N = 13 years) eider nests were checked annually during

1990-2006 at Tvärminne (excluding 1992-1993, 1995 and 2000). The mean annual mortality rate of adult females during the same period was $2.48 \pm 1.99\%$ (range: 0-6.52%). The annual mortality rate showed a significant positive trend with time ($r_s = 0.78$, N = 13, $P < 0.01$; Fig. 7). In 2004-2006, 17% (N = 9) of the carcasses showed marks of predation by white-tailed eagles (opened breast/belly, scalped head), 27% (N = 13) by American minks (bite marks on neck), while most of the carcasses (56%, N = 29) typically found close to eider nests were too old to determine the exact cause of death.

Predation model
The residuals of both the male and female regressions were normally distributed based on the Lilliefors test. The estimated survival of both males and females was 100% (95% CI: 87-112%). The estimated predation rate was 8% (95% CI: -23-38%) for males and 19% (95% CI: -3-42%) for females during the peak eagle population of 2004.

Discussion

Population development, sex ratio and breeding success during recent decades
Our study adds to the growing number of studies indicating that population declines are often asso-
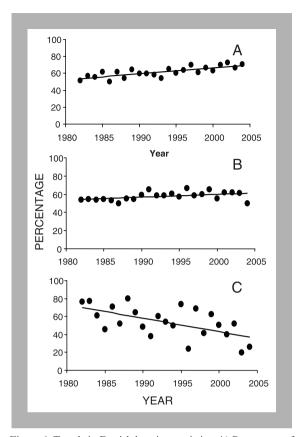
Figure 6. Trends in Danish hunting statistics. A) Percentage of males among adult eiders in the Danish hunting bag during the winters of 1982/83-2004/05 (1982 = winter 1982/83). B) Percentage of males among juvenile eiders in the Danish hunting bag during the winters of 1982/83-2004/05 (1982 = winter 1982/83). C) Percentage of juvenile eiders in the Danish hunting bag during the winters 1982/83-2004/05 (1982 = winter 1982/83). The lines show significant linear regression equations fitted to the data.
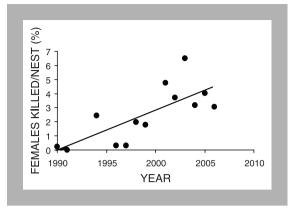

Figure 7. Number of fresh female carcasses divided by the total number of counted nests found during breeding population censuses at Tvärminne in 1990-2006. The line indicates the linear regression equation fitted to the data for illustrative purposes only.

ciated with dramatic changes in the sex ratio of a population, especially in populations with a male bias (e.g. Lens et al. 1998, Hall et al. 1999, Helle et al. 1999, Walters et al. 1999, Afton & Anderson 2001, Ewen et al. 2001, Steiffeten & Dale 2006). In the remainder of the discussion, we will evaluate plausible explanations for the observed change in sex ratio and its association with population decline.

Both migration and hunting data show that the proportion of females has decreased in the Baltic eider population during the last two decades. This decreasing proportion of females is already discernible among first-winter birds in the Danish hunting bag. However, the proportion of adult females has decreased more strongly than that of first-winter females, indicating that the main reason for this change in sex ratio is increased mortality of adult females, but that slight selection for male bias seem

to occur already prior to maturity (see Figs. 6A-B). This increased male bias prior to maturity may be due either to the primary production being male biased or increased mortality of juvenile females. Although the primary sex ratio of the Baltic breeding population is unknown, the latter alternative seems more likely, given the swift change in adult sex ratio, and sex ratios at hatching close to unity in other eider populations (Swennen et al. 1979).

Since clearly more males are hunted in the wintering areas, hunting is not likely to be the reason for this observed change in sex ratio, and hunting statistics primarily reflect the current sex ratio. This conclusion is also supported by our data showing that the mortality of breeding eider females has increased sharply in the western Gulf of Finland during the last 15 years (see Fig. 7). Our findings thus support Kilpi et al. (2003), who suggested that the reduced survival of breeding females has caused the male bias in the western Gulf of Finland. This reduced survival may be caused by higher breeding stress and predation of adult females. Our results show that carcasses often show signs of predation. Similar results were found in the northern Baltic proper in 2005, where 4.5% (70 out of 1,543) of the breeding females were found dead on the breeding islands, whereas only one dead male was found (Lehikoinen et al. 2006a). Thus our results support the hypothesis that the mortality of breeding females could be the key factor explaining the often found male bias in Anatidae populations (Blums & Mednis 1996).

