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The role of male mate-guarding in pre-laying Common Eiders *Somateria m. mollissima* in the northern Baltic Sea

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During the two weeks prior to laying on the Finnish breeding grounds in the central Gulf of Finland, Baltic Common Eider males escorted their females constantly. Towards the start of laying, males increased their vigilance by reducing their feeding rate from 70% to 0%. Concurrently, they lost weight. During the same time period, females kept their feeding rate constant at around 75%. Upon laying start, the initially even sex ratio of the population temporarily became male-biased when females disappeared to nests and emancipated males were still around. Yet, experimentally widowed females, feeding alone at this stage, were not harassed by the emancipated males and kept their clutch size and body weight similar to those of their previous nesting years. However, the hatching rate of the widows showed progressive decrease with the number of days from mate loss to laying. The viability of their mates' sperm varied from 1 to at least 20 days and this correlated with the proportion of viable eggs in their clutches. We suggest that male mate guarding is for fertilization assurance rather than for female protection during the pre-laying period at northern breeding grounds. – We did not observe any instance of paired males actively pursuing extra-pair copulations (EPC). We suggest that an inter-sexual conflict over copulations exists in our study population. Females may need repeated copulations because of variation in the duration of sperm viability. Males apparently rely on intense mate guarding as a means to safeguard paternity, resulting in a high rate of male refusals over mate solicitations (40%).

1. Introduction

Like most European waterfowl, the pair bonds of Common Eider *Somateria m. mollissima* form on the wintering grounds, and the male follows the homing female to her breeding grounds in spring (reviewed e.g. by Rohwer & Anderson 1998, Owen & Black 1990). Within the Baltic, Eiders overwinter in the Danish Straits, where birds from different Baltic populations mix (Noer 1991, Tiedemann & Noer 1998). The sex ratio on the wintering grounds is male-biased at 55–60% (Swennen *et al.* 1979, Noer *et al.* 1995). This ratio prevails in the migrating flocks to the Finnish sea territories in spring (Kilpi *et al.* 2003), but is levelled off upon arrival on the breeding islets where flocks brake into individual pairs clustering in ice-free water stretches at a sex ratio roughly 50:50 (Hario *et al.* 2002). When laying starts and females disappear to the nests, the sex ratio in waters temporarily turns to male-biased until males leave for moult migration.

Ice disappearance is among the most important proximate factors affecting laying start in the north (Nakashima 1986). Because its timing can vary by up to one month on the Finnish coast (Hario & Selin 1988), females need to wait for an unpredictable period between arrival and laying. Eiders are exceptional in that the female relies entirely on her body reserves for both laying and incubation (Milne 1976). Her reserves stem from the hyperphagia on the wintering grounds, during which period the male escorts her constantly. While waiting on the breeding grounds for the laying start she is continuously engaged in feeding, but this is for the maintenance only (Hario & Öst 2002).

Escorting males appear to be defending an area around their female. This behaviour has been interpreted as males protecting their mate from disturbance by other males while the female is feeding (Ashcroft 1976). This "protection" is thought to ultimately lead to improved nutritional condition of the laying hen (Ashcroft 1976, Milne 1976, Spurr & Milne 1976), possibly enhancing her breeding result as well (Black 1996). Other reasons suggested for this behaviour, called male mate guarding, are to prevent other males from copulating with her, to prevent interference with copulations, and to strengthen the pair bond (McKinney 1961, 1965).

Eiders are socially monogamous showing communal display but no forced copulation behaviour unlike many other waterfowl species (McKinney 1961, McKinney & Evarts 1997, own obs.). Paired females have never been observed soliciting extra-pair copulations (EPC) from extra-pair males – a feature common to all waterfowl (McKinney & Evarts 1997). As Eiders have no biparental care, males are considered to invest only in mate guarding and fertilization. The Common Eider is a game species for which spring harvest of males (or spring shooting) is still a common practice in many parts of the world. Premature breaking of a pair bond by widowing the female is claimed not to compromise female fecundity because of the facultative polygamy of females (Kalchreuter & Aebischer 2001). Widowed females are thought to receive sperm through copulations from emancipated males whose females already are incubating.

