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Parental care influences the feeding behaviour of female eiders *Somateria mollissima*

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We compared the feeding behaviour of lone tenders, multi-female tenders and post-breeding, non-tending eider females *Somateria mollissima* in the northern Baltic. Few prey species are available for eiders in the Baltic; in the non-breeding season adults prefer blue mussels *Mytilus edulis*, whereas small ducklings feed primarily on gammarids *Gammarus* spp. Infections by the acanthocephalan parasite *Polymorphus minutus* occur when eiders feed on gammarids and this infection may be fatal if the host's resistance is low. The mussel beds and areas with gammarids are close together but do not overlap. Assuming that females always should prefer blue mussels to gammarids we tested the following predictions: (i) non-tending females should exclusively feed on mussels, (ii) lone tenders may be forced to feed like their young, and (iii) multi-female tenders may occasionally utilise mussels, thereby mitigating constraints associated with consumption of unprofitable gammarid prey. Tending females foraged like their young, whereas non-tending females fed on mussels throughout the brood-rearing season. Individually marked females fed on mussels immediately after losing their brood, suggesting that a conflict between female and duckling feeding needs exists during early brood-rearing. However, later in the season all females and young fed on mussels. Multi-female tenders achieved no obvious foraging benefits compared to lone tenders, indicating that crèching in eiders may have primarily evolved for other reasons.

1. Introduction

Crèching behaviour, or brood amalgamation, is particularly common among waterfowl (Kehoe 1989), and has been studied extensively in the eider *Somateria mollissima* (e.g., Gorman & Milne 1972, Bédard & Munro 1976, Munro & Bédard 1977a, 1977b, Schmutz *et al.* 1982, Bustnes & Erikstad 1991a, 1991b). Eadie *et al.* (1988) reviewed the hypotheses that have been proposed to explain both pre- and post-hatch amalgamation and presented a theoretical framework for the evolution of these behaviours. Females in poor body condition may abandon their young, in order to replenish their body reserves more efficiently than those tending broods (Eadie *et al.* 1988, Kehoe 1989). The benefit to abandoning females is further emphasised if ducklings are unable to feed in the same habitat as adults, forcing mothers to use duckling feeding habitats (Bustnes 1996). The crèching system of eiders where several females may jointly care for young may allow females flexibility as to feeding method and site, while still participating in brood care. Several studies have reported differences in the feeding behaviour of eider females and ducklings (Pethon 1967, Gorman & Milne 1972, Cantin *et al.* 1974). In our study area in the Baltic, small ducklings mainly feed on a few (5) species of amphipods (*Gammarus* spp.) (Lehtonen & Hario 1994, Hollmén *et al.* 1996), whereas adult birds in the non-breeding season almost exclusively feed on blue mussels *Mytilus edulis* (Bagge *et al.* 1973, Nyström *et al.* 1991, Öst & Kilpi 1998). The Baltic Sea is brackish and relatively few prey species are available for eiders; this contrasts to truly marine habitats, where more prey species are available (Pethon 1967, Gorman & Milne 1972, Cantin *et al.* 1974, Nehls 1991, Guillemette *et al.* 1992). Adult eiders prefer blue mussels, probably because mussels occur in sufficient biomass in the Baltic (Kautsky 1981) to offer the birds an even energy return (Guillemette *et al.* 1992, Guillemette & Himmelman 1996). Gammarid consumption makes the birds susceptible to infections by the intestinal parasite *Polymorphus minutus*, as they are an intermediate host (Hario *et al.* 1992, Hollmén *et al.* 1996). The importance of *Polymorphus minutus* infection is controversial (Hario *et al.* 1995), but heavy loads of this parasite can be potentially dangerous for females, especially if the female is already emaciated due to breeding stress. Although animals in good body condition appear to be able to tolerate a parasite load, infections can be fatal if the host's resistance is lowered due to physiological stress (Hollmén *et al.* 1996).

