



BIO-3910

MASTER'S THESIS IN EVOLUTION AND BEHAVIOUR BIOLOGY

The role of white wing bands in parental care and mate choice in
the female Common eider (*Somateria mollissima*)



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1. ABSTRACT

The female Common eider (*Somateria mollossima*) is a drab, lightly coloured bird, easily distinguished from the brightly ornamented male. Unlike the male, the female has white bands on the tips of her wings, and these white wing bands have been shown to reflect individual quality in previous studies. In this study the potential role of the white wing bands in parental care and mate choice is studied, predicting that females without wing bands should tend for their brood less often, and get less interest from males, when compared to females with normal wing bands. The size of the wing bands was manipulated in two different studies, to explore if it influenced the females' brood tending behaviour and the interest from males respectively, during breeding season. The study of brood tending behaviour did not indicate a clear connection between experimental manipulation of the wing band size and brood tending behaviour. However, the natural variation in wing band size did relate to parental care, where females with larger natural wing bands tended for their brood more often than females with smaller wing bands. The study of male interest showed that males preferred females in the control group, with visible white wing bands, more often than females with removed wing bands. These results indicate that the white wing bands of the female Common eider play a role in both parental care and male mate choice.

2. INTRODUCTION

Traditional evolutionary theories concerning sexual selection in conventional sex-roles expect males, but typically not females, to signal their individual quality. These signals could be extravagant ornaments (colours, sounds, shapes or sizes), behaviour or chemical signalling that seems to be costly and have no beneficial function in terms of natural selection (Amundsen et al. 1997, Amundsen 2000b). Darwin was well aware that females of many animal species were ornamented, and he explained this as either ‘sex role reversal’, when the female is more ornamented than the male, or ‘the laws of inheritance’, when the female is equally or less ornamented than the male (Darwin 1871, Amundsen 2000a). However, more recent studies on female ornamentation show that also females’ quality and condition could be signalled through ornaments, and that even if these ornaments seem to be drab male-like ornaments they may not be just a by-product directly inherited from their ornamented father (Andersson 1994, Amundsen 2000b). Many species of seabirds have conspicuous crests or colourful beaks in both sexes, and among fish, similar colourful appearances in the two sexes are very common. This is also found in a number of invertebrate taxa (Amundsen 2000b). Female-specific traits may also evolve by natural selection through social interactions, for example where females bearing an honest “badge of status” in competition with conspecifics, may gain fitness by avoiding physical injury from direct confrontation (Darwin 1871, West-Eberhard 1983). Males of species with conventional sex-roles are expected to be selective in choosing a mate if female quality is highly variable, as in bluethroats (*Luscinia s. svecia*) (Amundsen et al. 1997). Many studies have examined the role of female ornamentation in relation to individual quality, and some have found significant relationships (ornamentation and parental care: Møller 1993; Linville et al. 1998; but see Hill 1993; Cuervo et al. 1996; Rhode et al. 1999; Smiseth and Amundsen 2000; ornamentation and body size: Amundsen et al. 1997; ornamentation and hatch date/reproductive success: Ruusila et al. 2002; Hanssen et al. 2006; but see Hill 1993; ornamentation and parasitism: Potti and Merino 1996). One of the reasons for the relatively few results may be that most of these studies have been conducted on ornaments that are present, and presumably selected for, in males, which may make it difficult to distinguish between correlated responses and selection for trait expression in females (Hanssen et al. 2006). It may be more beneficial to explore female ornamental traits and quality in species where the female ornament is not expressed in males, and where it cannot influence female quality in the period when the measurements are taken, like in the Common eider.

The Common eider (*Somateria mollissima*) (hereafter referred to as “eider”) is a long lived, iteroparous species with high adult survivorship, delayed sexual maturity (Coulson 1984) and a strong female philopatry to breeding areas (Cooch 1965, Reed 1975, Wakeley and Mendall 1976, Anderson et al. 1992). The eider is a large ground nesting sea duck (50-71cm long, weight 1500-2800g, Cramp and Simmons 1977) with a circumpolar distribution and breeds in coastal areas in arctic, boreal and some temperate regions (Cramp and Simmons 1977, Bustnes and Tertitski 2000). The females start breeding at age 2-3 (Swennen et al. 1990), are seasonally monogamous and usually mate at the wintering area, from where the males follow the females to their breeding grounds (Waldeck et al. 2008). The females’ plumage is brown and grey while the males’ plumage is more colourful. Unlike the male, the female has two bands of white, unpigmented feather tips on their wings, and these feathers are produced during moult, shortly after breeding in August-September (Carney 1992). Individual variation in physical characteristics (e.g. colour intensity, size of ornaments) may be used to judge the quality, condition or status of the individual, which may be important when selecting partners or evaluating competitors (Espmark et al. 2000). White feather tips in female eiders may for instance, reveal overall feather quality, as the absence of melanin in white parts of the feather weakens it (Burt 1986). In a previous observational study, Hanssen et al. (2006) found that the size of the white fringes in the wing feathers of female eiders correlated with previously experienced reproductive costs and immune function. Later the same researchers found that an immune challenge the previous year lead to smaller white fringes in the white feathers in female common eiders (Hanssen et al. 2008).