In this study, we aim to explore the validity of the "protection hypothesis" during the pre-laying period on the breeding grounds. We further discuss another function of male mate guarding, viz. the assurance of fertilization, whether costly for male or not.

2. Material and methods

2.1. Behavioural data

As a part of a long-term study on the reproductive biology of the Common Eider, the behaviour of paired females and their mates was followed daily from their arrival in April until the end of the egg laying period in May 1996–99 at the Söderskär Game Research Station in the central Gulf of Finland (60 °07' N, 25 °25' E). Behavioural observations were conducted from a lighthouse tower in 3-hour sessions, using binoculars (10×) or telescopes (20–40×). Pairs were chosen randomly by scanning the surrounding loafing sites and selecting the first pair entering the water after resting for at least 30 minutes. Each pair was monitored throughout one foraging cycle. A foraging cycle consisted of a feeding bout and a subsequent resting bout (see Guillemette *et al.* 1992), usually starting when the pair entered the water from a loafing spot and ending when the pair returned to one. Females had been colour ringed during previous study years. Due to the elevated lighthouse position in close proximity to the eiders, the colour ring combination of females were readily identifiable.

The males were not colour ringed, but in all cases the putative male of an established pair was the only male escorting the female constantly during the one-hour long feeding bouts and the intermittent resting bouts (see later), and the presence of the male did not provoke threatening behaviour from the female associated with him.

Feeding rate was measured as the percentage duration of diving activities during a feeding bout.

A feeding bout is the time devoted to active food intake during a foraging cycle, i. e. the time required to fill up the esophagus before entering a resting bout (see Guillemette *et al.* 1992). Eiders in the Gulf of Finland feed on mussels which they secure primarily by diving. There is no tide in the Baltic Sea, this prohibiting the easy exposure of mussel beds for surface feeding (for further details of behaviour sampling, see Hario & Öst 2002).

Solicitation and copulation rates are the number of solicitations and copulations per hour during one feeding bout. The numbers of within-pair and extra-pair activities were scored separately. The reactions of paired females and paired males towards the soliciting partner were noted (whether accepting or not).

All the measured variables were related to the proximity of the start of laying and start of incubation for each female, based on direct observations. Females usually lay a clutch of four to five eggs, the incubation starting upon laying the penultimate egg. Focal observations were made from 15 days before egg laying till 3 days after the start of laying.

2.2. Removal of the male protection

In our earlier study from 1994 investigating parentage of Common Eider clutches and productivity of widowed females, we removed by shooting the escorting male from 11 nesting females on the same study islands (Hario *et al.* 2002; license no. LUO 62/1994). This happened during the population laying period, starting upon the ice break-up and ending when the last females completed laying. The study simulated spring harvest of males. We use data obtained in this study of widowed breeders to explore the sperm storage duration of males. DNA was extracted from blood samples from females and from liver tissue samples from males and from vascular areas in egg shell membranes. Genotypes were obtained from each sample at three bi-parentally inherited microsatellite loci developed from eiders (Fields & Scribner 1997). We only use data of eight families where both alleles at each locus in the offspring were present in corresponding loci of the putative parents.

We calculated the sperm storage duration in days from the day of male removal to the day when the egg was laid (sperm age). Sperm age is known to affect egg viability in such a way that the older the sperm the earlier the embryo mortality (or no fertilization at all; Birkhead & Møller 1992). We define "sperm viability" as the proportion of viable eggs in a clutch relative to the sperm age.

The effect of widowing on female condition and productivity was measured as the percentage difference in widows' clutch size, hatching success and body weight between the experiment year and the mean of each individual's previous breeding career (1–12 years, median 10 years). This difference was related to the length of the period of being a widow (days from mate loss to laying; 0–26 days, median 6 days).

Measurements of reproductive performance of widows (laying dates, clutch size, 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 clutch were conducted according to the procedures described in Laurila and Hario (1988). The remaining members of the study population in 1994 (32 breeding females) were used as controls.