The populations of the main predators of eiders, eagles and minks, have clearly increased during the

last decades in southern Finland (Kauhala 1996, Stjernberg et al. 2005). The mink invaded the archipelago already in the 1970s (Kauhala 1996), whereas the number of eagles have been increasing rapidly especially since the 1990s (Stjernberg et al. 2005). Kilpi & Öst (2002) showed that white-tailed sea eagles may have dramatic effects on local eider populations. However, females also face severe die-offs caused by pathogens and disease (e.g. avian cholera; Christensen et al. 1997, Franson et al. 2000, 2002, Desholm et al. 2002), but there are no indications that these die-offs would have become more common recently (Kilpi et al. 2003).

Our modelling produced unrealistic survival estimates and the results were non-significant, probably due to unrealistic parameterisation of the model given the coarse-grained data available. However, the important point is that a mere 11% increase in female mortality compared to that of males at the end of the study period could explain the observed change in the sex ratio. In recent years about 5% of breeding females have been found dead already in the middle of the incubation period, so female mortality is likely to be even higher at the end of the breeding season. Nevertheless, based on our model, eagle predation in itself does not explain the biased sex ratio, but other important factors such as minks and breeding stress may also have contributed to the increased female breeding mortality.

In addition to predation of breeding females, hunting could also partly explain the population decline of Baltic eiders. In particular, Danish winter hunting affects a notable proportion of the whole wintering population. Nevertheless, the number of hunters has declined, and the hunting bag in 2000 was only 63% of the top hunting bags of the 1980s and 1990s (Christensen 2005, Hario & Rintala 2006). Thus hunting in itself is not likely to explain the collapse of Baltic eiders.

Assessed by the Danish hunting bag data, the proportion of juveniles in the wintering areas has decreased during the last decades, which indicates that the breeding success has decreased. This finding also renders it unlikely that enhanced survival of male ducklings would be the reason for the increased male bias (*cf*. Cooch et al. 1997). It seems rather more likely that the survival of female offspring may have been impaired during the current population decline. The increased male bias in the population can negatively affect the breeding success already prior to laying. Excess males may only attempt extra-pair copulations with already paired females

(Steele et al. 2007), and these attempts can be harmful for females preparing for breeding. Harassments typically involving groups of males have become more common with increasing male bias (Hario et al. 2002, Steele et al. 2007).

The decrease in breeding success is probably affected by several interacting factors. The most likely explanation is that there are ever fewer successfully reproducing females in relation to males. A decreased proportion of successfully reproducing females, mainly due to increased mortality on the breeding grounds, will directly affect offspring production, provided that the average reproductive output of successfully breeding females has not increased. Increased predation risk in the breeding areas has significantly increased nest failure on islands depredated by eagles (Kilpi & Öst 2002). Based on data from our study site in the western Gulf of Finland, there is no trend in total fledgling production (fledged young per female) during the last 15 years (Lehikoinen et al. 2006b). However, this census method does not consider breeding females which have died before the young fledge. Thus increasing mortality of breeding females decreases the proportion of young produced per breeding attempt.

The winter distribution of ringing recoveries of Finnish eiders differed significantly between the population increase and decrease phases. However, in spite of statistical significance, we do not believe that a 24-km shift in the central point of the recoveries has large biological relevance to wintering eiders. Since most of the recoveries are based on hunted birds, the distribution of recoveries is strongly affected by the distribution of hunters. Based on the Danish hunting statistics, Noer et al. (1995) found that hunting intensity has been decreasing in eastern Denmark, around the Island of Sjælland, between 1970 and 1980s, which may explain the slight southwestwards shift in the central point of recoveries found in the present study. A similar change has, however, not occurred according to the data from the period 1980-2000 (Christensen 2005). Nevertheless, despite the minor shift in average location, eiders from the Gulf of Finland seem on the whole to have used the same general wintering areas since the 1970s.