Female eiders feed very little, or, not at all during laying and the 24–26-day incubation period (Korschgen 1977, Hario 1983, Parker & Holm 1990). The breeding stress female eiders face is extreme; they lose about 46% of their body mass from prelaying to hatching (Parker & Holm 1990, Erikstad *et al.* 1993). In exceptional cases females may even die due to starvation during the later phases of incubation (pers. obs.). Although females get rid of their parasites during continuous incubation, they are in poor condition and susceptible to new infections (Thompson 1985). If the host's resistance is low and the transmission of parasites is fast, the interaction between breeding anorexia and heavy infection can be fatal for a female (Hario *et al.* 1992 and pers. obs.). The parasite load of females can equal the prebreeding level in less than three days of feeding after completed incubation (Thompson 1985, Hario *et al.* 1992). Accordingly, a female may not have enough time to replenish her body reserves after completed incubation before the infection can reach a destructive stage.

We studied the foraging behaviour of females and ducklings during the brood-rearing season in the northern Baltic. We wanted to know whether or not there are general differences in feeding behaviour between brood-caring females and non-tending females. We also wanted to compare the feeding behaviour of females tending the brood alone (hereafter lone tenders) and females attending multi-female broods ("crèches"). Assuming that females always should prefer blue mussels to gammarids, either because of the risk of *Polymorphus* infection or because of the possibly lower energetic value of gammarids, we predicted that: (i) non-tending females, either brood abandoners or females having lost their brood at an early stage, should exclusively feed on blue mussels, (ii) lone tenders may be forced to feed in the same manner and use the same feeding habitat and food items as the ducklings, and (iii) multi-female tending may to some extent free females to modify their behaviour, and they may utilise mussels as well.

2. Methods

2.1. Study area

The study was carried out in the tideless Baltic Sea, west of the Hanko Peninsula (60°N, 23°E), SW Finland, close to the Tvärminne Zoological Station in 1994–1996. A map of the study area is presented in Kilpi *et al.* (1990). About 1 500 pairs of eiders breed annually in the area and the population has remained fairly stable for the last decade. Eiders breed on islands covered with pine (*Pinus sylvestris*) and spruce (*Picea abies*) woodland and on treeless islets (Kilpi & Lindström 1997). The study site is a complex of islands, islets, and small skerries forming a fine-scaled mosaic of feeding patches for eiders (Öst & Kilpi 1997). Most eider broods feed close to the seashore, which can be divided into a filamentous algal zone (0.2–2 m) dominated by *Cladophora* spp. and a fucus zone (2–5 m) dominated by *Fucus vesiculosus* (Kiirikki 1996). Gammarids are abundant in these two littoral zones (Hario *et al.* 1992). Larger mussels, suitable as food for adult eiders occur in mussel beds which range in depth from about 4–12 m with highest biomass observed at ca. 8 m (Olli Mustonen, pers. comm.). Mussels less than about 3 mm long are attached to filamentous algae and are not found in the mussel beds (Sunila 1981). It is noteworthy that the mussel beds and the seashore habitats are only a few meters apart (Öst & Kilpi 1997).

2.2. Foraging behaviour

The foraging behaviour of eider females and ducklings was observed from suitable vantage points in the Tvärminne archipelago during the brood-rearing season. The females were grouped in the following categories: (a) non-tending females, feeding at approximately the same sites as broods, (b) lone tenders, and, (c) multi-female tenders. All observed multi-female tenders were of broody or associate status (*sensu* Bédard & Munro 1976). The observed non-tending females were either brood abandoners or failed nesters, because few nonbreeders occur in our study area (pers. obs.). We used focal animal sampling (Altmann 1974), one bird from the group was randomly chosen for detailed recording of its foraging behaviour. Observation started once a foraging brood or non-tending female was spotted and ended when the bird under study stopped foraging or was lost out of sight. The following information was tape-recorded: (1) total observation time, (2) flock composition, (3) distance to the nearest shore, (4) the feeding mode (diving, up-ending or bill-dip), (5) number of feeding bouts (dives, up-endings and bill-dips), and, (6) duration of dives. Distance from shore was estimated visually in the field by the same person (M. Ö.) to minimise variation by observer. The position of feeding flocks was recorded on maps each day. Recordings of the foraging behaviour of a particular brood or non-tending female were done only once from a specific vantage point during one day. Thus, we eliminated the possibility of choosing the same focal bird twice. By rotating observation locations we also tried to reduce the risk of sampling the same birds more than once during a certain study period (early vs. late brood-rearing period, respectively). The same vantage point was used approximately every week.

