

The cost of mate guarding in the Common Eider

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A male biased sex ratio in Finnish Common Eiders (*Somateria mollissima*) results in unmated males interacting with eider pairs. We quantified the effects of mate guarding on other behaviors. Mated males spent less time feeding and performed fewer dives than unmated males in 2003, but not in 2004. A cold winter in 2003 implies that eiders arrived on the breeding grounds in poorer condition making feeding more critical. Mated males were dominant over unmated ones, winning two thirds of their aggressions. Mated males had fewer aggressive encounters but spent a greater proportion of their time in aggression. Mated males also seemed to spend extensive energy guarding their mate during infrequent but intensive “harassments”, lasting up to 165 minutes, in which 6 to 23 males chased one female. Harassments became more frequent later in the season, when females started incubating and the male bias was most pronounced. These harassments, and the fact that unmated males often approached other ducks, suggest that unmated males are trying to access females. Given the current trend of increasing male bias, both the cost of being mated and the fitness benefits of an alternative mating strategy may increase.



1. Introduction

Like many waterfowl, male Common Eiders (*Somateria mollissima*) do not participate in nest building, incubation, or parental care. Their fitness, thus, is largely dependent on fathering as many ducklings as possible and living to breed another year. Because they are a long lived species, with an estimated yearly survival close to 85% (Yoccoz *et al.* 2002), surviving is especially important in lifetime fitness (Clutton-Brock 1988,

Lindén & Møller 1989, Clark & Ydenberg 1990, Stearns & Kawecki 1994). Males can increase fitness during the breeding season by insuring that they are the father for all the eggs laid by their mate and perhaps by fathering other eggs through extra pair copulations. A further increase in fitness might result from protecting the female from interference during foraging in the period preceding incubation (e.g. Ashcroft 1976, Ankney & McInnes 1978). Female eiders are capital breeders, forming eggs out of their body reserves, and incubating

alone with no feeding during a 24–26 day incubation period (Goudie *et al.* 2000). Females lose up to 32–46% of their body weight during incubation (Korschgen 1977, Parker & Holm 1990) and their condition after the ducklings hatch affects their nest success (Hanssen *et al.* 2003) and their strategy for rearing the ducklings (Bustnes *et al.* 2002, Öst *et al.* 2003). This strategy in turn affects the survival prospects of the young (Bustnes & Erikstad 1991). Thus, entering incubation with maximum reserves is important.

Male eiders must guard their mates during preincubation to either prevent disturbance of the female by other males during feeding (Christensen 2000) or to prevent copulations with other males (Hario & Hollmén 2004). As a result, males may experience a negative energy balance during the breeding season; in some species, the magnitude of lipid reserves used by breeding males equals that of females (Hipes & Hepp 1995). The difficulty of mate guarding in eiders is accentuated by two factors. First, in some areas, the sex ratio is heavily male biased. In the Baltic Sea, migrating eiders are approximately 56% male (Kilpi *et al.* 2003), and this excess of males is maintained on the breeding grounds in the western Gulf of Finland, although a balanced sex ratio occurs further east (Hario & Hollmén 2004). Single males often approach paired ducks as well as any single females, so that females are near several males much of the time. Second, eiders typically dive to 10 m depth for their food, primarily benthic invertebrates (Goudie *et al.* 2000), and thus are below the surface for up to a minute (Ydenberg & Guillemette 1991). While in winter, the time on the surface is just long enough to recover from the lack of respiration during the dive (Ydenberg & Guillemette 1991), and digest the food (Guillemette *et al.* 1992); during spring, the need to guard the female may result in fewer and shorter dives. Unmated males, on the other hand, are not constrained in the length or number of their dives, and may enjoy a nutritional benefit by not having to guard a female. This benefit could lead to increased survival.

Body condition of eider females following incubation is significantly negatively correlated with the severity of the preceding winter as indicated by the Northern Atlantic Oscillation index (NAO, Lehikoinen *et al.* 2006). This is presumably true for males as well and indicates that eiders

cannot consume enough food on the breeding grounds to make up for a severe winter. The preferred food in the Baltic, blue mussel (*Mytilus edulis*), is energetically marginal because of its small size (Öst & Kilpi 1997), the high shell content (Bustnes 1998), and the need to crush the hard shells and to heat the food up to body temperature. Body condition and survival of eiders is further compromised by periodic outbreaks of disease and parasites (Hollmén *et al.* 1999, 2000, 2002).