Seasonal trends in sex ratio
Female waterfowl are extremely philopatric to breeding areas unlike males, which follow the females after mating in the wintering areas and guard

their mate until the incubation starts (Cooke et al. 1975, Greenwood 1980, Lessells 1985), and these differences are also well documented in eiders (Baillie & Milne 1989, Swennen 1990, Bustnes & Erikstad 1993, Tiedemann et al. 1999). The most accurate counts from the 2000s clearly demonstrate that the sex ratio changed continuously during the migration period. During the early migration period, the population was highly male biased, which indicates that unpaired males tend to migrate as early as possible to maximise the potential time for extra-pair copulation in the breeding areas. During the peak migration, the sex ratio was still male biased, but to a lesser degree than during the early migration. The sex ratio during the peak migration most likely represents the average adult sex ratio of the population, since the peak migration has an emphasis on the successfully breeding cohorts. After the peak migration, the sex ratio again shifted into more pronounced male bias. This may be caused by late-migrating unpaired males which are searching for mates or, alternatively, this may be a methodological artefact of the onset of incubation, which decreases the proportion of actively moving females in the local population at HALIAS. The former explanation seems more likely, however, since the timing of the second peak in male bias precedes the mean onset of egg-laying at Tvärminne close to HALIAS, where egg-laying typically begins in late April (Öst 1999, Hario & Öst 2002, Lehikoinen et al. 2006b; see Fig. 3).

After the second male peak, the proportion of males again decreased. The same trend was apparent also in 1979-1983, when the proportion of males was around 30-40% towards the end of the migration period. This increase in the proportion of females during the incubation period is likely due to migration of non-breeding subadult females, possible augmented with a hitherto unknown fraction of non-breeding adults (cf. Coulson 1984). This is supported by the fact that non-breeding subadult waterfowl migrate later than the breeding adults in spring (reviewed by Johnson et al. 1992). Eider females do not start breeding until they are at least two or three years old (Cramp & Simmons 1977). According to Cramp & Simmons (1977), immature eiders often spend their summer near wintering areas or intermediate maritime localities. This seems to apply to males in the Gulf of Finland, since only small numbers of subadult eider males are seen during spring migration at Hanko. Subadult males need not follow females until they reach maturity,

and may thus spend their summer elsewhere. However, the increase in the proportion of females at the end of the migration period suggests that considerable numbers of non-breeding subadult females return to their future breeding areas. Although non-tending females, including failed nesters, brood abandoners and an unknown fraction of non-breeders, are not tolerated within eider broods in our study area (Öst et al. 2003), females returning to their natal area may be involved in nest prospecting, during which it may also be important to monitor the breeding success of adult females (cf. Boulinier & Danchin 1997, Danchin et al. 1998). Thus it seems that the sex ratio, especially at the end of the migration, reflects the proportion of non-breeding subadults, and thereby the breeding success during the most recent years. Stronger female bias at the end of the migration period in 1979-1983 compared to that in 2001-2005 indicates weaker breeding success at the turn of the decade of 1990-2000 than during 1970-1980. This conclusion is also corroborated by the Danish hunting bag data, which indicate decreasing breeding success since the mid-1980s. The third male peak in the sex ratio already indicates the onset of autumn migration of males (Lehikoinen & Vähätalo 2000, Tiainen et al. 2001).

Stronger female than male philopatry could also explain differences in the sex ratio based on migration censuses and hunting bag data. According to migration counts, the sex ratio was clearly female biased in the early 1980s, but based on hunting statistics the sex ratio was already slightly male biased. Migration counts may underestimate the numbers of subadult non-breeding males and thus the total proportion of males, as it seems that mainly non-breeding females, but not males, return to their future breeding areas. On the contrary, the hunting statistics seem to give a relatively reliable estimate of the annual sex ratio of eiders. This is supported by recorded sex ratios of dead eiders found during a few larger oil spill accidents in the wintering areas since 1980s. The annual sex ratio of oil spill victims and that of eiders included in the hunting statistics has been similar (T.K. Christensen, unpubl. data).

To conclude, the Baltic eider population has become male biased during the last two decades and the proportion of males has been on the increase until recently. The increased male bias seems to be a reflection of the declining and poorly reproducing population of the Baltic Sea. The observed male bias, reduced breeding success and population

decline may all be linked to increased female breeding mortality. We strongly encourage further empirical and theoretical studies on the impact of hunting and predation and the role of decreased breeding success and sex biased mortality, to better understand the rapid changes occurring in the Baltic eider population.

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