Albeit the mussel beds and areas where gammarids are abundant are close together, they do not overlap. Therefore longer dives farther off shore indicated that a bird was feeding on mussels, whereas shorter dives closer to the shore or the use of other techniques than diving (bill-dipping/up-ending) suggested that a bird was feeding on gammarids.

Using the field maps as references, we measured the depth of the water at seven preferred feeding sites by non-tending females in 1994 (five depth readings at each site). From these locations we collected blue mussel samples with a triangular bottom scraper (*see* Öst & Kilpi 1997). Out of the sample, 30 mussels were randomly chosen and measured to the nearest 0.1 mm using a Vernier calliper.

In 1994, most ducklings died during their first week of life, so all the data were for broods with small ducklings aged 1–10 days. Therefore we could only observe non-tending females in late June 1994. By contrast, 1995 was a good production year for eiders; the approximately 1 500 nesting pairs in the study area reared about 2 000 fledglings. Hence we were able to observe the foraging behaviour of all three female categories throughout the brood-rearing period in 1995. Because ducklings survived until fledging in 1995 we were also able to study how duckling foraging behaviour changed as they grew. The size of ducklings was estimated visually in the field by relating the length of the duckling's body to the length of the female's head while swimming. In this manner the ducklings were classified in four size classes. The age of these ducklings was not precisely known, because the individual variation in growth rates is considerable (Hario & Selin 1989). Regardless, the size of ducklings rather than their age is decisive in determining the type of food ducklings are able to ingest.

The gizzard and intestines of breeding female eiders are subject to rapid weight loss during laying since they contribute nutrients to egg synthesis (Korschgen 1977, Parker & Holm 1990). Due to this muscle atrophy, postbreeding females might be unable to eat hard-shelled prey shortly after incubation (Korschgen 1977). To determine if female eiders that had completed incubation were able to feed on mussels, we recorded the feeding behaviour of individually wing-tagged females in 1996 (*see* Öst 1999). We focused on females that had successfully hatched a brood, but which soon afterwards were observed as non-tending females. We recorded the duration of dives, the distance to the nearest shore, and number of days between observation and estimated hatching. The hatching day was either determined directly by observing signs of hatching, or, indirectly by a water-test, where the incubation stage is established by the way the egg floats in a bucket of water (Kilpi & Lindström 1997).

2.3. Data analysis

Some individuals were timed many times during a feeding session (more than 20 dives), while some individuals were timed only a few (2–3) times. To avoid pseudoreplication, we used the mean dive duration per bird instead of using all records in the analyses.

The quantitative variables (distance from the nearest shore, dive duration) were analysed by ANOVA, and pairwise comparisons of means were done with *post hoc* Tukey's test. For two sample comparisons we made use of independent, two-tailed *t*-tests. Parametric tests were used when

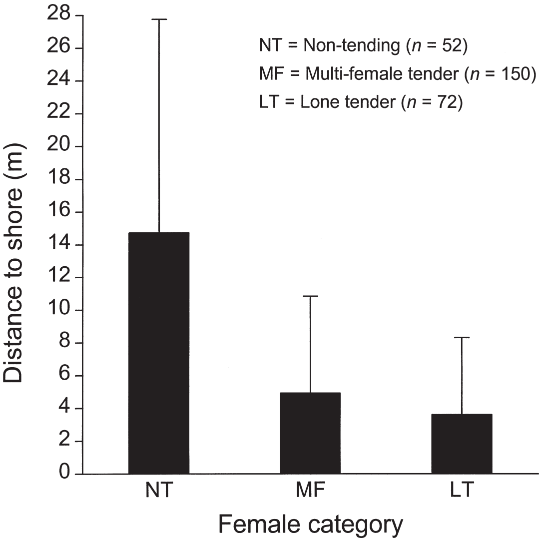

Fig 1. Mean distance (+ S.D.) to the nearest shore while foraging for different female categories during the early brood-rearing season in 1994 and 1995 (pooled data).

the data conformed to a normal distribution (Wilk-Shapiro test) and the variances were homogenous (Bartlett's test for homogeneity of variances). The statistical analysis of distance to the nearest shore was done on log $(x + 1)$ transformed data to correct for non-normality.