Eiders are extreme capital breeders, subject to substantial costs prior to hatching (Parker and Holm 1990), and the female does not eat during the entire incubation period. The body mass of females increase by about 20% before egg laying (Erikstad and Tveraa 1995) and decrease by about 46% during incubation through the loss of stored lipid and protein (Parker and Holm 1990, Erikstad and Tveraa 1995, Øst et al. 2002, Hanssen et al. 2003a). Recovery after hatching is therefore likely to be an important fitness consideration. Indicative of the importance of condition recovery, Bustnes and Erikstad (1991), Kilpi et al. (2001), Bustnes et al. (2002) and Hanssen et al. (2003b) found that brood-rearing strategies in eiders are associated with differences in body condition. Females in poor body condition are more prone to abandon their brood.

Eiders are social birds and female social groups typically form during the breeding season when some females amalgamate their broods (Öst 1999, Öst et al. 2002, 2003, 2005). This is a common form of alloparental care in birds, but also in other taxa of animals. For example, female sperm whales form “babysitting” groups so that some females can dive to optimal feeding areas without leaving their young unattended and vulnerable to predation (Whitehead 1996). Female primates also form social relationships with female kin, to decrease predation risk (Sterk et al 1997). Some eider females rear their young on their own while others pool their broods and sometimes share brood-rearing duties. Brood-tending-associations form during a few days of intense social interaction, as females depart the nesting islands with their newly hatched broods (Öst and Kilpi 2000). Roughly half of the eider females abandon their own ducklings to the care of other females (Bustnes and Erikstad 1991). Females with large broods are less willing to abandon the young to other females than those with small broods (Erikstad et al. 1993). The crèching system of eiders, where several females may jointly care for young, allow females flexibility as to feeding method and site, leaves more time for feeding and less time for scanning for predators, while still participating in brood care (Öst and Kilpi 1999, Öst et al. 2002). This is regarded as beneficial for both genetic and adoptive parents and the young (Eadie et al. 1988). This formation in eiders is characterized by aggression and the presence of dominance hierarchies (Öst 1999), and the females forming the coalitions with each other are unrelated (Öst et al. 2005). The spatial position of ducklings depends on their mother’s status in the female dominance hierarchy (Öst and Bäck 2003).

Ornamental display of quality in females is not expected to evolve by sexual selection, unless the males become a limited resource for which females may compete (Emlen and Oring 1977). In eiders this is not the case, but Hanssen et al. (2006, 2008) suggested that the information contained in the white wing bands of females may be important for males as they perform courtship and mate guarding for several months before breeding and male reproductive success is solely dependent on the fecundity of their female partner. Information about female quality should be of importance for male fitness, and females with large white wing bands, reflecting good individual quality (Hanssen et al. 2006, 2008), should get more attention from males than females with smaller wing bands. The strongest evidence of males choosing females based on ornamental traits is in crested auklets (*Aethia cristatella*) (Jones and Hunter 1993). In cardinals (*Cardinalis cardinalis*), Linville et al. (1998) found that males preferred colourful females over drab females and that these females also provide more food for their offspring than do drab mothers, providing evidence of direct benefits from mating

with ornamented females. Also, Skarstein and Folstad (1996) reported that bright red female arctic charr had fewer deleterious parasites than drabber females, suggesting that the bright red might reflect individual quality in the female. Male attraction and female competition functions of female ornaments are not mutually exclusive. Both of these functions are fundamentally aspects of competition among females to mate with the best males (Amundsen 2000b).

The main objective of this study was to examine whether the white wing bands of the female Common eider (*Somateria mollissima*) could affect alloparental care and male interest. The hypothesis was that the removal of the white wing bands affects the female brood tending behaviour and male attention. It was expected that a female with masked white bands would tend her own ducklings less often than a female with natural white bands, and the females with natural white bands would garner more male attention than those with removed white bands.

3. MATERIALS AND METHODS

3.1 Study area, study species and experimental manipulation

The study was conducted on Grindøya (Fig. 1a), a small island of the coast of Tromsø, Northern Norway (69°49'N, 18°15'E). The island is approximately 0.65 km² and some 200 pairs of Common eider (*Somateria mollissima*) breed here (personal observations). In the study of brood tending behaviour, during the breeding season in May-July 2007, the island was visited daily from the start of egg-laying, in mid-May, to determine the laying date and clutch size of the breeding females. The nests were found by visually searching the island for nests. The female eider covers her first eggs thoroughly with grass and leaves, making them hard to discover at the 1-2 egg stage. The eider lays one egg per day (Watson et al. 1993, Hanssen et al. 2003a), so when no new eggs had been laid during a two day period we assumed that the clutch was complete. The females produce from three to six eggs and clutches of four and five eggs are most common (Hanssen et al. 2003a). The females were captured with a snare at day 5 and at day 20 after laying the first egg. As a part of a study at the Norwegian Institute for Nature Research (NINA) the eiders were weighed, wing band measures were taken, blood samples were collected, eiders with leg rings were registered and unringed birds were ringed with a metal leg ring for identification purposes. Every egg was measured in length and breadth to the nearest ± 0.1 mm using a vernier calliper. At day 20, the females' white wing bands were measured to the nearest 0.1 mm.