We conducted this study to assess whether there was a benefit to unmated males that might partially offset the loss of fitness due to not breeding. We reasoned that mated male eiders would be able to forage less than unmated males because of the need to guard their females. We predicted that they would spend less time diving and have shorter dives. Also, mated males should spend more time being vigilant, actively looking around for rival males.

2. Methods

Observations were carried out on a well studied population of eiders in the archipelago of the western Gulf of Finland of the Baltic Sea, in the vicinity of the Tvärminne Zoological Station (59° 50' N, 23° 15' E), near Hanko, Finland.

We used scan samples of focal males to quantify behavior. Observations were made using a spotting scope from elevated positions on islands near foraging eiders. From each observation point in 2004, we first recorded sex ratio of all eiders visible and concurrently noted the number of harassment groups, groups of several males chasing one female. For scan samples, conducted in both 2003 and 2004, one male, either mated or unmated, was selected at random from those visible. Although many of the females in this population are color ringed, the males are not, but pairs generally stayed apart from big groups and it was easy to follow an individual male. Behavior of the focal male was recorded at 30 second intervals for an hour. Behaviors that we recorded included feeding, flying, swimming, walking, preening, aggression, resting, and vigilance. As we were interested primarily in foraging versus mate guarding, and because flying and walking were rare behaviors, we pooled flying, walking, swimming, and vigilance

into one category that represents behavior in which mate guarding is possible. This pooling procedure also reduced the effect of potential observer bias, since swimming and vigilance especially are behaviors subject to interpretation problems. We also pooled resting and preening, as these are both behaviors in which the bird is presumably paying less attention to its surroundings. Feeding was reported when the male was either under water, dabbling (rare), or handling food on the surface. Aggression involved chasing another duck or pecking at it. In addition to these instantaneous scan samples, we continuously recorded all instances where a focal male approached or was approached by another eider, all aggressive encounters and the outcome of each, and the number and duration of each dive, even if they did not occur on the 30 second point.

Observations were divided into a preincubation period when few if any females were on nests, and an incubation period during which more and more females were on nests skewing the observable sex ratio further towards males. The exact dates of these observation periods were chosen so as to match the spring phenology of each study year. Preincubation observations were made from 18 to 24 April in 2003, and 7 to 21 April in 2004. Observations during incubation were made 6 to 17 May in 2003 and 25 to 30 April in 2004. Males sometimes swam out of sight or joined a large group in which distinguishing individuals was impossible, effectively terminating the string of observations. We excluded observation strings with less than 10 minutes from the analysis. We scanned 96 males in 2003 and 71 in 2004. The overall study population includes about 3,000 adult eiders, and observation sites were scattered throughout the study area, looking different directions from at least 10 different islands, so that repeated observations of the same individual were unlikely.

Because the scan data were proportions, they were arcsine transformed (Sokal & Rohlf 1995). Resulting variables were approximately normally distributed (Shapiro Wilk's test). A multivariate analysis of variance (MANOVA) was performed on the four transformed variables: resting or preening, vigilant or moving, aggression, and feeding. Multivariate tests are more powerful when dependent variables are intercorrelated (Zar

1999), as is the case for time budget data. All interactions among independent variables (year, mated status [mated, unmated], and period [incubation or preincubation]) were initially included, but because period was not significant, either alone or in its interactions with the other variables, it was removed from the analysis. The multivariate analysis was followed by univariate tests on the transformed variables.

Three of the variables recorded continuously, aggressive interactions per hour, approaches per hour, and dives per hour, were not normally distributed, so we analyzed these with the non-parametric Scheirer-Ray-Hare extension of the Kruskal Wallis test (Sokal & Rohlf 1995), which is a non-parametric analog of ANOVA based on ranked variates with three independent factors (year, mated status, and period) plus their interactions. Average dive length was normally distributed and was analyzed with ANOVA with year, mated status, period, and their interactions as independent variables. Sex ratio and the number of harassments per female as counted at the beginning of scans in 2004 were both normally distributed and were analyzed with linear regression.