We used logistic regression to model the feeding technique of females. Logistic regression is a suitable method for representing data in the form of proportions (Collett 1991) as it is more informative and powerful than analysis as a three-way table or loglinear models (Sokal & Rohlf 1995). The response variable in our logistic regression model was binary: females only diving or females using additional techniques to diving (i.e. diving and bill-dipping/up-ending or only bill-dipping/up-ending). The predictor variables in our model were year and the three categories of females. The overall fit of regressions was tested with likelihood ratio tests (analysis of deviance). Good fit is achieved if the deviance is close to the degrees of freedom and the p-value is insignificant. By calculating odds ratios (odds ratio = $e^{\text{parameter estimate}}$) it is possible to characterise the quantitative effects of the predictor variables on the feeding technique of females. The significance of the parameters of the model was tested with Wald's test, which is based on the confidence interval of the odds ratio. A parameter is different from zero ($p < 0.05$) if 1 is not included in the 95% confidence interval of the odds ratio. Because we were unable to gather data on the feeding technique of females of all the categories during the late brood-rearing period in 1995, we compared the feeding technique of females during late brood-rearing with a chi-square test, and the same method was used to analyse the feeding mode of ducklings.

Numerical values are expressed as means ± S.D. In cases with slightly asymmetric distributions, we present median values instead (Sokal & Rohlf 1995).

3. Results

3.1. Distance from shore

Females of the different breeding categories foraged at different distances from the shore during the early brood-rearing season (duckling age 1–15 days) (two-way ANOVA, $F_{2,268} = 48.67$, $p < 0.001$). The difference between years was nonsignificant ($F_{1,268} = 2.89$, $p = 0.09$), as was the interaction of year and category ($F_{2,268} = 0.76$, $p = 0.47$). Non-tending females foraged significantly further off from the nearest shore than lone tenders or multi-female tenders (Tukey's test, df = 268, $p < 0.001$ in both comparisons). Lone tenders foraged closest to the shore and multi-female tenders took an intermediate position, but the differences between these female categories were nonsignificant (Tukey's test, df = 268, $p = 0.17$, Fig. 1). The foraging sites of non-tending females ranged in mean depth from 3.4 to 9.5 m (seven sites, five depth readings from each site). At these sites, blue mussels were abundant. The mean size of mussels ranged from 8.2 ± 1.8 mm ($n = 30$) at the site with the smallest mussels to 19.6 ± 6.6 mm ($n = 30$) at the site with the largest mussels. The variation between sites was significant (one-way ANOVA, $F_{6,203} = 20.5$, $p < 0.001$), but was not correlated with the depth ($r = -0.27$, $n = 7$, $p = 0.56$). Therefore the variation probably reflects a heterogeneous size distribution of mussels at the sampling sites.

Later in the rearing season (late June–July) when the ducklings were ca. one month old, the differences in distance from the shore between foraging tending and non-tending females had almost disappeared. The results concerning lone tenders and multi-female tenders are based solely on the 1995 data, while for non-tending females data for both years were pooled due to small sample sizes. Lone tenders, multi-female tenders and non-tending females foraged significantly farther off shore during the late breeding season (non-tending females: $t_{77} = -4.9$, $p < 0.001$; lone tenders: $t_{110} = -7.1$, $p < 0.001$; multi-female tenders: $t_{111} = -3.5$, $p < 0.001$). The females of the different categories foraged at different distances to shore (Kruskal-Wallis test, $H_2 = 8.3$, $p < 0.05$). Multi-female tenders ($\bar{x} = 17.5 \pm 18.6$ m, $n = 15$) foraged significantly closer to the shore than non-tending females (37.2 ± 27.0 m, $n = 27$) and lone tenders (31.9 ± 38.2 m, $n = 63$; Kruskal-Wallis comparison of mean ranks, $p < 0.05$), but there were no differences between lone tenders and non-tending females (Kruskal-Wallis comparison of mean ranks, $p > 0.05$).

Larger ducklings foraged further from shore (logdistance = 1.05 + 0.35 × (size class); $r^2_{225} = 0.31$, $p < 0.001$).