In the study of brood tending behaviour, in 2005 and 2007, the females were randomly placed in a control group or an experimental group where the females' wing bands were covered with a 10% solution of nyanzol D in hydrogen peroxide to make them less conspicuous. The females incubated for 22-26 days (Erikstad and Tveraa 1995) and the newly hatched ducklings go to sea to feed with their mother within 24 hours. Before the ducklings and the mother left the nest, they were tagged with colour-coded tape tags so as to distinguish between the females and connect females and ducklings while observing their behaviour after leaving the nest. The tags were attached to the back of their head with superglue.

The study of male interest was also conducted on Grindøya (Fig. 1), during May-June 2008. During the breeding season the females incubate almost constantly, while males, both those who have mated and others hoping for a chance to mate, patrol the seashore. When a female comes down to the water either for preening or drinking (Crisuolo et al. 2000), or because she has been scared off the nest, males flock around her, showing their colourful throats and

making their characteristic mating call. The females were captured with a snare and their white wing bands (Fig. 2a) were measured to the nearest 0.1 mm. Females were randomly placed in a control group and an experimental group where the females' white wing bands were cut completely off with scissors (Fig. 2b).

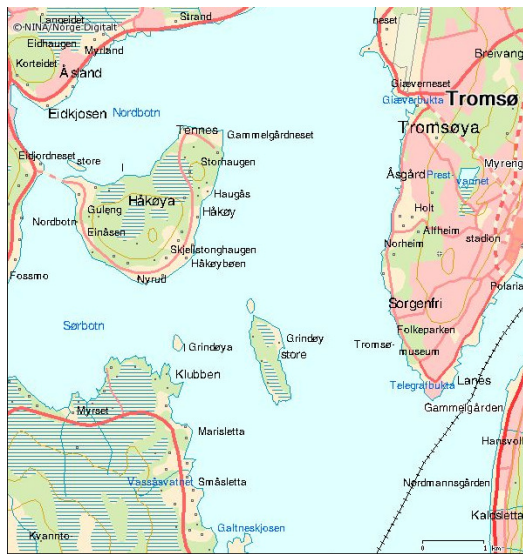


Figure 1a: Map of the study area, Grindøya



Figure 1b: Map of the surrounding areas around Grindøya where the Common eiders disperse

3.2 Study of brood tending behaviour

The study was conducted in surrounding areas around Tromsø in 2007. After hatching the eiders disperse over a large area in the fjords surrounding Grindøya, 72 km of coastline (Bustnes and Erikstad 1991) (Fig. 1b). In eiders parental care is either abandonment, care of young by a single female or joint care by two or more females. Tenders are females observed caring for young alone or with other females during the first week after hatching (Bustnes and Erikstad 1991). About 40% of the eider females abandon their own ducklings to the care of other females, and this usually occurs within the first two days of leaving the nest (Bustnes and Erikstad 1991, Kilpi et al. 2001). Females and ducklings with colour coded tape tags were observed in their natural habitat every day from mid June to mid July 2007, and the brood tending behaviour was registered. I classified the females as to whether they were abandoners or tenders. Abandoners are females known to have left the colony with young and then observed during the first week after hatching not caring for young. In this study I did not distinguish between the ones exclusively caring for their own young and the ones tending multiple broods with other females, i.e. crèching. Data from a similar study in 2005 from the

same colony on Grindøya was also used further in the statistical analysis and data presentation.

3.3 Study of male interest

This study was conducted on Grindøya (Fig. 1a), during May-June 2008. To observe males and females in their natural habitat and to register how many males showed an interest in each of the females that came to the shore, we released the females after registering wing band size and started a stopwatch as the female landed on the water. I registered the number of males (1) when the female landed on the water, (2) after 30 seconds, (3) after 60 seconds and (4) after 120 seconds. After this time most females tended to return to their nests, so I chose not to register interest longer than 120 seconds.



Figure 2a: The white wing bands of the female eider



Figure 2b: The wing of the female eider after cutting of the white wing bands.

3.4 Data analysis

To analyze the data collected we used the Statistical Analysis Software, SAS, version 9.2 (SAS Institute Inc. 1999). The following parts of the white wing bands were measured on both the right and the left wing: (1) Inner width and (2) outer width. To simplify the analysis and get a common value for the white wing bands we calculated the mean of the wing band measurements of the left wing.