The outcome of aggressive encounters (wins, losses) was analyzed with logistic regression. The dependent variable used in logistic regression was the proportion of wins of all aggressive encounters (logit link function), and the independent categorical variables were year, mated status, period, and the interaction between mated status and period. Significance testing was based on analysis of deviance, and to compensate for obvious overdispersion judged by the larger residual deviance as compared to the residual degrees of freedom (ratio 2.76), F-tests rather than chi-square tests were applied (Crawley 2002). We also present odds ratios and their associated 95% confidence intervals. The confidence limits of the odds ratios were adjusted for overdispersion by multiplying the standard errors of the parameter estimates by the square root of the ratio of residual deviance to the residual degrees of freedom (Collett 1991).

3. Results

The multivariate MANOVA revealed significant differences in the overall time activity budgets for

mated status and the interaction between year and mated status (Pillai's trace = 0.15, $F_{4,160} = 7.18$, $P < 0.001$ for mated status, Pillai's trace = 0.063, $F_{4,160} = 2.69$, $P = 0.03$ for status \times year). In the univariate analyses, there was no consistent difference between mated and unmated male eiders in the proportion of time spent feeding (Two-way ANOVA: $F_{1,163} = 0.039$, $P = 0.85$). However, the interaction between year and mated status was significant ($F_{1,163} = 4.59$, $P = 0.03$). Unmated males fed more than mated males in 2003, but less in 2004 (Fig. 1 a). Similarly, unmated males dove more per hour than mated males in 2003 and less in 2004 (Scheirer-Ray-Hare test on interaction male status \times year: $H_{1,166} = 5.98$, $P = 0.01$, Fig. 1 b). The average length of a dive was not significantly different between the two mated classes ($F_{1,79} = 0.76$, $P = 0.39$), although there was a significant interaction between mated status and period ($F_{1,79} = 6.00$, $P = 0.02$). Mated males had shorter dives only after incubation had begun (Fig. 1 c). During this period, the males classified as unmated included males with mates that were incubating, and the proportion of males had increased (see Fig. 3).

Mated males did not differ from unmated males in the proportion of time spent resting or preening (Two-way ANOVA: $F_{1,163} = 1.69$, $P = 0.20$), or time spent vigilant, including moving ($F_{1,163} = 2.85$, $P = 0.09$). The interactions between year and mated status were also non significant for these two variables ($P > 0.4$).

Unmated males were clearly subordinate in aggressive encounters to mated males. Our logistic regression model showed that mated males had a significantly higher probability of winning aggressive encounters compared to unmated males (Logistic regression: Δ Deviance = 273.42, $F_{1,119} = 102.32$, $P < 0.001$, Fig. 2 a); the odds of winning an encounter was on average 3.27 times higher for mated males (95% adjusted CI of odds ratio: 2.39–4.48). Focal males, irrespective of mating status, were also generally more inclined to win aggressive encounters after the onset of incubation (Logistic regression: Δ Deviance = 35.94, $F_{1,118} = 13.45$, $P < 0.001$, Fig. 2 a); the odds of winning an encounter was on average 1.83 times higher than during pre-incubation (95% adjusted CI of odds ratio: 1.33–2.52). There was also a significant interaction between mated status and period: although the probability of winning encounters was

