WITHIN-SEASON AND BETWEEN-YEAR VARIATION IN THE STRUCTURE OF COMMON EIDER BROODS[1]

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Abstract. I studied within-season and between-year variation in Common Eider (*Somateria mollissima*) brood structure, by censusing broods for four years in the northern Baltic. I also examined within-season patterns of female aggressiveness, and explored whether between-year patterns could be related to female body condition at hatching. Multi-female tending was initially the dominant brood rearing strategy. Moreover, 25–38.1% of the lone-tended broods had more than six ducklings indicating that they may contain adopted young. The number of ducklings per female increased with brood size, exposing some newly hatched ducklings to chilling due to unfavorably high ratios of ducklings to brooding females. Lone tenders became proportionally more common, the proportion of two-female tended broods was stable, and the proportion of broods with more than two females rapidly decreased during the season. Female aggression decreased in frequency over time, so the decline of broods with more than two females may relate to female aggressiveness. Family units began to break up when ducklings were 7 weeks old. Multi-female broods were initially more common in years when females were in good condition at hatching and less common in years when females were in poor condition. However, multi-female broods decreased in frequency over time in all years except the poorest year; multi-female tending strategy was most common in poor years and least common in good years. These between-year patterns may result from differences in body condition between lone tenders and multi-female tenders, indicating that female body condition may affect brood-caring decisions.

Key words: Baltic Sea, body condition, brood structure, Common Eider, lone tending, post-hatch brood amalgamation, Somateria mollissima.

INTRODUCTION

Brood amalgamation results in offspring being reared by adults other than their genetic parents. Some of the hypotheses put forward to explain the phenomenon have viewed it as a nonadaptive epiphenomenon (Savard 1987). Alternatively, brood amalgamation has been considered adaptive, entailing benefits to the donor and/or recipient females, or for the young themselves (the social benefit hypotheses; Eadie and Lyon 1998). Recently, Eadie and Lyon (1998) proposed that brood amalgamation may be a function of two separate processes, brood desertion and brood adoption.

Post-hatch brood amalgamation is particularly common among waterfowl (Eadie et al. 1988, Beauchamp 1997, 1998), yet in Anatids it has often been regarded as a nonselected consequence of accidental brood mixing, enhanced by predation (Munro and Bédard 1977a, 1977b) or by intraspecific aggression and territoriality (Williams 1974, Patterson et al. 1982, Savard

1987). The variation in brood amalgamation behavior among Anatids is considerable, making it difficult to draw generalized conclusions about its function for this group (Eadie and Lyon 1998). In some groups, such as geese and shelducks, mated pairs may adopt foreign ducklings (Patterson et al. 1982, Choudhury et al. 1993). In other waterfowl, such as scoters and goldeneyes, amalgamated broods consist of single females tending nondescendant young (Savard 1987, Kehoe 1989). Eiders have a unique parental care system where many females may jointly care for young, and thus a variety of combinations of females and young can be found (Gorman and Milne 1972, Bédard and Munro 1976).

The factors affecting brood abandonment in Anatids are controversial (Bustnes and Erikstad 1995, Pöysä 1995). Evidence supporting the energetic salvage strategy hypothesis has been presented for Common Eiders (*Somateria mollissima*) (Bustnes and Erikstad 1991). According to this hypothesis, females in poor body condition more likely abandon their brood to the care of conspecific females (Eadie et al. 1988). Brood abandonment increases the donor female's survival at the expense of current season's repro-

duction. If body condition affects brood-caring decisions, annual differences in female condition may be reflected in the structure of broods.

The status of females in eider broods with several females is hierarchic, and agonistic interactions among females maintain this hierarchy (Bédard and Munro 1976, Schmutz et al. 1982). Brood amalgamation in eiders is assumed to take place mainly during the ducklings' first week of life (Munro and Bédard 1977a), but the number of females in multi-female broods may vary throughout the breeding season (Ahlén and Andersson 1970, Bédard and Munro 1976). When ducklings approach fledging, family units disintegrate spontaneously (Munro and Bédard 1977a).

This paper describes the compositional structure of Common Eider broods in the northern Baltic. Very few descriptions of this structure exist for the Baltic (Hildén 1964). Firstly, I focused on structural changes during the breeding season. I discuss whether female aggressiveness may influence the within-season pattern, by presenting data on the frequency of female aggression during different phases of brood rearing. Secondly, I studied between-year variation in brood structure, and examined whether these patterns were related to female body condition at hatching. No detailed study on annual variation in brood structure has yet been made.