Study of brood tending behaviour: Since the dependent variable tending/abandoning is a binary response variable, these data were analyzed using logistic regression, and all values are

based on type III SS (sums of squares). We tested to see if (1) the experiment of covering the females' wing bands, (2) the size of the wing bands and (3) the two factors combined had any effect on the tending behaviour. The year of study (2005 and 2007) was also included as a factor in the analysis.

Study of male interest: The data was analyzed using Logistic regression with Poisson response distribution and Log link function, and all the values are based on type III SS (sums of squares). We tested to see if (1) the experiment of cutting off the females' wing bands, (2) time, (3) date, (4) the size of the wing bands and (3) and (4) combined had any affect on the number of males showing interest in each female.

4. RESULTS

4.1. Study of brood tending behaviour

In this study 36 individuals were included, with 17 controls and 19 treated. Of these, only 14 were observed again and included in the statistical analysis. I found that 10 of these females cared for their young and 4 did not. Also included in the analysis were data from 2005.

Twenty-eight individuals, 14 controls and 14 treated were included and of these 18 individuals were observed again and included in the statistical analysis. In this study, 5 of the females cared for their young and 13 females did not.

4.2. Study of male interest

In this study 30 individuals were included, 16 controls and 14 treated. Each of these was observed at four times; (1) when the female landed on the water, (2) after 30 seconds, (3) after 60 seconds and (4) after 120 seconds.

4.3 Data analysis

Study of brood tending behaviour: The logistic regression analysis of tending/abandoning behaviour resulted in a model (Table 1) where the experiment of colouring the females' wing bands did not significantly ($P=0.91$) influence whether the females tended or abandoned their young. However, the size of the wing bands before manipulation ($P=0.01$) significantly influenced whether the females tended or abandoned their young. The interaction between the experiment and wing band size did not affect brood tending ($P=0.44$).

Table 1: Analysis of brood tending behaviour in eider females, in relation to experimental masking of wing bands and natural wing band size.

Variable	Experiment	DF	Estimate	Std Error	ChiSq	P > ChiSq
Intercept		1	-3.2613	1.7088		
Experiment	0	1			0.0139	0.9058
Size of wing bands		1	0.6839	0.3241	4.4524	0.0110

The probability of tending increases with wing band size (Fig. 3). Figure 5 also show the observed amount of females tending (1) and abandoning (0) their brood, and their wing band size.

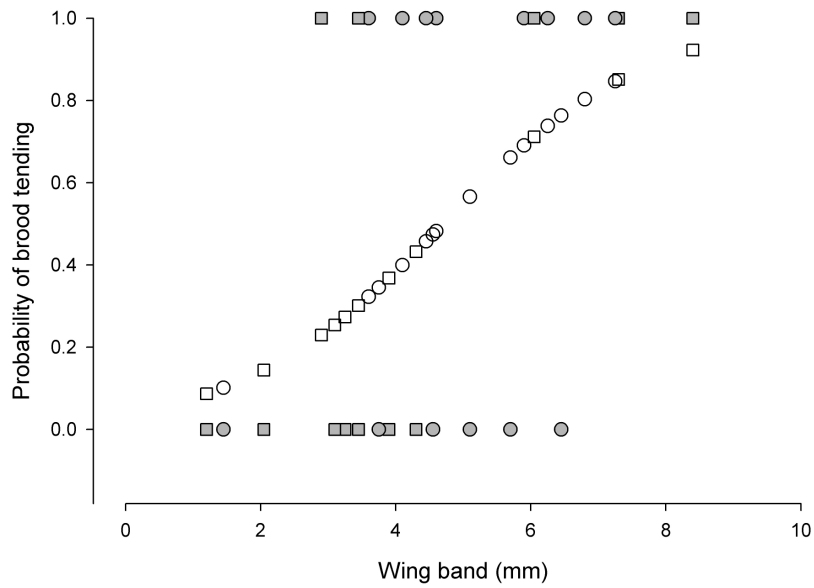


Figure 3: Probability of brood tending as a function of wing band size. Grey values- Observed values (0= abandoning females, 1=tending females). Squares- Females in control group. Circles - Masked females.

Study of male interest: I calculated the mean number of males in each of these groups at the four different times. At time 60s I registered the most number of males in the control group (4.50) and at time 30s I registered the most number of males in the experiment group (2.71) (see fig. 4).