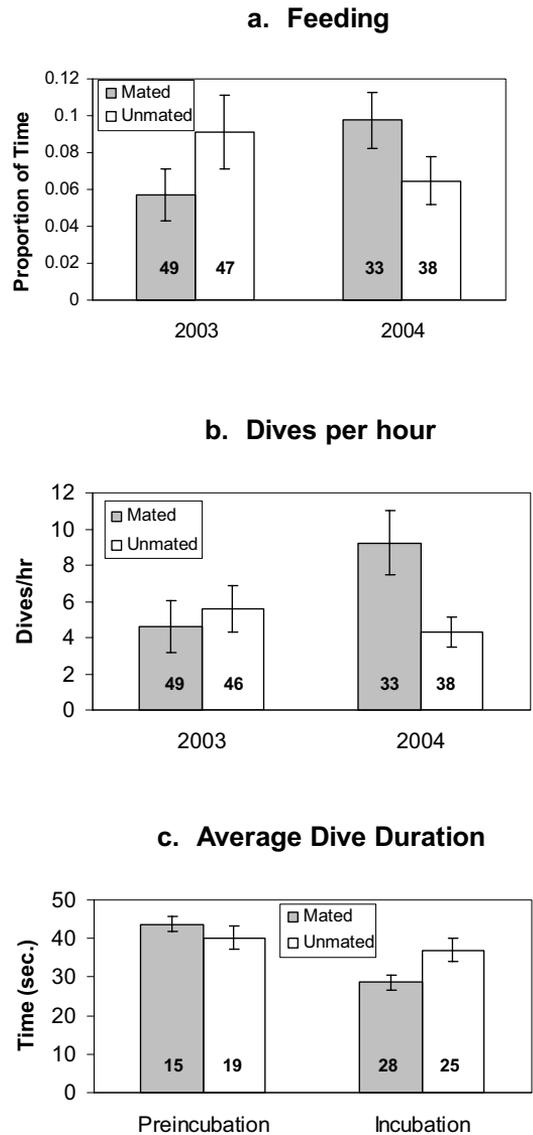


Fig. 1. Feeding behavior including (a.) proportion of time mated and unmated eiders spent feeding during scan samples, (b.) number of dives of mated and unmated males, and (c.) the duration of dives of mated and unmated males. Error bars are standard errors and sample size is shown within the bars.

higher for mated males throughout the season, the odds of winning was less skewed towards mated males after the onset of incubation (Logistic regression: Δ Deviance = 10.33, $F_{1,117} = 3.87$, $P = 0.05$, Fig. 2a). There were no annual differences in the outcome of aggressions (Logistic regression: Δ Deviance = 7.86, $F_{1,120} = 2.94$, $P = 0.09$).

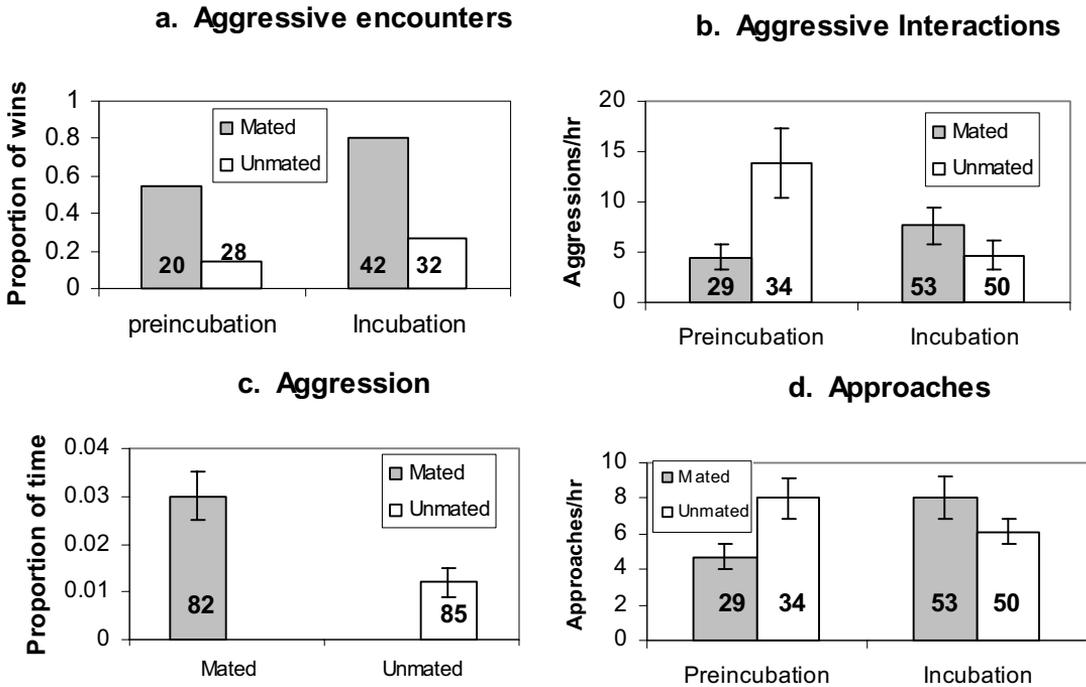


Fig. 2. Aggressive behavior of focal males, including (a.) the proportion of time a focal male won an aggressive encounter, (b.) the number of individual aggressive encounters of focal males, (c.) the proportion of time spent in aggression from scan samples, and (d.) the number of times a focal male approached or was approached by another eider. Error bars are standard errors and sample size is shown within the bars.