3.2. Feeding technique

Diving was the primary feeding technique of female eiders throughout the brood-rearing season. During the early brood-rearing period, females also fed by up-ending and bill-dipping, indicating a non-mussel diet. Our logistic regression model of female feeding techniques during early brood-rearing had a good fit (deviance = 0.96, df = 2, $p = 0.62$, Table 1). The predictor variable year was significant ($p < 0.01$): the probability of diving was generally higher in 1995 than in 1994 (Table 1). Lone tenders and multi-female tenders used additional techniques to diving more often than non-tending females ($p < 0.01$, Table 1, Fig. 2). There were no significant differences in feeding technique frequencies between lone tenders and multi-female tenders ($p = 0.11$, Table 1, Fig. 2).

Later in the breeding season females of all the categories fed almost exclusively by diving (Fig. 3). All the data on tending females were from 1995 whereas the data on non-tending females from 1994 and 1995 were pooled (only one observation of non-tending females from 1995). The frequency of foraging modes did not differ among the groups during the late brood-rearing season ($\chi^2_2 = 2.2$, $p = 0.33$).

Ducklings changed their feeding mode as the season progressed. There were no differences between years in the frequency of feeding techniques of small ducklings ($\chi^2_1 = 1.6$, $p = 0.21$), so the data were pooled. The data on the feeding technique of larger ducklings could only be obtained for 1995. Diving was less frequent during early brood-rearing (frequency of occurrence 50%, $n = 69$) than later in the breeding season (frequency of occurrence 95%, $n = 77$) ($\chi^2_1 = 39.6$, $p < 0.001$).

3.3. Duration of dives

The duration of dives of the three female categories was different during the early brood-rearing season (two-way ANOVA, $F_{2,206} = 71.77$, $p < 0.001$). The difference between years was significant ($F_{1,206} = 32.11$, $p < 0.05$); within each female category the mean dive duration was longer in 1995 than in 1994 (Tukey's test, $p < 0.05$ in all cases). There was no year by category interaction ($F_{2,206} = 0.51$, $p = 0.60$). The dives of non-tending females were significantly longer than those of lone tenders and multi-female tenders in both years, but there were no differences in dive duration between the lone tenders and multi-female tenders (Tukey's test, $p < 0.001$ for all compari-

Table 1. Parameter estimates of the logit model for female feeding techniques. The response variable is the probability of a female using additional techniques to diving. Significant parameters set in boldface.

Parameter[a)]	Estimate	S.E.	p	OR	95% CI[b)] of OR
α_{year}	**–1.09**	0.39	0.005	0.34	0.16–0.73
$\beta_{\text{non-tend}}$	**–2.04**	0.75	0.006	0.13	0.03–0.56
β_{parental}	0.65	0.41	0.11	1.91	0.86–4.24

[a)] The coefficient α_{year} is the difference in logits of additional technique probability between years 1995 and 1994, $\beta_{\text{non-tend}}$ is the difference in logits of additional technique probability between non-tending females and brood-caring females (i.e. lone tenders and multi-female tenders) and β_{parental} is the difference in logits of additional technique probability between lone tenders and multi-female tenders.

[b)] A coefficient is different from zero when 1 is not included in the confidence interval of the odds ratio (Wald's test).

