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DOES SEX-SPECIFIC DUCKLING MORTALITY CONTRIBUTE TO MALE BIAS IN ADULT COMMON EIDERS?

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Abstract. Adult sex ratios of waterfowl often show male bias, usually explained by differential female mortality during breeding. However, the sex ratio among first-winter Common Eiders (*Somateria mollissima*) in Europe is already male biased; thus, the breeding mortality hypothesis cannot be the sole explanation for this phenomenon. To clarify when the observed male bias originally arises, we studied the sex ratio of hatched eider ducklings and the sex ratio of ducklings found dead prior to fledging in a wild and free-ranging population. The hatching sex ratio did not deviate from equal (50% females, $n = 418$). In contrast, the sex ratio of duckling carcasses was female biased (59%, $n = 118$), suggesting that survival of female ducklings is lower than that of males. Consequently, the adult-male bias found in many ducks may be established already during the early phases of life, despite an equal sex ratio at hatching.

Key words: Baltic Sea, Common Eider, duckling, sex-biased mortality, sex ratio.

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¿Contribuye la Mortalidad Vinculada al Sexo de los Pichones al Sesgo hacia los Machos en los Adultos de *Somateria mollisima*?

Resumen. La proporción de sexos en los adultos de especies de anseriformes frecuentemente exhibe un sesgo hacia los machos, lo que usualmente se explica por una mortalidad diferencial de las hembras durante la reproducción. Sin embargo, la proporción de sexos de los individuos de la especie *Somateria mollissima* ya está sesgada hacia los machos durante su primer invierno, por lo que la hipótesis de la mortalidad relacionada con la reproducción no puede ser la única explicación de este fenómeno. Para determinar el momento de aparición del sesgo hacia los machos, estudiamos la proporción de sexos en pichones recién eclosionados y en pichones encontrados muertos antes de emplumar en una población silvestre en la que los individuos se mueven libremente. La proporción de sexos al momento de la eclosión no se desvió significativamente de la igualdad (50% hembras, $n = 418$). En contraste, la proporción de sexos de los pichones muertos estuvo sesgada hacia las hembras (59%, $n = 118$), lo que sugiere que la supervivencia de los pichones hembra es menor que la de los pichones macho. En consecuencia, el sesgo hacia los adultos macho observado en muchos patos podría establecerse durante las primeras etapas de vida, a pesar de que al momento de la eclosión la proporción de sexos es igual.

There is strong theoretical support that equal sex ratio in animal populations is an evolutionarily stable strategy (Fisher 1930, Charnov 1982). However, the sex ratio of the adult population may not always be equal because of differential mortality of the sexes at various life stages. Whereas adult males are thought to suffer a higher mortality rate as a consequence of, for instance, inferior immunocompetence caused by testosterone (Folstad and Karter 1992), sex-specific mortality during early life, while common in birds and mammals (Clutton-Brock et al.1985, Røskaft and Slagsvold 1985, Griffiths 1992), remains poorly understood and controversial (reviewed by Bize et al. 2005). This controversy is especially apparent in birds, some studies of which have reported higher mortality of male nestlings, most notably because of greater food requirement, leaving them more vulnerable to starvation (Clutton-Brock et al. 1985, Arroyo 2002, Hipkiss et al. 2002). Other studies have reported higher mortality of female nestlings (Swennen et al. 1979, Bize et al. 2005), perhaps due to their lower competitiveness at acquiring food resources or because of their higher exposure to deleterious sex-linked recessive alleles, the effects of which may be most evident under food-deprived conditions (Bize et al. 2005).

According to sex allocation theory, females should adjust the sex ratio of their offspring and bias it toward the rarer sex, which has a greater rate of reproductive returns (Fisher 1930). Recent empirical findings have indeed confirmed that females of several bird species are capable of facultative sex ratio manipulation (Svensson and Nilsson 1996, Nager et al. 1999, Badyaev et al. 2002). In sexually dimorphic species, the reproductive success of one sex is more dependent than the other on the amount of parental resources, and hence, high-quality females typically produce a surplus of the bigger and more expensive sex, while low-quality females produce a surplus of the smaller sex (Kalmbach et al. 2001, Alonso-Alvarez and Velando 2003).

In waterfowl, most of which show seasonal monogamy, secondary sex ratios at hatching seem close to unity (Swennen et al. 1979, Blums and Mednis 1996, Cooch et al. 1997), whereas tertiary sex ratios are often male biased (Blums and Mednis 1996, Lehikoinen et al. 2008). This has been explained mainly by increased female mortality during the breeding season (Blums and Mednis 1996).