Unmated males also had more aggressive encounters per hour than mated males during the preincubation period, but not during the incubation period (when the unmated category included males mated to females on nests) (Scheirer-Ray-Hare test on interaction male type \times period: $H_{1,159} = 8.859$, $P = 0.003$, Fig. 2 b). On the other hand, scan data showed that mated males spent more of their time in aggressive encounters than unmated males ($F_{1,163} = 20.39$, $P < 0.001$, Fig. 2 c). Note, however that the proportion of time in aggression was small, in the range of 1–3%. The number of times an unmated male approached or was approached by another eider showed a similar pattern to the aggression data: unmated males had more approaches during pre-incubation, but less during incubation (Scheirer-Ray-Hare test on interaction male type \times period: $H_{1,159} = 4.76$, $P = 0.03$, Fig. 2 d).

In addition to one-on-one encounters between eiders, we also saw groups of 6–23 males following and chasing a mated pair. During these “harassment” episodes, the presumed mated male was nearly continuously trying to stay near the female,

causing him to spend most of his time chasing off the other males. These bouts were highly variable in length and intensity, lasting from 5 to 165 minutes, and both the individual male members and group size also varied considerably. It was apparent that the mated male spent a great deal of energy and was not able to forage for the entire time. These harassment groups occurred infrequently enough so that they were rarely seen during scan sampling, but they became more frequent later in the incubation period, as females on nests biased the sex ratio towards males (Fig. 3). Therefore they represented a much greater cost for males mated to females who nested late in the season.

4. Discussion

The benefit to unmated males of having more time for feeding occurred in only one year of our study. Unmated males spent more time feeding compared to mated males in 2003, but not in 2004. This result was consistent in two analyses: scan samples

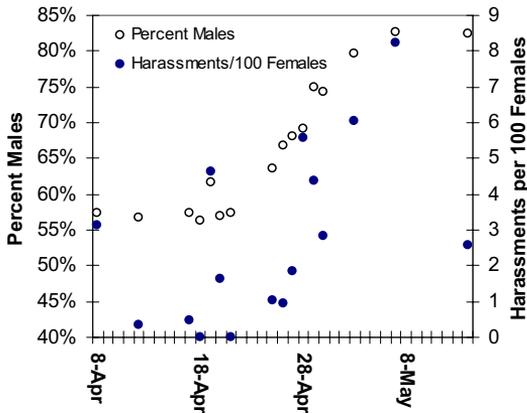


Fig. 3. Sex ratio (percentage of eiders that were males) and number of harassment groups visible per 100 females during spring 2004. Harassments were counted during an initial scan of all eiders visible. Sex ratio is a significant predictor of the number of observed harassments per 100 females (Linear regression: Number of harassments per 100 females = $3.72 \times$ proportion of males $- 2.84$, $F_{1,15} = 13.86$, $P = 0.002$, $R^2 = 0.50$).

showing proportion of time in different behaviors and the number of dives per hour, emphasizing that the result shows a real difference between the years. Mated males had shorter dives during the incubation period, when more unmated males were available, suggesting that dive length may have been constrained by needing to be on the surface to guard their mate. The amount of food available was not a greater constraint in 2003 as annual sampling of blue mussels, the most common food item for eiders, showed a 21 percent reduction between 2003 and 2004 with a sharper reduction (65 percent) near the center of the study area (Mats Westerborn, unpublished data). However, the severity of the preceding winter affects the condition of breeding females (Lehikoinen *et al.* 2006), and thus probably condition of males. Since winter 2002/2003 was much colder than winter 2003/2004 (A. Lehikoinen, unpublished data), males were likely in weaker condition during spring 2003 than in 2004 and the time spent feeding may have been more critical. Furthermore, in 2003, an epidemic swept through the study population resulting in at least 100 deaths, based on carcasses we found on the edges of islands. The causative agent is unknown but a similar episode in 1998 at Utö, Archipelago Sea, killed thousands of males

and also females (Hollmén *et al.* 2003). Carcasses we collected were emaciated, indicating that the disease, combined with a cold winter, may have affected eiders' condition. Thus, the benefit of being unmated may be important in replenishing reserves in seasons in which there are other stresses on body condition.