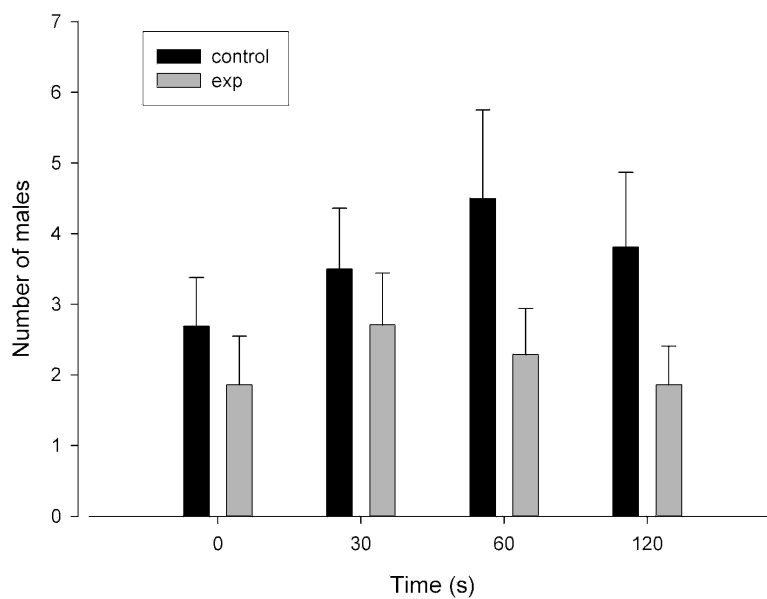


Figure 4: Mean number of males in the control- and the experimental group, at the four different times. There was 16 females (N) in the control group and 14 females (N) in the experiment group.

I analyzed interest from males in each of the four time intervals separately (table 2). The analysis show that the experiment had a significant influence on the number of males at time 60s (P= 0.003) and 120s (P= 0.005). The date showed to have a significant influence on the interest from males at time 30s (P= 0.008) and 120s (P= 0.031). The original size of the wing bands did not seem to significantly influence the interest from males at any of the four times.

Table 2: Analysis of male interest in eider females in relation to experimental removal of wing bands, date and natural wing band size, at the four different times.

Time	Parameter	DF	Est.	Std. error	Wald 95% conf. lim.		Chi-Sq	P-value
Start	Intercept	1	1.65	0.79	0.10	3.21	4.35	0.04
	Experiment	1	0.35	0.26	-0.15	0.86	1.90	0.17
	Date	1	-0.02	0.02	-0.06	0.02	1.36	0.24
	Size of wing bands	1	-0.05	0.09	-0.24	0.13	0.34	0.56
30 s	Intercept	1	2.97	0.70	1.60	4.34	18.02	< 0.0001
	Experiment	1	0.21	0.21	-0.22	0.64	0.94	0.33
	Date	1	-0.05	0.02	0.09	0.01	7.12	0.008
	Size of the wing bands	1	0.07	0.08	0.23	0.08	0.87	0.35
60 s	Intercept	1	1.82	0.66	0.53	3.11	7.63	0.01
	Experiment	1	0.66	0.22	0.23	1.09	8.99	0.003
	Date	1	-0.03	0.02	-0.06	0.007	2.47	0.12
	Size of the wing bands	1	-0.03	0.08	-0.17	0.12	0.12	0.73
120 s	Intercept	1	1.70	0.76	0.22	3.18	5.10	0.024
	Experiment	1	0.68	0.24	0.20	1.16	7.76	0.005
	Date	1	-0.04	0.02	-0.09	-0.004	4.66	0.03
	Size of the wing bands	1	0.06	0.08	-0.09	0.21	0.57	0.45

5. DISCUSSION

Previous studies done on the ornamentation of the Common eider (*Somateria mollissima*) and its function have shown that the white wing bands indicate individual quality. Large wing bands is associated with large clutch size (Hanssen et al. 2006), also, females with large clutches have higher capacity to increase incubation and brood-rearing effort (Hanssen et al. 2003a). Additionally, females with larger wing bands show better tolerance of reproductive costs (Hanssen et al. 2006) and have better body condition (as body condition is a sign of better tolerance of reproductive costs) and may therefore also be less prone to abandon their brood (Kilpi et al. 2001 and Öst 1999). I wanted to examine if the experimental masking of the wing bands had an influence on whether the females rear their own brood or abandon it. I also wanted to examine if the wing bands had an influence on male interest, making males choose females with natural wing bands more often than females with experimentally removed wing bands.

5.1 Brood tending behaviour

The experiment of masking the females' wing bands with a 10% solution of nyanzol D in hydrogen peroxide did not influence the brood tending behaviour, however, the females with naturally larger wing bands did tend for their young more often than females with smaller wing bands. Interestingly, the size of the wing bands was related to brood tending behaviour also in the manipulated group where the wing bands shouldn't be visible. This could mean that the condition dependent factors underlying the size of the wing bands affect brood tending behaviour and not the size of the wing bands per se. Alternatively, as the colour solution used to manipulate the females' wing bands may not have been as long lasting as expected, and may have dissolved earlier than anticipated, the wing bands may have been visible also in the manipulated birds.