METHODS

STUDY AREA

The study was carried out in the northern Baltic, east of Hanko (60°N, 23°E), southwest Finland, close to the Tvärminne Zoological Station, in 1995–1998. The study site is a complex of islands, islets, and small skerries (Öst and Kilpi 1997). Eiders breed on small, open islands and on larger, wooded islands covered by spruce (*Picea abies*) and pine (*Pinus sylvestris*) (Kilpi and Lindström 1997). The area holds about 1,500 breeding pairs. Broods with small young forage mainly on amphipods (*Gammarus* spp.) in the littoral zone (Hario et al. 1992). Larger ducklings utilize blue mussels (*Mytilus edulis*), so broods move to the mussel beds farther from shore as ducklings grow. The mussel beds occur on hardbottoms at depths of 3–12 m (Öst and Kilpi 1997). Habitat patches suitable for small ducklings (i.e., with gammarids) and the preferred patches of adults (mussel beds) are close

together but do not overlap (Öst and Kilpi 1997).

CENSUSES OF BROODS

Broods were observed from vantage points on islands along a fixed census route with binoculars and a 30× spotting scope. The same vantage points were used in all years and censuses were made in good weather, when waves did not interfere with observations. The first census was made at peak hatching, which occurs at the end of May-beginning of June, depending on the phenology of the year. Thereafter, censuses were carried out with intervals of about one week until most ducklings had dispersed to the outer archipelago zone. Because the census dates each year were adjusted to the phenology of the year, the censuses represent equivalent phases of the annual breeding cycle. Although mixing of broods with young born before and after peak hatching adds some noise to the data, hatching is generally very synchronous. For example, 50% of all females trapped in 1998 ($n = 81$) hatched within less than 4 days. Complete series of censuses (6) were accomplished in 1997 and 1998. Only three complete censuses (census 1, 2, and 5) were made in 1995. In 1996, only the first two censuses were made because high duckling mortality led to a rapid disappearance of almost all broods. Female status within multi-female broods (Bédard and Munro 1976) was not determined during the censuses, because this is time-consuming and requires that broods are at close observation distances. Lone tenders, two-female broods, and broods with more than two females were analyzed separately. The number of fledged young each year was counted in August immediately prior to fledging.

I tried to attain a minimum estimate for females adopting young, although the extent of adoptions is impossible to determine exactly without marked ducklings. The error is smaller for lone tenders than for multi-female broods, in which the origin of young is more mixed. The mean clutch size in the area is 4.4 on open islands and 5.2 on wooded islands (Kilpi and Lindström 1997). The proportion of clutches with more than six eggs in 1995–1998 varied between 3.9% in 1995 ($n = 51$) and 5.7% in 1996 ($n = 154$), the annual mean ($\pm$ SD) being 5.0 $\pm$ 0.8% ($n = 4$ years). Many of these nests were undoubtedly parasitized. I made the assumption that lone tenders with more than six

ducklings may have adopted young. The estimate is conservative due to duckling mortality, and thus underestimating the extent of adoptions, especially towards the end of the breeding season. I therefore derived estimates for the first census only.

DATA ON FEMALE BODY CONDITION AND AGGRESSIVENESS

Nesting females were trapped with hand-nets, weighed to the nearest 10 g on a Pesola spring balance, and the length of the radius-ulna was measured with a steel ruler to the nearest 1 mm to obtain a measure of structural size. Trapping was timed to coincide with, on the average, the last week of incubation, both to minimize disturbance and to reduce variance in the time females had been incubating. The final weight of females at hatching was calculated from these weight data combined with knowledge of incubation time of trapped females each year. Incubation time was determined directly by observing signs of hatching at the nest, or by a water-test, where the incubation stage is established by the way the egg floats in a bucket of water (Kilpi and Lindström 1997). Females do not eat during incubation, and consequently they lose 10–30 g of their body weight per day. Weight loss is slightly curvilinear, so body weight and time incubating were log-transformed. In addition, weight loss is faster on open islands, and also year-dependent, so separate regression equations for weight against incubation time were used for females trapped on open and wooded islands for different years, to correct the estimate of weight at hatching (Kilpi and Lindström 1997). Female weight at hatching divided by radius-ulna length was used as a simple condition index.