2.3. Male body condition

In order to establish a body condition index for males we divided the cube root of the body weight by the length of the radius and ulna (Saino *et al.* 1997) of seven males shot in the simulation study in 1994. Males were weighed immediately after collection to the nearest 10 g using a spring scale. Every male had their abdominal organs and the intestines intact after the rifle shot, making the comparison of weight indices feasible.

2.4. Statistical analyses

Individually known females and their males were used as the sampling unit in all statistical analyses. We used Pearson correlation to scrutinize the relationship between dependent variables (feeding rate, copulation rate) and independent variables (duration of the feeding bout, laying proximity). In the calculation of the correlation coefficients we used transformed data: log (y+1) transformation to account for zero counts in the dependent variables, and arcsine transformation for reaching normality in the proportional data. Spearman rank correlation was applied to data with small sample size (male body condition, sperm duration, widows' reproduction parameters). Regression was fitted to data to obtain coefficient of determination, R^2. Differences between means were tested with one-way ANOVA. The similarity of variances was tested with Bartlett's test; when found heteroscedastic, a non-parametric test was applied. Mean values are given with standard errors, tests are two-tailed, and significance level is set at 0.05. All analysis was done using SYSTAT 5.0 software package.

3. Results

A total of 102 hours of behavioural observation was obtained on 70 different pairs during 1996–99, comprising 70 foraging cycles (mean duration 87 ± 7 min). Results of the four study years were pooled as there were no between-year differences in the duration of the feeding bout (ANOVA, $F_{3,66} = 0.79$, $P = 0.50$), in the feeding rate of the females ($P = 0.07$) nor the males ($P = 0.06$), in the interaction rate ($P = 0.32$) nor in the copulation rate ($P = 0.45$).

The ice brake-up at Söderskär took place on 2 May 1996, 30 March 1997, 24 April 1998, and 10 April 1999. Females never entered the islets until the ice connection to the mainland had broken up. The median number of days they were waiting between arrival and laying commencement were 3, 11, 4 and 6 in 1996–99, respectively. These are minimum figures, as arrivals could escape notice due to adverse spotting conditions, inclement weather, concealments etc. The individual variation in time between arrival and laying was also large, ranging from 1 to 24 days. Population nesting synchrony, however, was roughly similar over the four years, with 50% of nests initiated within 8–10 days.

Prior to laying, the sex ratio in waters around the monitoring islets averaged 1.03 males per 1 female, i.e. 50.7% males (SD = 0.06, n = 19 counts averaging 97 individuals, range 49–142 ind.). There were no between-year differences in the ratio (ANOVA $F_{3,15} = 0.58$, $P = 0.64$). After the laying start, the sex ratio rapidly turned to male-biased being 1.91 already at the annual median laying start (SD = 0.18, n = 4 counts averaging 131 individuals, range 101–156) and ending up in 3–7 times more males than females prior to male departure.

3.1. Feeding rate

The feeding bout duration of females and their mate coincided highly significantly (Pearson $r = 0.996$, $n = 70$, $P < 0.0001$). The feeding rate (intensity) of females averaged 74.3 ± 2.7%, whereas it was only 24.3 ± 3.2% in males (Mann-Whitney $U = 3961.0$, $P < 0.001$). This was due to males significantly decreasing their feeding rate from 70% at the start of monitoring to 0% at the time of laying (Fig. 1, $r = 0.592$, $n = 70$, $P < 0.001$). This was reflected in concurrent decrease in male body weight index (Fig. 2, Spearman $r = -0.750$, $n = 7$, $P < 0.05$). No temporal trend was found in the feeding rate of females in relation to proximity of laying (Fig. 1, $r = 0.022$, ns, $n = 70$).

3.2. Effects of mate loss on female condition and productivity

The remating response of the widows of the 1994 experiment varied greatly. Four of the 11 nesting widows were actively seeking rapid mate replacement after mate loss, by copulating with alien males. Yet, they did not form permanent pair bonds with any of the new mates but were feeding alone and none of the resulting progeny in their broods was found to be sired by the last male. The seven widows that did not try to remate were never seen soliciting copulations. They, too, were always feeding alone. As a whole, males showed very little interest to the lone widows.