The Common Eider (*Somateria mollissima*) is a monogamous and sexually size-dimorphic species (males are approximately 15% heavier than females; Cramp and Simmons 1977). Eider populations on the Baltic Sea have faced a dramatic decline in breeding numbers and a rapidly increasing male bias in adult sex ratio (up to 71:29) during the past 10–15 years (Kilpi et al. 2003, Hario and Rintala 2006, Lehikoinen et al. 2008). Even though increased mortality of breeding females partly explains the increased male bias (Lehikoinen et al. 2008), some additional bias originates prior to maturity, since the sex ratio of juveniles in the wintering areas is already male biased (~57% males). This bias among juveniles has increased in parallel with the shift in adult sex ratio (Lehikoinen et al. 2008). Our goal was to clarify the timing of the presumed early male bias by determining the sex ratio at hatching and among naturally deceased prefledged ducklings, respectively. Although previous data suggest an even sex ratio at hatching among eiders (Swennen et al. 1979), female-biased secondary sex ratios would appear adaptive from a sex allocation theory perspective under the strongly male-biased operative sex ratio of the current Baltic breeding population.

METHODS

The study site, the Tvärminne Archipelago, is situated in the western Gulf of Finland, in the Baltic Sea (59°N, 23°E). For a detailed description of the study area, see Öst (1999) and Öst and Kilpi (2000). We estimated incubation stage by using the egg-floating method (Kilpi and Lindström 1997), and we used this information to visit nests to sample ducklings at their projected hatching dates (hatched ducklings stay in their nest only about 24 hours). We collected a few down feathers from each hatched or hatching duckling found in the nest for DNA analysis in 2003 and 2005–2006; ducklings were weighed to the nearest 1 g, and DNA samples were then stored in a freezer for later analysis. In 2005–2006, we also measured the tarsus length of each duckling with a vernier caliper to the nearest 0.1 mm. In 1996–2000, we determined the sex of ducklings found dead in the study area by the presence or absence of bulla tympaniformis of the syrinx (Broman 1942). The dead ducklings were found on average three weeks after the mean hatching date for that year (range: 1–6 weeks). We determined the sex of hatched ducklings by using the DNA test described by Griffiths et al. (1998).

STATISTICAL ANALYSIS

We performed two-tailed exact binomial tests to analyze whether the observed overall sex ratios of hatchlings and dead ducklings departed from parity. We investigated whether hatchling sex ratios showed annual variation by using logistic regression, with the proportion of males (logit link function) as the dependent variable, and year as a fixed effect. Significance testing was based on analysis of deviance, and since there was no apparent overdispersion (ratio of residual deviance to residual degrees of freedom < 2; Collett 1991), chi square tests were applied. Both hatchling weight and tarsus length fulfilled the assumptions of parametric tests (normally distributed variables, equal variance between the sexes). These data were analyzed with general linear mixed models (GLMM), using the restricted maximum-likelihood method, and executed in S-Plus Version 6.1 (Insightful Corporation, Seattle, Washington) using the lme algorithm (Pinheiro and Bates 1999). This method was chosen because it enables the fitting of random terms; in our case, the measurements of ducklings from the same brood are correlated, so we used a random effects

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TABLE 1. Annual sex ratio and the number of hatched ducklings in Common Eiders, Finland, in 2003 and 2005–2006, and *P*-values for exact binomial tests to analyze whether the observed sex ratio differed from parity.

Year	Male %	*n*	*P*
2003	50.0	128	1.00
2005	47.8	182	0.60
2006	51.9	108	0.77
Total	49.5	418	0.88

TABLE 2. The number of male and female Common Fider ducklings found in the Tvärminne Archipelago, finland, in 1996–2000.

Year	Males	Females	Female %
1996	10	6	37.5
1997	4	4	50.0
1998	4	8	66.7
1999	11	20	64.5
2000	19	32	62.7
Total	48	70	59.3

structure with ducklings nested within brood. In addition to analyzing sexual differences in our morphological measurements, we also included year and the interaction between year and sex as fixed effects in modeling to control for any year effects. We present numerical values as means ± SD, and a significance level of $P \leq 0.05$ was used throughout the analyses.