I examined female aggressiveness during brood rearing using data on females individually marked with a wing-tag in 1997–1998. These females were peak breeders, nesting on both open and wooded islands in the study area. When a focal female was encountered, brood structure was recorded, including status of all participating females (lone tenders, broody, associate and visiting females in multi-female broods). Broody females lead the group during movements, they do most of the vocalization and vigilance behavior, and brood the young. Associate females are less active but nevertheless tend to stay close to the ducklings, whereas visiting females stay at the fringe of the brood

(Bédard and Munro 1976). I observed the females for varying lengths of time (median = 5 min, range 0.5–32 min), recording the number of aggressive encounters of the marked bird, and the initiator of these encounters. Because the focus was on aggressiveness during brood rearing, observations of females without young were excluded. Focal watches varied in length because the determination of status sometimes required a lot of time, whereas in other cases the bird was soon lost from sight. I also determined the time period between observation of a female and the estimated day her brood had hatched. For each female, I calculated the frequency of aggression during the early vs. late brood rearing season, defined as the total number of aggressive encounters per total observation time during that study period. The dividing line between the periods was set at 15 days posthatch, corresponding to the time the first and second brood censuses were made. I made a total of 285 observations of 90 marked individuals, but only a part of these data were used to avoid pseudoreplication (see Data Analysis).

DATA ANALYSIS

Because the broods encountered during consecutive censuses each year were largely the same, the observations from different censuses were dependent. Because it was impossible to individually recognize broods during these mass sampling events, statistical tests for dependent observations could not be used. I therefore treated the data as independent observations in the analysis. To compensate for the inflated sample sizes associated with independent tests, I used an α level of 0.01 to decrease the probability of committing a Type I error. I examined within-season trends in brood structure with Spearman rank correlations based on census-specific overall values. I restricted these trend analyses to the years with a complete series of censuses, 1997 and 1998. A chi-square test was used for the analysis of adoptions in different years. I used a log-linear model to compare the incidence of multi-female vs. lone tending during the first two censuses in different years. My data were organized as a three-way contingency table, in which the three classifying factors were female category (multi-female broods vs. lone tenders), year, and census. I fitted models, starting from the most complex model (Sokal and Rohlf 1995) assuming an interaction among all factors (Table

TABLE 1. The estimated mean weight of trapped Common Eider females at hatching, the mean body condition index (weight at hatching/radius-ulna length), sample size of trapped females, and the number of fledged young in 1995–1998. Observations of females trapped in more than one year were excluded. The number of young produced is the total number in the study area, which held approximately 1,500 breeding pairs.

Year	Weight at hatching (g)	Body condition	n	Fledged young
1995	1,566 ± 107	14.6 ± 1.0	45	2,000
1996	1,287 ± 176	11.9 ± 1.5	58	100
1997	1,416 ± 129	13.3 ± 1.1	107	1,000
1998	1,516 ± 105	14.0 ± 0.9	69	600

3). A model gave a reasonably good fit if the log-likelihood statistic had a P-value exceeding 0.1. The results of the log-linear analysis were compared with the data on female body condition in different years.

The data on female aggressiveness contained dependent observations, because some females were observed during both the early and late brood rearing season. I therefore included only females observed during both periods in the analysis. For these females, I compared the frequency of aggression during early vs. late brood rearing using a Wilcoxon's signed-ranks test. Kruskal-Wallis ANOVA using two-tailed probabilities was applied to test for differences in independent quantitative variables, because these variables did not fulfill the assumptions of parametric tests. The data on female body condition included some observations of females trapped in more than one year. Altogether 40 trappings (12.5%) out of the total sample of 319 trapped females in 1995–1998 dealt with females captured at least twice. These 40 observations were excluded to make the observations among years completely independent. Numerical values are expressed as means ± SD.

RESULTS

FEMALE CONDITION

The mean body-condition index of females varied between years (Kruskal-Wallis test, H_3 = 100.7, P < 0.001). The condition index was significantly higher in 1995 and 1998 than in 1997, and the index was lowest in 1996 (Kruskal-Wallis comparison of mean ranks, P < 0.05) (Table 1). In years when females were in good condition at hatching, fledgling production was usually high (Table 1). However, females were in good condition in 1998 but the reproductive output was low. Judged by female condition at hatching, the years can be ranked in the order 1996, 1997, 1998, and 1995; 1996 being an extremely poor and 1995 a very good year.