There seemed to be no progressive change in clutch size ($r_s = 0.229$, ns, $n = 11$) or body weight ($r_s = 0.236$, ns, $n = 11$) with the time span from mate loss to laying i.e. the time of being without male protection, whereas a tendency of a declining hatching rate was noted ($r_s = 0.473$, ns; Fig. 3). This was linked with the viability of the original male's sperm, as the share of viable eggs in a clutch tended to decrease with increasing age of the

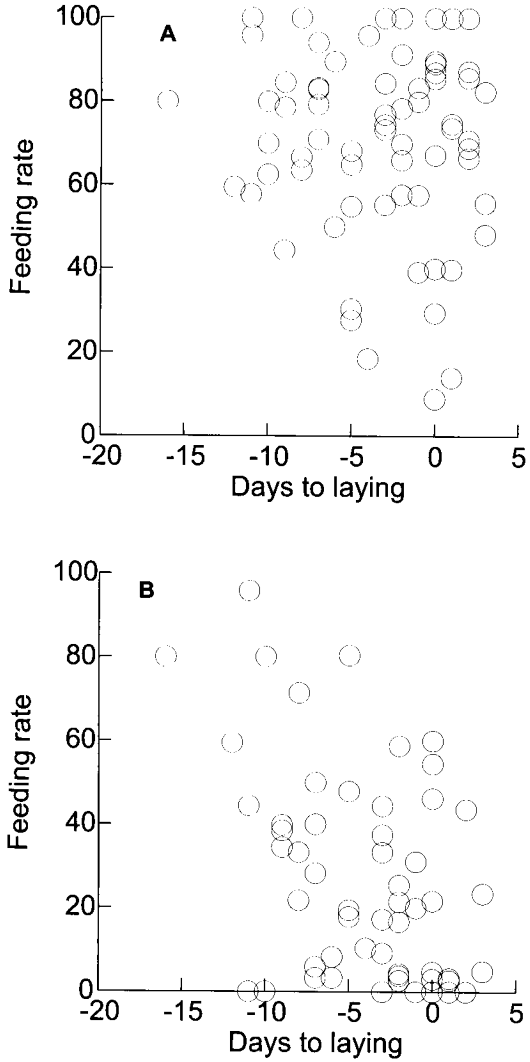

Fig. 1. Female feeding rate (time proportion of active foraging during a feeding bout) (A) and male feeding rate (B) in relation to the laying proximity of the pair. The day the first egg is laid is referred to as day 0, days before this are preceded by a minus sign, and days after by a plus sign.

sperm ($r_s = -0.578$, n = 8, $P < 0.1$; Fig. 3). The sperm viability ranged from at least 20 days to only one day (one male shot after copulation at the initiation of the egg laying; the first egg was then fathered by him, but the rest of the clutch remained unfertilized). Despite the comparatively high proportion of explainable variance (51%) in sperm age over fertilization rate in Fig. 3, there is a marked individual variation in sperm duration, too, as judged from the scatter in data points on day 7 and 1 in Fig. 3.

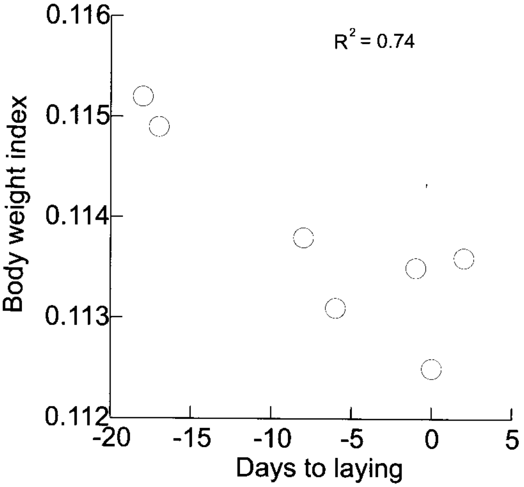

Fig. 2. Body weight index of males in relation to the laying proximity of their mates.