RESULTS

A total of 418 hatched ducklings were sexed, and the hatchling sex ratio in 2003 and 2005–2006 was close to equal (50% females, $n = 211$), not significantly deviating from a 50:50 ratio (Table 1). There were also no signs of annual variation in hatchling sex ratios (logistic regression, Δ deviance = 0.46, df = 2, $P = 0.79$), with the proportion of males ranging between 48% and 52% (Table 1).

The hatching weight of ducklings did not differ between males (74.7 ± 6.3 g, $n = 198$) and females (74.2 ± 5.7 g, $n = 201$; GLMM: $F_{1,78} = 2.1$, $P = 0.15$, $n = 122$ broods), and there were no year effects nor any interaction between sex and year (GLMM, both $P > 0.3$). Tarsus length of ducklings did not differ between males (33.7 ± 1.5 mm, $n = 138$) and females (33.6 ± 1.6 mm, $n = 144$; GLMM: $F_{1,53} = 3.5$, $P = 0.07$, $n = 89$ broods), and there were no year effects nor interaction between sex and year (GLMM, both $P > 0.1$).

In contrast to hatching sex ratio, the sex ratio of the ducklings found dead in 1996–2000 was significantly female biased (59% females, $n = 70$ out of 118; exact binomial test: $P = 0.05$). The annual variation in sex ratio of dead ducklings was not analyzed statistically due to small sample sizes (Table 2).

DISCUSSION

The sex ratio at hatching of Common Eiders did not differ from an even ratio. A plausible corollary of this result is that primary sex ratios at ovulation are also likely to be equal (van den Burg et al. 2002), even though we should emphasize that the sex ratio of unhatched eggs, representing only 8% ± 15% of all eggs in our sampled broods ($n = 141$), could still be biased (Cichon et al. 2005). Nonetheless, we can safely conclude that female eiders produce equal numbers of male and female hatchlings, despite the strongly male-biased adult sex ratio. Our finding of an equal sex ratio at hatching, previously documented in eiders by Swennen et al. (1979), seems consistent with sex allocation theory, considering that there were no significant sex differences in morphological measurements among hatchlings, which may reflect equal costs of resource allocation to males and females. Similar to our findings, Swennen et al. (1979) were also unable to find sex differences in hatchling body mass, despite notable sexual size-dimorphism in adult Common Eiders. Our argument of roughly equal resource costs of producing males and females is further strengthened by the fact that eider ducklings are self feeding and precocial, which contrasts with many studies of sex-specific resource allocation in sexually dimorphic species, where parents typically feed the young (Kalmbach et al. 2001, Alonso-Alvarez and Velando 2003). However, we cannot exclude the null hypothesis that an even hatchling sex ratio simply reflects the inability of females to facultatively adjust the sex ratio; the evidence for adaptive control of offspring sex in birds is scant and controversial (Blums and Mednis 1996).

There are also other adaptive explanations as to why females may favor an even sex ratio. Since the main contributor to the recent rapid change in the sex ratio of Baltic eiders is probably increased female mortality, either at the juvenile stage (this study) or during breeding (Lehikoinen et al. 2008), average female life span is currently shorter than that of males. However, despite their longer expected life span, per capita reproductive fitness of males has likely decreased due to an aggravated lack of partners for successful breeding, as indirectly indicated by intensified male-male competition during breeding (Steele et al. 2007). Thus, from the female perspective, the fitness benefits of producing long-lived males with highly skewed lifetime reproductive success may equal those of producing females, whose lifetime reproductive success shows less variance.

Perhaps our most important result was that the mortality of female ducklings was significantly higher than that of males. The female-biased mortality rate in ducklings (59%) is sufficient to explain the entire male surplus (approximately 57%) among first-winter birds in the wintering area (Lehikoinen et al. 2008). Thus, the sexual differences in mortality rates may level off once the ducklings fledge and gradually leave the study area (Swennen et al. 1979). Annual variation in the sex ratio of dead ducklings was not evaluated due to small sample size. However, we believe that this female bias in duckling mortality is characteristic of years with average or above-average duckling survival (1997–2000), since the only aberrant year with a slight male bias in duckling mortality, notwithstanding the low annual sample size, was 1996. This year represents an atypical year, since more than 90% of the ducklings died in an epidemic (Hollmén et al. 2002). Although hatching and post-mortem sex ratios were not determined during identical time periods (hatching: 2003–2006, post-mortem: 1996–2000), this discrepancy should not bias our results, considering only weak annual variation in annual hatching sex ratios and the continuing male bias in the adult sex ratio during the last decade (Lehikoinen et al. 2008). On a more general note, our result indicates that differential mortality among the sexes may occur prior to maturity, and this could contribute substantially to the observed male bias in waterfowl.