WITHIN-SEASON AND ANNUAL VARIATION IN BROOD STRUCTURE

An average brood at peak hatching had slightly more than two females, 8–12 ducklings, and the ratio of ducklings to females was about 5:1 (Table 2). The mean number of ducklings, females, and the ratio of ducklings to females in broods decreased significantly during the breeding season in both 1997 and 1998 (Table 2).

Brood composition differed among years in the first census, when the impact of variable duckling mortality was still insignificant. Both the mean number of ducklings (H_3 = 22.4, P < 0.001) and females (H_3 = 17.9, P < 0.001), as well as the mean ratio of ducklings to females (H_3 = 11.9, P < 0.01) differed among years. The number of ducklings and the ratio of ducklings to females in broods were significantly higher in 1997 compared with 1995 and 1996, but did not differ significantly from the intermediate year 1998. The number of females was significantly higher in 1997 and 1998 than in 1996, whereas the number of females in 1995 did not differ significantly from any other year (Kruskal-Wallis comparison of mean ranks, P < 0.05) (Table 2).

The number of ducklings per female increased with brood size: the ratio of ducklings to females in broods correlated positively with duckling number in the first census in all years (r_s ≥ 0.58, n = 179 to 282, all P < 0.001). However, this ratio may have an upper limit because the brood may have too few females to brood all the young against chilling. Ducklings depend on brooding for one to two weeks. One female can brood 10 newly hatched young according to a conservative estimate, so broods exceeding a ratio of 10 ducklings per female during the first census would not provide adequate brooding for all ducklings (Mendenhall 1979). The proportion of these "excess" young potentially exposed to chilling was 9.0% in 1995, 5.0% in 1996, 3.2% in 1997, and 5.1% in 1998. For all years, these young constituted 5.7% (n = 571) of all observed young in the first census.

The proportion of lone tenders with more than six ducklings in the first census varied between

TABLE 2. The mean ± SD (n) number of ducklings and females in broods, and the average ratio of ducklings to females for all censuses 1995–1998. Dash indicates lack of data. All differences between censuses were significant in both 1997 and 1998 ($r_s \leq -0.94$, all $P < 0.01$).

| Census	Ducklings brood⁻¹				Females brood⁻¹				Ducklings female⁻¹			
	1995	1996	1997	1998	1995	1996	1997	1998	1995	1996	1997	1998
1	9.4 ± 9.2 (280)	8.3 ± 6.7 (282)	11.7 ± 9.4 (179)	11.4 ± 11.2 (260)	2.1 ± 1.3	2.1 ± 1.3	2.5 ± 1.8	2.5 ± 1.7	4.9 ± 5.0	4.6 ± 3.9	5.2 ± 4.0	4.8 ± 4.0
2	6.5 ± 6.3 (222)	4.8 ± 5.2 (109)	6.9 ± 7.4 (257)	7.9 ± 8.9 (275)	1.5 ± 0.7	2.1 ± 1.4	1.7 ± 0.9	1.7 ± 0.9	4.7 ± 5.0	2.5 ± 2.1	4.3 ± 4.0	4.9 ± 5.8
3	—	—	5.8 ± 4.9 (317)	5.2 ± 4.9 (309)	—	—	1.6 ± 0.7	1.6 ± 0.7	—	—	3.8 ± 3.2	3.4 ± 3.1
4	—	—	5.1 ± 5.8 (362)	4.0 ± 3.7 (276)	—	—	1.6 ± 0.8	1.5 ± 0.6	—	—	3.4 ± 3.5	2.8 ± 2.4
5	6.3 ± 7.9 (246)	—	4.2 ± 5.2 (362)	3.2 ± 2.6 (249)	1.2 ± 0.5	—	1.4 ± 0.6	1.4 ± 0.6	5.7 ± 7.5	—	3.0 ± 2.8	2.4 ± 2.0
6	—	—	3.9 ± 4.3 (316)	2.8 ± 2.4 (202)	—	—	1.1 ± 0.5	1.3 ± 0.5	—	—	3.2 ± 3.3	2.2 ± 1.7
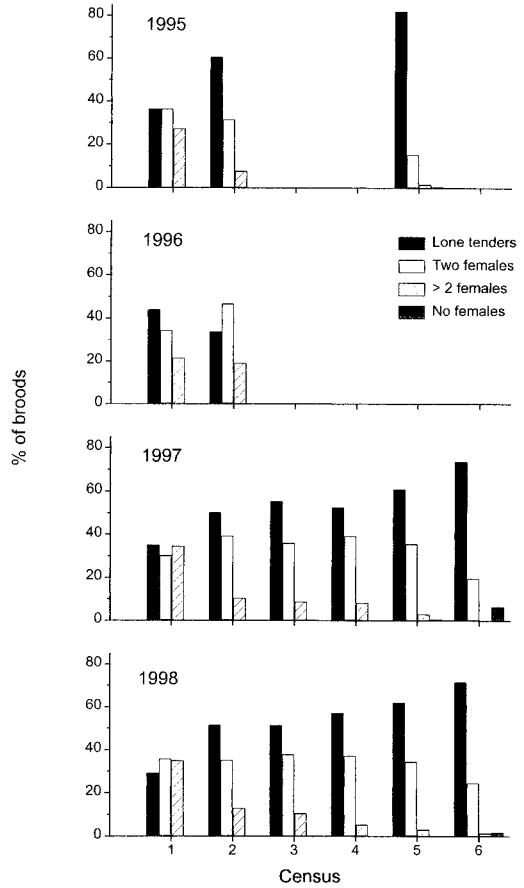
FIGURE 1. The proportion of broods tended by lone tenders, two females, more than two females, and broods without tending females in the censuses 1995–1998.