The question is what purpose the wing bands may have in female-female interactions in a crèche system. It has been suggested that individual variation in physical characteristics (e.g. colour intensity, size of ornaments) may be used to judge the quality, condition or status of the individual (Espmark et al. 2000), and as Öst et al. (2005) states, the coalition formations in female eiders are not formed between relatives and is characterized by frequent aggression and the presence of female dominance hierarchies. As females seem to evaluate each others' status during the brood rearing period (Öst et al. 2003), and as the spatial position of ducklings depends on their mother's status in the female dominance hierarchy (Öst et al.

2007) and the white wing bands signal individual quality (Hanssen et al. 2006), it is not unlikely that the white wing bands of female eiders may play an important role in female-female interactions in the crèche system. Females may use the size of the wing bands to evaluate whether to cooperate in brood rearing with a female or not. Females using ornaments as badges of status is not only seen in eiders. Such a function of female showiness has received indicative support in field studies of dotterels *Charadrius morinellus* (Owens et al. 1994), capuchinbirds *Perissocephalus tricolour* (Trail 1990) and hummingbirds *Amazilia* spp. (Wolf 1969, Bleiweiss 1985). The crèching system of eiders, where several females may jointly care for young, allow females flexibility as to feeding method and site, leaves more time for feeding and less time for scanning for predators, while still participating in brood care (Öst and Kilpi 1999, Öst et al. 2002). Therefore, as the survival prospects of a female's offspring may depend on the mutual dominance relationships of females in the crèche (Öst and Bäck 2003), the females would benefit from evaluating the cooperating females' condition before joining a crèche, or allowing other females to join.

5.2 Male interest

The experiment of cutting of the females' wing bands significantly affected male interest at time 60s and time 120s, which might indicate that males flock around any female entering the water and might need some time to evaluate each of the females' quality. After further evaluation males seemed to conclude that the females with removed wing bands, and thus supposedly of low quality (Hanssen et al. 2006), were of less interest than the females with natural wing bands. Alternatively, the males might consider the females without wing bands to be immature females, which have not yet developed the characteristically white wing bands. At time 30s and 120s the date was negatively related to the amount of males showing interest in females. This seems likely as the amount of males present at the seashore at Grindøya decreases later in the breeding season, when males leave to feed and moult at other locations around Tromsø (personal observations). The method used to manipulate the females' wing bands in this part of the study may have been better compared to using the colour solution used in the study of brood tending behaviour, as this manipulation is permanent until the females moult and grow new feathers a few months later.

The question is what purpose the females' white wing bands may have in male mate choice. Only a handful of experiments have aimed at testing the potential function of female showiness in mate choice of species with conventional sex roles (Amundsen 2000b), and even

less have been done on species where the female trait is not expressed in the male (Hanssen et al. 2006). Still, there is evidence of males choosing ornamented females in species where the two sexes carry similar extravagant ornaments (crested auklets: Jones and Hunter 1993), and in species where the female carry a reduced version of the male ornament (house finches: Hill 1993 and bluethroats: Amundsen et al. 1997). Evidence of direct benefits to the male when choosing an ornamented female over a less ornamented female have been shown in northern cardinals (*Cardinalis cardinalis*), where the colourful females provide more food to the offspring than drab females, and thus provides for an increased chance for offspring survival (Linville et al. 1998). Evidence of potential indirect benefits is found in the pied flycatcher (*Ficedula hypoleuca*), where females with a white forehead patch had fewer parasites (Potti and Merino 1996). The information contained in the white wing bands of female eiders may be important for males as they perform courtship and mate guarding for several months before breeding, and male reproductive success is solely dependent on the fecundity of their female partner (Hanssen et al. 2008). Information about female quality should thus be of importance for male fitness, and it would be beneficial for the male to choose a female with large wing bands as this female would be in good health and have large reproductive capacity (Hanssen et al 2006, 2008). Also, it is likely that the male benefits from being choosy since eider females in good condition are more likely to hatch their eggs (Hanssen et al. 2003a, Hanssen et al. 2006) and care for their own young (Bustnes and Erikstad 1991, Hanssen et al. 2003a), and young cared for by their own mother have a higher probability of survival (Bustnes and Erikstad 1991).

5.3 Conclusion and further research

The results shown in this study indicate that the white wing bands of the female eider may have a function in both brood rearing and male-female interaction. It seems like these wing bands are used to reveal information about the females' individual quality to both interested males and cooperating females. However, even though we still might not understand the complete role of the wing bands, this study gives clear predictions for further research. As few studies have been done on female-female interactions and the use of ornaments in interactions between cooperating female eiders during breeding season, it would be favourable to further study this in detail. Also, too little is known about the use of female ornaments to signal individual quality to interested males, so the relationship between wing bands and male interest should be the focus of further research.