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Is it possible to generalize our findings of differential mortality between the sexes during early life, considering that the current sex ratio of adult Baltic Common Eiders has recently become increasingly skewed towards males (Kilpi et al. 2003, Lehikoinen et al. 2008), a condition that is perhaps atypical of waterfowl in general? The results of our study are closely paralleled by those of Swennen et al. (1979), from a Dutch Common Eider population in the Wadden Sea, in which the population-wide sex ratio at the time was, to the best of our knowledge, temporally stable and typical of eiders. Swennen et al. (1979) observed an equal sex ratio at hatching, whereas captive-reared ducklings showed a clearly female-biased mortality in their first four weeks of life. Our study is the first to document this female-biased duckling mortality in the wild.

Why do female eider ducklings suffer from higher mortality, considering that the larger sex is usually considered more vulnerable because of higher food requirements, and thus higher risks of starvation (Clutton-Brock et al. 1985, Røskaft and Slagsvold 1985, Griffiths 1992)? Although the opposite mortality pattern has been observed in birds of prey, it has been attributed to a competitive advantage of the larger sex (Arroyo 2002, Hipkiss et al. 2002), which is unlikely to apply to eiders. Overt aggression among eider ducklings is rare, and the spatial position of ducklings in crèches is uncorrelated with their weight or relative size at hatching (Öst and Bäck 2003); thus other mechanisms causing female-biased duckling mortality, operating after ducklings have left the nest, need to be considered.

One such common mechanism is heterozygote inferiority (underdominance). In birds females are heterogametic (ZW) and males are homogametic (WW). Thus, any harmful recessive gene alleles in the W chromosome (e.g., affecting duckling immune responses), will more often affect females than males (Trivers and Willard 1973, Myers 1978). In Common Eiders, pathogens may be linked with underdominance effects, as they constitute a major mortality factor and in some years may kill the majority of ducklings during their first three weeks of life (Hollmén 2002, Hollmén et al. 2002). Some avian studies have documented female-biased susceptibility to disease (Swennen et al. 1979) or parasites (Bize et al. 2005) at the juvenile stage.

An alternative hypothesis for female-biased mortality is that females may be physiologically less resistant to parasites or have higher predation vulnerability than males because of sex differences in demand of nutrients (Martins 2004, Bize et al. 2005). Although both sexes have similar body size and weight at hatching, males are the larger sex as adults. The size dimorphism likely appears during early duckling growth (Rodehutscord et al. 2006). In Zebra Finches (*Taeniopygia guttata*), the growth rate of female nestlings was lower under food-deprived conditions, whereas in males, growth rate was unaffected by food availability (Martins 2004). Common Eider crèches are hierarchically structured with respect to the relative spatial position of both females (Öst et al. 2007) and their young (Öst and Bäck 2003). Lower growth rate in female ducklings could thus lead to a lower ranking in crèches exposing them to higher predation risk, as indicated by the fact that in Common Eiders, relative body condition attained as ducklings within cohorts rather than absolute body condition, predicts subsequent survival and recruitment into the breeding population (Christensen 1999).

The relative importance of mechanisms underlying the higher mortality rate of female offspring is still unclear. Female ducklings may be more susceptible to infection, or they may be at a disadvantage when competing for food resources in the brood, although this latter alternative seems unlikely based on direct observation (Öst and Bäck 2003). The risk of starvation may also show interesting interactions with both predation risk and susceptibility to disease. For example, Swennen (1989) observed that, whereas gull predation pressure on eider ducklings showed little annual variation, predation success was strongly correlated with greater dispersion of ducklings when food availability was low. If female ducklings are more emaciated than male ducklings, they are more likely to occupy peripheral positions in the brood, rendering them more susceptible to gull attacks (Mendenhall and Milne 1985, Swennen 1989), and poor body condition is also linked with suppressed immunocompetence (reviewed by Gershwin et al. 1985).

In conclusion, a notable change in secondary sex ratio towards a male bias occurs during prefledging in Baltic Common Eiders. We argue that this finding may represent a more general phenomenon in Anatinae than previously believed; however, more experimental studies on sex-specific differences in duckling mortality patterns under natural conditions are urgently needed.

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