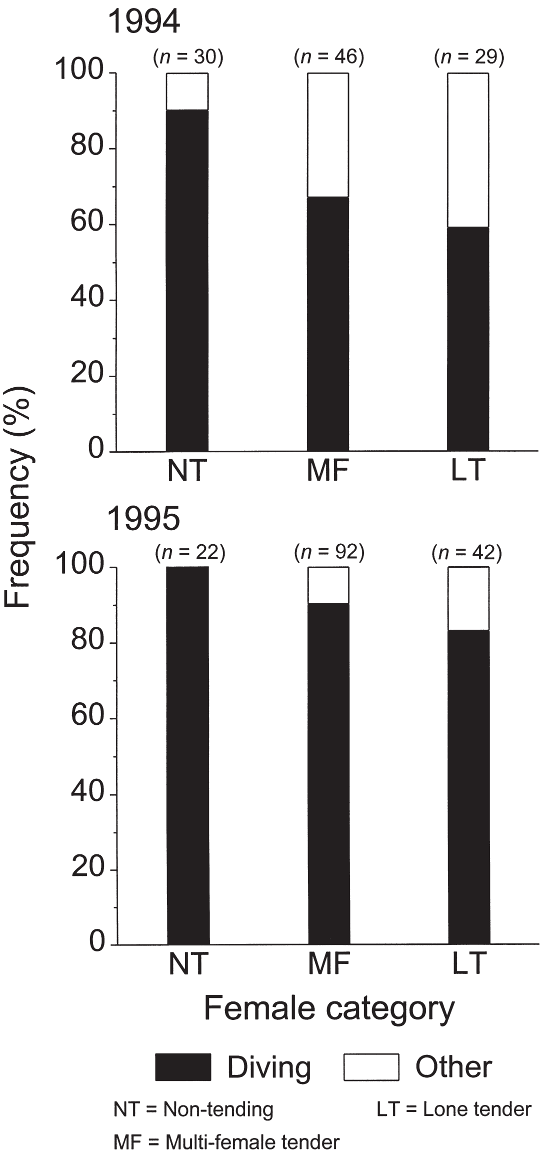

Fig. 2. The frequency of feeding techniques among different female categories during early brood-rearing in 1994 (upper panel) and in 1995 (lower panel). The feeding techniques of females were classified as either only diving or using additional techniques to diving ("other methods").

sons involving non-tending females, $p > 0.05$ for all comparisons of the lone tenders and multi-female tenders, Fig. 4). Lone tenders had the shortest mean dive duration in both years. In 1994, the diving times of the lone tenders even approached those of small ducklings ($t_{44} = 1.92, p = 0.06$, Fig. 4).

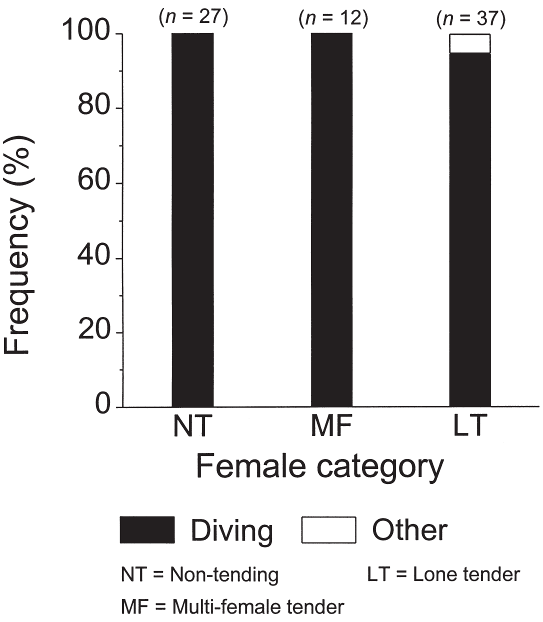

Fig. 3. The frequency of feeding techniques among different female categories during the late brood-rearing season. The data on lone tenders and multi-female tenders are from 1995, and the data on non-tending females were pooled for both years.

With this exception, however, females of all the categories performed significantly longer dives than small ducklings during early brood-rearing.

There were no differences in diving times among females of different categories later in the rearing season (non-tending females (both years pooled): 40.6 ± 9.4 s, $n = 28$; lone tenders (1995): 38.4 ± 14.0 s, $n = 23$, multi-female tenders (1995): 27.3 ± 13.1 s, $n = 2$; one-way ANOVA, $F_{2,50} = 1.28$, $p = 0.29$). Female of all the categories performed longer dives than during early brood-rearing.

Ducklings performed longer dives as they grew (diving time = –1.46 + 11.2 × (size class), $r^2_{60} = 0.67$, $p < 0.001$, Fig. 5). Ducklings of the two largest size classes constituted 65.4% of all observed young during the late breeding season in 1995 ($n = 78$). These ducklings performed dives of equal duration to the females observed at the same time in 1995 (females (all the categories pooled): 37.6 ± 13.7 s, $n = 26$; ducklings: 35.5 ± 12.0 s, $n = 31$; $t_{55} = 0.61$, $p = 0.54$), strongly indicating that both females and ducklings at this stage exclusively fed on a mussel diet.