Also, compared to controls, the clutch size of widowed breeders (4.55 ± 0.69) was similar to that of controls (4.47 ± 0.76; one-way ANOVA, $F_{1,41}$ = 0.087, ns) whereas the hatching rate (53.2 ± 38.9%) was significantly lower than that of controls in 1994 (81.1 ± 31.3%; $F_{1,41} = 5.77$, $P = 0.042$; for details see Hario *et al.* 2002).

3.3. Solicitation and copulation rates

During 1996–99, we recorded 41 within-pair solicitations by the female, averaging 0.33 ± 0.06 per pair per hour (n = 70). We also recorded 14 non-mate solicitations by four single females on two paired males. All these took place prior to laying start of the population.

Of the 41 within-pair solicitations, 16 (39%) were refused by the male. Copulation rate averaged 0.23 ± 0.05. Due to the many zero counts, there was no relationship with laying proximity (r = –0.070; Fig. 4). Of the 14 non-mate solicitations, 11 were refused by the male (79%), the rates differing significantly ($\chi^2_1 = 6.531$, $P = 0.011$). One paired male refused six solicitations from three single females; he was not involved in any of the three EPCs recorded during this study. The other paired male first refused five solicitations from two females (one of which was among the three

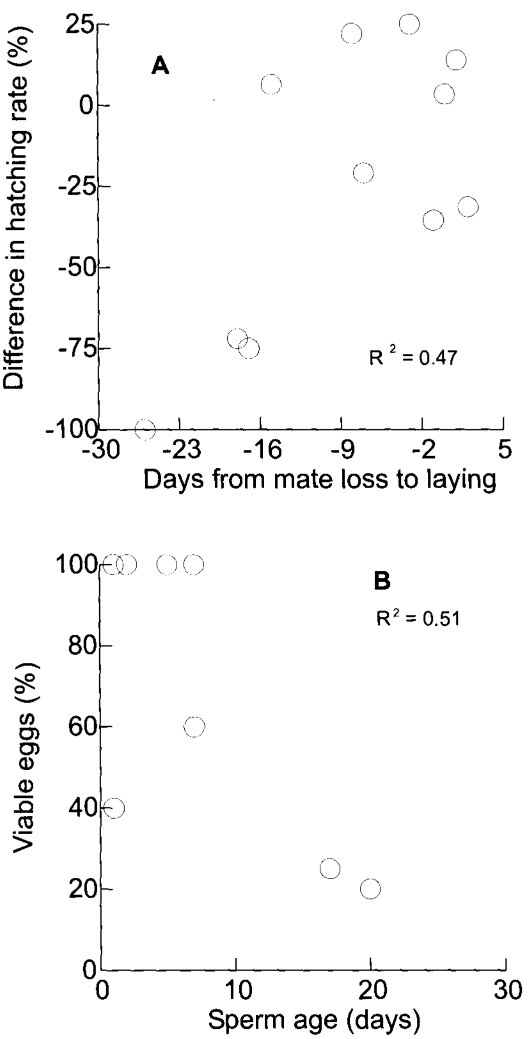

Fig. 3. The amount of difference in hatching rate (compared to the previous breeding career of the female) in relation to the number of days from mate loss to laying (A). The relationship between the sperm duration (i.e. the time span from the last copulation to the laying date) and the percentage amount of viable eggs in the clutch (B).

afore mentioned females soliciting the previous male), but was finally involved in all the three EPCs after persistent sexual harassment fy the females. He finally divorced his initial mate at the time she was laying her first egg and started to mate-guard the other one of the single females with whom he subsequently bred. It is noteworthy that no paired females were soliciting EPCs, and no EPC seemed to be male-initiated.

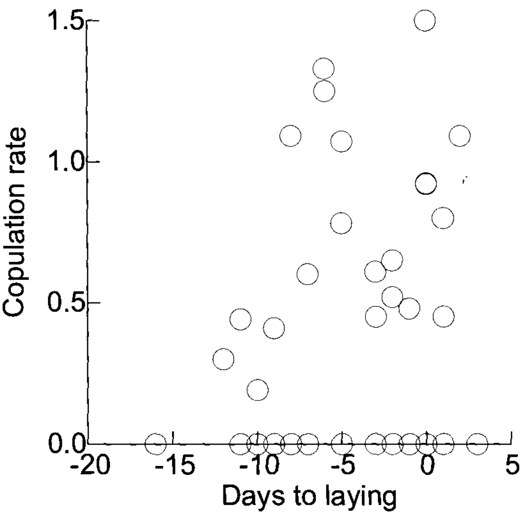

Fig. 4. Copulation rate (number of copulations per pair per hour during one feeding bout) in relation to the laying proximity of the pair.