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7. REFERENCES

- Amundsen, T., Forsgren, E. and Hansen, L. T. T.** 1997. On the function of female ornaments: male bluethroaths prefer colourful females. *Proc. R. Soc. Lond. B.* **264**: 1579-1586.
- Amundsen, T.** 2000a. Why are female birds ornamented? *Tree.* **15**: 149-155.
- Amundsen, T.** 2000b. Female ornaments: genetically correlated or sexually selected? In: Espmark, Y., Amundsen, T. & Rosenqvist, G. (Eds.), *Animal Signals: Signalling and Signal Design in Animal Communication*, pp. 133-154. Tapir Academic Press, Trondheim.
- Andersson, M.** 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Anderson, M. G., Rhymer, J. M. and Rohwer, F. C.** 1992. Philopatry, dispersal and the genetic structure of waterfowl populations. In: Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A., Krapu, G. (Eds.), *Ecology and management of breeding waterfowl*, pp. 365-395. Minneapolis, MN: University of Minnesota Press.
- Bleiweiss, R.** 1985. Iridescent polychromatism in a female hummingbird: is it related to feeding strategie? *Auk.* **102**: 701-713.
- Burt, E. H. J.** 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on Wood Warblers. *Ornit. Monogr.* **38**: 1-126.
- Bustnes, J. O. and Erikstad, K. E.** 1991. Parental care in the common eider (*Somateria mollissima*): Factors affecting abandonment and adoption of young. *Canadian Journal of Zoology.* **69**: 1538-1545.
- Bustnes, J. O. and Tertitski, G. M.** 2000. Common eider *Somateria mollissima* in: *The status of marine birds breeding in the Barents Sea region. Norsk Polarinstitut, Rapportserie nr 113 pp 46-47.* Norsk Polarinstitut, Tromsø.

- Bustnes, J. O., Erikstad, K. E. and Bjørn, T. H.** 2002. Body condition and brood abandonment in Common eiders breeding in the high arctic. *International Journal of Waterbird Biology*. **25**: 63-66.
- Carney, S. M.** 1992. Species, Age and Sex Identification of Ducks using Wing Plumage. Washington, D.C.: U.S. Department of the Interior, U.S. Fish and Wildlife Service. (<http://www.npwrc.usgs.gov/resource/birds/duckplum/index.htm>).
- Cooch, F. G.** 1965. The breeding biology and management of the northern common eider in the Cape Dorset area, N.W.T. Canadian Wildlife Service. Wildl Manag Bull 2. 68 p.
- Coulson, J.C.** 1984. The population dynamics of the eider duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. *Ibis*. **126**: 525–43.
- Cramp, S. and Simmons, K. E. L.** 1977. *Somateria mollissima* Eider. The Birds of the Western Palearctic (Ed. by S. Cramp & KEL Simmons): 595-604.
- Criscuolo, F., Gauthier-Clerc, M., Gabrielsen, G. and Le Maho, Y.** 2000. Recess behaviour of the incubating Common Eider *Somateria mollissima*. *Polar Biology*. **23**: 571-574.
- Cuervo, J. J., de Lope, F. and Møller, A. P.** 1996. The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behavioral Ecology*. **7**: 132–136.
- Darwin, C.** 1971. The decent of man, and selection in relation to sex. J., Murray, London.
- Eadie, J. M., Kehoe, F. P. and Nudds, T. D.** 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Canadian Journal of Zoology*. **66**: 1709-1721.
- Emlen, S. T., and Oring, L. W.** 1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science*. **197** (4300): 215-223.

Espmark, Y., Amundsen, T. and Rosenqvist, G. (Eds.). 2000. Animal Signals: Signalling and Signal Design in Animal Communication. Tapir Academic Press, Trondheim.

Erikstad, K. E. Bustnes, J. O. and Moum, T. 1993. Clutch-size determination in precocial birds: A study of the Common eider. *Auk*. **110**: 623-628.

Erikstad, K. E. and Tverraa, T. 1995. Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*? *Oecologica*. **103**: 270-274.

Hanssen, S.A., Erikstad, K.E., Johnsen, T.V. and Bustnes, J.O. 2003a. Differential investment and costs during avian incubation determined by individual quality: an experimental study of the common eider *Somateria mollissima*. *Proc. R. Soc. Lond. B*. **270**: 531-537.

Hanssen, S.A., Folstad, I. and Erikstad, K.E. 2003b. Reduced immunocompetence and cost of reproduction in common eiders. *Oecologia*. **136**: 457-464.

Hanssen, S. A., Folstad, I. and Erikstad, K. E. 2006. White plumage reflects individual quality in female eiders. *Animal Behaviour*. **71**: 337-343.

Hanssen, S. A., Hasselquist, D., Folstad, I. and Erikstad, K. E. 2008. A label of health: a previous immune challenge is reflected in the expression of a female trait. *Biology Letters*. **4** (4): 379-381.

Hill, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the house finch. *Evolution*. **47**: 1515–1525.

Jones, I. L. and Hunter, F. M. 1993. Mutual sexual selection in a monogamous seabird. *Nature*. **362**: 238-239.

Kilpi, M., Öst, M., Lindstrøm, K. and Rita, H. 2001. Female characteristics and parental care mode in the crèching system of eiders, *Somateria mollissima*. *Animal Behaviour*. **62**: 527-534.