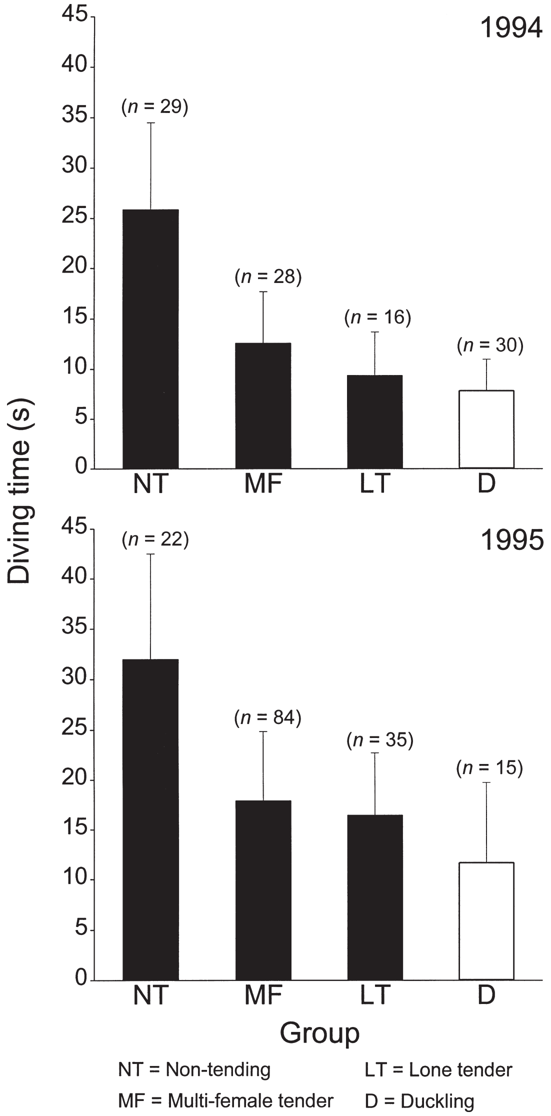

Fig. 4. Mean duration of dives (+ S.D.) of the different female categories and small ducklings during early brood-rearing in 1994 (upper panel) and in 1995 (lower panel).

3.4. Data on individually marked females (1996)

The mean dive duration of females that had completed incubation but soon lost their brood was 46.1 ± 11.4 s (*n* = 7 females), and these females foraged a median distance of 20 m (range 6–100 m) from the nearest shore. The median number of days between observation and estimated hatching was only 5 days (range 0–16 days, *n* = 7).

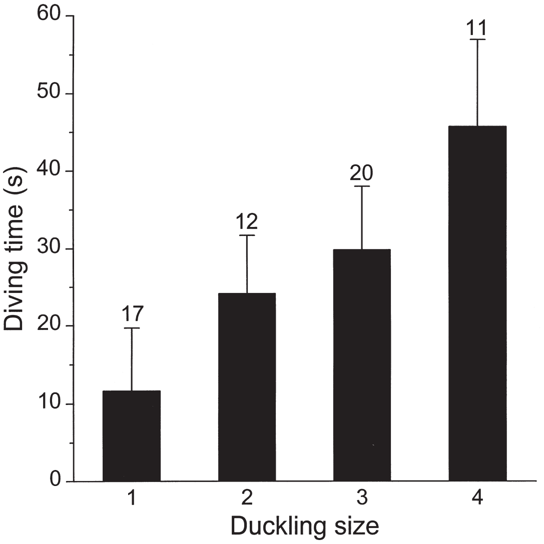

Fig. 5. Mean diving times (+ S.D.) of ducklings in relation to their size. The ducklings were grouped in four size classes in the field by relating the length of the duckling's body to the length of the female's head while swimming. Sample size above the columns.

4. Discussion

We showed that the preferred feeding habitat and feeding mode of females and small ducklings are different during early brood-rearing, indicating a difference in preferred food items (*see* Hario *et al.* 1992). The ducklings exert an influence on the females involved in brood care, by forcing these females to feed like their young. In contrast, non-tending females fed on a mussel diet throughout the breeding season. Individually marked, post-breeding non-tending females performed long dives outside the littoral zone shortly after losing their brood, which suggests that they fed exclusively on mussels. By choosing mussels brood abandoners and failed nesters can avoid parasite infection associated with gammarid consumption, which may be harmful for a female suffering from breeding anorexia. Alternatively, mussels may be energetically more favourable than amphipods, although we do not have sufficient data on the energy intake rate of eiders feeding on these two prey items. This difference between tending and non-tending females is one reason why Baltic eider females in poor condition may increase their own survival by abandoning their brood. Additionally, females might reduce foraging costs associated with brood care by joining multi-female broods. However, the benefit accruing to these females remains unclear, because there were no significant differences in foraging behaviour between lone tenders and multi-female tenders. We also showed that the conflict between female and duckling needs disappears later in the season, as the ducklings changed to a mussel diet and the broods gradually moved seawards. The shift in the diet is clearly reflected in the diving times of ducklings, which gradually increased with duckling size.