4. Discussion

According to our results, the role of male mate guarding in Common Eiders on the northern breeding grounds seems to be for fertilization assurance rather than for protecting the female from disturbance by other males. Widowed females were fully capable of foraging without male protection, and their body weight and clutch size relative to their previous breeding careers showed no response to the time spent alone after mate loss. Yet, their hatching rate tended to decrease over time along with the length of time since last copulation. The sperm viability seemed unpredictable also in terms of individual variability.

The male mate guarding was very intense. The male was present for 99% of the feeding bout duration of the female. The feeding rate of the male remained significantly lower than that of the female and decreased towards the start of laying. Most males practically ceased feeding and only guarded the mate. However, when the female entered the resting bout, often the male did not. Instead, he started up-ending on the shoreline, hastely eating algae (*Cladophora* sp.) while keeping watch of the female. The palatability and nutrient value of algae are presumably poor compared to mussels, and this foraging tactic probably implies that he was significantly food-deprived. His meagre meals could not compensate for the energetic loss entailed during mate guarding, resulting in a loss of body weight.

There were no indications of paired males pursuing EPCs. Monogamy is the basic mating system in most waterfowl, and, despite the male-biased sex ratio in many species, there seems to be no incidences of true polygamy (McKinney & Evarts 1997). We did not witness any cases in which male-display would have led to an extra-pair copulation despite the fact that males readily gave the cooing call and movement (see McKinney 1961) when approaching alien females. Instead, there were three cases of female-initiated extra-pair copulations by single females.

In our spring hunting experiment, there were no instances of physical or sexual harassment by neighbouring males, and most females remained unpaired, others trying to re-mate. Yet, re-mating took the form of rapid mate replacement, and none of the new mates were proven to have fertilized any of the offspring. Males apparently rely on intense mate guarding as a means to safeguard paternity. The energetic cost of mate guarding may conflict with pursuing EPCs, while saving the male from being cuckolded himself. Thus, EPC or non-mate copulations do not seem a valid secondary reproductive strategy for Common Eider males. This is possibly linked with the high frequency of male refusals for female solicitations, too.

Females, on the other hand, seem to seek repeated copulations from their mate because one copulation may not be enough to fertilize her entire clutch. The viability of sperm was found to vary from 1 day to at least 20 days. Therefore, a single copulation does not guarantee fertilization of the entire clutch. A female could compensate for ejaculates of poor quality by soliciting copulations repeatedly (Hunter *et al.* 1993).

Apparently, from the female's point of view, male presence on the northern breeding grounds is mainly for the fertilization assurance. The timing of the ice break-up can vary by up to one month or more in the northern Baltic (Hario & Selin 1988). Arctic-nesting birds evolved to avoid mammalian predators by postponing laying until the ice connection to the mainland has broken up. This phenomenon of postponing laying according to ice disappearance is known to indigenous people of the Arctic (Nakashima 1986). Because of this unpredictability in timing of clutch initiation and in sperm viability, it would pay for the female to have her own mate with her throughout the pre-laying period, especially as there are no extra males arriving at north at the initial stage of breeding. Duration of the rapid follicle growth is 6 days plus 4–5 days for laying the clutch (Alisauskas & Ankney 1992). During this roughly 10-day period females may not need to invest much anymore in their breeding as they rely heavily on endogenous energy and protein in ovogenesis (Korschgen 1977). Most females spend only a few days on the breeding grounds before entering the laying stage. Exogenous sources may then be used for the maintenance mainly (Hario & Öst 2002), and male mate guarding does not contribute substantially to building the fat reserves of the female at that stage.