Mated males are likely to expend more energy in aggressive encounters than unmated males. Although continuous data indicated that mated males had fewer aggressive encounters per hour during the preincubation period (Fig. 2 b), the overall scan data showed more time was spent on aggression than for unmated males (Fig. 2 c). These apparently contradictory results can be reconciled if aggressive encounters lasted longer for mated males, suggesting that they might use more energy. Mated males usually win these encounters; their win ratio was 55 and 80 percent in preincubation to incubation periods, respectively (Fig. 2 a). This is not unexpected as in other species of waterfowl, unmated males are often subordinate to mated ones (e.g., Stahl *et al.* 2001), and mated dabbling duck males during the winter are reported to win up to 96 percent of their encounters with unmated males (Thompson & Baldassarre 1992). This suggests that if mated males are guarding their mate from extra pair copulations, they are usually successful. These data include aggressive interactions with other mated males so it does not mean that they lose some encounters with unmated males. The fact that unmated males occasionally win encounters, (8 to 30 percent of encounters, Fig. 2 a), and that they approached or were approached more than mated males during preincubation, suggests that they are attempting to displace a mated male. The higher win ratio of focal males during the incubation period is not biologically meaningful as focal males were chosen at random. The lowered win ratio of mated males during incubation probably results from the fact that some of the males they encountered were actually mated to females already on nests and thus were more dominant males.

The aggressive behavior of unmated males and the frequency with which they approach other males suggest that they may occasionally be successful in copulating with a female or replacing a mated male. Hario and Hollmén (2004) hypothesized that Common Eider females may actively so-

licit extra-pair copulations to ensure sperm viability, although this hypothesis remains untested empirically. Thus, being unmated may represent an alternative mating strategy.

Although scan data indicates that the cost in missed feeding opportunities for mated males may only occur after severe winters, the infrequent but intensive harassment groups may cause an energy expenditure much greater than differences seen in scan data and could result in much higher energy costs for mated males. These can consist of up to 2.75 hours of nearly continuous aggression for a mated male (and escaping for the female), and could easily represent a significant stress to males and females. On a more general note, male harassment is likely to represent an important but as yet unrecognized contributor to the well-known decline in reproductive output with advancing laying date, as late-nesting pairs will be disproportionately affected by harassment (Fig. 3). The sex ratio in the western Gulf of Finland has become increasingly male biased since the early 1980s, when the population was slightly female-biased (A. Lehtikoinen *et al.*, unpublished data). If this trend in sex ratio continues, male-male competition will increase and the energetic demands of fending off harassment groups could have an effect on survival of males.

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Parin vartioinnin kustannukset haahkalla

Vesilintujen tapaan haahkat pariutuvat talvehtimisaikoinaan ja muuttavat pareittain pesimäalueilleen. Koirasvoittoinen haahkojen sukupuolijakauma aiheuttaa vuorovaikutuksia pariutumattomien koiraiden ja pesivien parien välillä. Me tutkimme puolison vartiointiin liittyvää käyttäytymistä lajin pesimäalueilla Suomessa. Pariutuneet koiraat ruokailivat ja sukelsivat harvemmin kuin pariutuneet koiraat vuonna 2003, mutta tilanne oli päin vastainen vuonna 2004. Kylmän talven 2003 jälkeen haahkat saapuivat pesimäalueilleen huo-

nossa kunnossa, jonka takia ruokailu pesimäalueilla oli tärkeää. Pariutuneet koiraat olivat dominoivia suhteessa pariutumattomiin voittaneita kaksikolmannesta näiden välisistä aggressioista. Pariutuneet koiraat kohtasivat myös harvemmin aggressioita, mutta viettivät näissä enemmän aikaa kuin pariutumattomat.

Osa pariutuneet koiraista joutui ajoittain pannotamaan runsaasti energiaa vartioidessaan puolisoaan pariutumattomien koiraiden häirintäryhmiltä. Näissä häirintäryhmissä havaittiin kuudesta 23 koirasta ja parin häirintä kesti pisimmillään 165 minuuttia. Häirintäryhmät yleistyivät naaraiden alkaessa nousta maihin hautomaan ja siten koirasvoittoisuuden lisääntyessä entisestään. Häirintä ja havainnot pariutumattomien koiraiden lähestymisestä naaraita kohtaan viittaavat, että pariutumattomat koiraat yrittävät kasvattaa kelpoisuuttaan parin ulkopuolisilla parittelulla. Kasvavan haahkan koirasvoittoisuuden sekä pariutuneen olemisen kustannuksien takia vaihtoehtoinen pariutumistapa voi yleistyä populaatiossa.

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