Parental care affects the feeding behaviour of eider females in the northern Baltic, although females are not inevitably forced to leave their young in order to feed, as is the case in areas where the spatial segregation between feeding areas suitable for adults and young is large (Gorman & Milne 1972). In the Ythan estuary of Scotland, for example, the large-scale spatial segregation results in large crèches and females form a rotating female cohort tending the ducklings (Gorman & Milne 1972). On the other hand, parental care had little effect on the foraging behaviour of females in northern Norway: all females irrespective of breeding status fed in the intertidal zone by dabbling (Bustnes 1996). In the St. Lawrence estuary of Canada, brood-caring females also fed entirely by dabbling and up-ending in the subtidal zone, but non-tending females dispersed "seaward", probably feeding on mussels by diving (Cantin *et al.* 1974). One important difference between northern Norway and our study area is the number of feeding options. In the Baltic, very few options are available: adults in the non-breeding season feed almost exclusively on blue mussels and small ducklings on gammarids (Lehtonen & Hario 1994, Hollmén *et al.* 1996, Öst & Kilpi 1998). With more feeding options available, the fitness costs of feeding on a non-mussel diet may be smaller for the females. Moreover, oceanic mussel beds are found at smaller depths than in the Baltic, and hence females are able to obtain mussels by dabbling (Pethon 1967, Bustnes & Erikstad 1988, 1990, Nehls 1995). Finally, thin-shelled Baltic blue mussels are presumably easier to utilise by postbreeding females with reduced gizzards than large and thick-shelled Atlantic *Mytilus edulis* (*see* Öst & Kilpi 1998). Our observations demonstrated that postbreeding females, which had completed incubation but soon lost their brood, fed on mussels shortly after hatch.

The body condition of female eiders influences the decision to abandon the brood (Bustnes & Erikstad 1991a, Öst 1999, *see also* Pöysä & Milonoff 1999). Brood abandoners may lay smaller clutches and have a lower body weight at hatching than females caring for young (Bustnes & Erikstad 1991a). Furthermore, the mean weight of those females that changed their behaviour has been shown to be higher in years when they cared for young (Bustnes & Erikstad 1991a, pers. obs.). However, brood abandonment also entails reproductive costs, because the young of abandoners may have a lower survival rate (Bustnes & Erikstad 1991a, Eadie & Lyon 1998). Caring for her own young should, therefore, be the preferred option of a female which resistance to parasite infection is sufficent, or, which is in good enough body condition to feed on prey of a lower energetic value.

We failed to detect significant benefits associated with foraging accruing to multi-female tenders. The feeding habitat, feeding mode and diving time of lone tenders and multi-female tenders were similar. All observed multi-female tenders in this study were of broody or associate status (Bédard & Munro 1976). We may hypothesize that broody females in multi-female broods with the strongest bonds to the ducklings would be forced to feed as their ducklings, whereas subordinate (associate or visiting) females would be able to escape this constraint to some extent and also feed on mussels. More elaborate observations of females of varying status are needed to determine if the foraging behaviour of subordinate and broody females in multi-female broods is different. Furthermore, there may be differences in the total activity budget of lone tenders and multi-female tenders. For example, lone tenders might be forced to devote a larger proportion of time to activities such as vigilance at the expense of feeding.

Parental care in precocial species has been considered less costly to parents than in altricial species, because parents do not feed their young (Schindler & Lamprecht 1987, Williams *et al.* 1994). This study showed, however, that eider females attending young are probably incurring a cost by foraging on amphipods with the ducklings, either because of an increased risk of parasite infection, or due to lower energetic intake. Accordingly, non-tending females immediately switched to a blue mussel diet after losing their brood, and pre-breeding females also exclusively feed on blue mussels if these are available (M. Hario & M. Öst, in prep.). Our study demonstrates that costs other than those directly related to brood care should also be taken into consideration when evaluating the entire parental effort.

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