Our results demostrate that there can be a conflict over copulations between males and females in the Common Eider. For the male, mate guarding during the final 2–3 pre-laying weeks makes the final effort in securing paternity. He has already invested a great deal of his body reserves, and his diet changes with accompanying decreases in absorption rates of nutrients (Hilton *et al.* 2000) can occassionally contribute to intestinal disturbances and harmful effects of infections and various other pathogens (Hollmén *et al.* 2003). Mortalities of Eider males, peaking around the laying start, have been reported on several occasions along the northern breeding areas in the Baltic (Grenquist *et al.* 1971, Hollmén *et al.* 2003). The physical investment of Common Eider males during breeding has not been measured, but it could be analogous to seabirds with pronounced courtship feeding.

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Haahkakoiraan puolisonvartioinnin merkitys pohjoisilla pesimäalueilla

Haahkan sukupuolten lukusuhde on koirasenemmistöinen (55–60 %) talvehtimisalueilla ja kevätmuuttoparvissa pohjoiseen, mutta keskisen Suomenlahden pesimäpaikoille linnut saapuvat valmiiksi pariutuneita ja odottelevat rantavesissä kiintojään irtoamista tasaisessa lukukusuhteesssa 50:50. Koiraiden puolisonvartiointi on tuolloin erittäin tiivistä. Söderskärillä koiraat olivat naaraan vanavedessä 99 % ajasta kahden viikon ajan ennen munintaa. Koiraiden ravinnonotto (mitattuna tehollisen sukeltelun osuutena ruokailujaksosta) oli aluksi 70-prosenttista, mutta väheni munintaa kohden jatkuvasti siten, että koiraat eivät lopulta ruokailleet enää lainkaan vaan pelkästään vartioivat naarasta. Niiden oma kunto (mitattuna normeerattuna ruumiinpainona) aleni huomattavasti samalla kun naaraat pitivät ruokailutehokkuutensa tasaisena 75 prosentissa.

Sukupuolten lukusuhde kääntyi nopeasti koirasvaltaiseksi naaraiden aloitettua muninnan. Ennen sulkasatomuutolle lähtöä koiraita oli enimmillään vuosittain (1996–99) 3–7 kertaa enemmän pesimävesillä kuin naaraita. Munintakaudella 1994 tehdyssä kevätmetsästyskokeessa koiraat eivät kuitenkaan pyrkineet parisuhteen ulkopuoliseen paritteluun leskinaaraiden kanssa, joiden ruumiinpaino ja pesyekoko säilyivät muuttumattomina naaraiden aikaisempiin suorituksiin nähden. Niiden kuoriutumistulos kuitenkin heikkeni sitä enemmän, mitä pitempi aika oli kulunut koiraan poistamisesta. Tämä johtui hedelmöitymättömien munien ja/tai varhaisten sikiökuolemien osuuden kasvusta niiden pesyeissä. Koiraiden sperman elinkyky heikkeni ajan myötä ja lisäksi se vaihteli yksilöllisesti epäennustettavasti. Koiraiden puolisonvartioinnin merkityksenä näytti olevan paremminkin hedelmöitymisen varmistaminen kuin naaraan ruokailurauhan takaaminen.

Naaraat tarjoutuivat omalle koiraalleen keskimäärin kolmen tunnin välein ruokailujaksoilla, mutta koiraat hylkäsivät tarjouksista noin 40 %. Naaraat nähtävästi tarvitsevan oman koiraansa mukanaan pohjoiseen varmistaakseen hedelmöitymisensä epäennustettavana aikana jäänlähdöstä munintaan. Naaraat pyrkivät kiinteään parisuhteeseen ja siinä runsaisiin paritteluihin. Koiraalle puolestaan tiivis puolisonvartiointi saattaa olla parempi taktiikka kuin parittelujen runsaus. Puolisonvartiointi on ilmeisesti siinä määrin suuri kustannus, ettei koiraalla ole varaa riskeerata isyyttään pyrkimällä parisuhteen ulkopuolisiin paritteluihin, joiden yhteydessä se saattaa itse joutua aisankannattajaksi.

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