Linville, S. U., Breitwisch, R. and Schilling, A. J. 1998. Plumage brightness as an indicator of parental care in northern cardinals. *Animal Behaviour*. **55**: 119–127.

Møller, A. P. 1993. Sexual selection in the barn swallow (*Hirundo rustica*). 3. Female tail ornaments. *Evolution*. **47**: 417-431.

NINA Kartportal/Norge Digitalt: <http://wms.nina.no/wms>

Öst, M. 1999. Within-season and between-year variation in the structure of common eider broods. *Condor*. **101**: 598-606.

Öst, M. and Kilpi, M. 1999. Parental care influences the feeding behaviour of female eiders *Somateria mollissima*. *Ann. Zool. Fennici*. **36**: 195-204.

Öst, M. and Kilpi, M. 2000. Eider females and broods from neighbouring colonies use segregated local feeding areas. *Waterbirds*. **23**: 24-32.

Öst, M., Mantila, L. and Kilpi, M. 2002. Shared care provides time-budgeting advantages for female eiders. *Animal behaviour*. **64**: 223-231.

Öst, M. and Bäck, A. 2003. Spatial structure and parental aggression in eider broods. *Animal Behaviour*. **66**: 1069-1075.

Öst, M., Vitikainen, E., Waldeck, P., Sundstrøm, L., Lindström, K., Hollmén, T., Franson, J. C. and Kilpi, M. 2005. Eider females form non-kin brood-rearing coalitions. *Molecular Ecology*. **14**: 311-317.

Öst, M., Jaatinen, K. and Steele, B. 2007. Aggressive females seize a central positions and show increased vigilance in brood-rearing coalitions of eiders. *Animal Behaviour*. **73**: 239-247.

Owens, I. P. F., Burke, T. and Thompson, D. B. A. 1994. Extraordinary sex roles in the Eurasian dotterel: female mating arenas, female-female competition, and female mate choice. *American Naturalist*. **144**: 76-100.

- Parker, H. and Holm, H.** 1990. Patterns of nutrient and energy expenditure in female Common eiders nesting in the high arctic. *Auk*. **107**: 660-668.
- Potti, J. and Merino, S.** 1996. Decreased levels of blood trypanosome infection correlate with female expression of a male secondary sexual trait: implications for sexual selection. *Proceedings of the Royal Society of London, Series B*. **263**: 1199–1204.
- Reed, A.** 1975. Migration, homing and mortality of breeding female eiders *Somateria mollissima dresseri* of the St. Lawrence estuary, Quebec. *Ornis Scand.* **6**: 41–7.
- Rohde, P. A., Johnsen, A. and Lifjeld, J. T.** 1999. Female plumage coloration in the bluethroat: no evidence for an indicator of maternal quality. *Condor*. **101**: 96–104.
- Ruusila, V., Pöysä, H. and Runkko, P.** 2002. Female wing plumage reflects reproductive success in common goldeneyes, *Bucephala clangula*. *Journal of Avian Biology*. **32**: 1–5.
- SAS Institute Inc.** 1999. The SAS System for Windows, release 9.2. Cary, North Carolina: SAS Institute Inc.
- Skarstein, F. and Folstad, I.** 1996. Sexual dichromatism and the immunocompetence handicap: an observational approach using Arctic charr. *Oikos*. **76**: 359-367.
- Smiseth, P. T. and Amundsen, T.** 2000. Does female coloration signal parental quality? A male removal experiment with the bluethroat (*Luscinia s. svecica*). *Behavioral Ecology and Sociobiology*. **47**: 205–212.
- Sterk, E. H. M., Watts, D. P. and van Schaik, C. P.** 1997. The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol.* **41**: 291-309.
- Swennen, C., Ursem, J. C. H. and Duiven, P.** 1993. Determinate laying and egg attendance in Common eiders. *Ornis Scand.* **24**: 48-52.
- Trail, P. W.** 1990. Why should lek-breeders be monomorphic? *Evolution*. **44**: 1837-1852.

Wakeley, J. S. and Mendall, H. L. 1976. Migrational homing and survival of adult female eiders in Maine. *J Wildl Manag.* **40**: 15–21.

Waldeck, P., Andersson, M., Kilpi, M. and Öst, M. 2008. Spatial relatedness and brood parasitism in a female-philopatric bird population. *Behavioural Ecology.* **19**: 67-73.

Watson, M. D., Robertson, G. J. and Cooke, F. 1993. Egg laying and laying interval in the common eider. *Condor.* **95**: 869-878.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology.* **58**: 155-183.

Whitehead, H. 1996. Babysitting, div synchrony and indication of alloparental care in sperm whales. *Behav Ecol Sociobiol.* **38**: 237-244.

Wolf, L. L. 1969. Female territoriality in a tropical hummingbird. *Auk.* **86**: 480-504.