25.0% in 1996 (31 out of 124 lone-tender broods) and 38.1% in 1997 (24 out of 63 broods). These values represent a minimum estimate of the proportion of lone-tender broods that may contain adopted young. The proportion of lone-tender broods with excess young did not differ among years ($\chi^2_3 = 3.6$, $P = 0.3$).

Depending on the year, 29–44% of broods were initially tended by single females (Fig. 1). Multi-female tending was thus initially the dominant brood rearing strategy. The proportion of lone tenders increased with time ($r_s = 0.94$, $n = 6$, $P < 0.01$ in both 1997 and 1998), whereas the proportion of two-female broods was stable (1997: $r_s = -0.37$, $n = 6$, $P > 0.4$; 1998: $r_s = -0.54$, $n = 6$, $P > 0.2$) (Fig. 1). In contrast, the proportion of broods with more than two fe-

TABLE 3. Log-linear models fitted to the incidence data on multi-female vs. lone tending in different years during the first two censuses. A model gave a reasonably good fit if the G-statistic had a P-value exceeding 0.1. Interaction terms are separated by $\times$, semicolons separate independent factors. The three classifying factors were year, female category, and census.

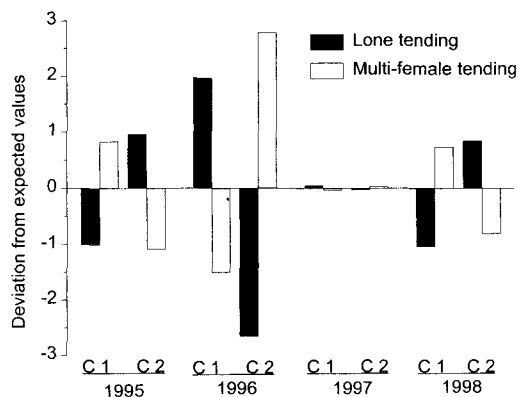| Model	G	P
Year $\times$ female category $\times$ census	−0.0	1.0
Year $\times$ female category; female category $\times$ census; year $\times$ census	28.0	<0.001
Year $\times$ census; female category $\times$ census	34.5	<0.001
Year $\times$ female category; female category $\times$ census	119.3	<0.001
Year $\times$ census; female category	76.3	<0.001
Female category $\times$ census; year	124.7	<0.001
Year $\times$ female category; census	161.1	<0.001
Year; female category; census	166.5	<0.001

FIGURE 2. Deviations between observed and expected frequencies of lone tenders and multi-female broods in the first two censuses in 1995–1998 (C 1 = census 1, C 2 = census 2). These deviations are described by the standardized residuals of the model testing for two-factor effects (year $\times$ category; category $\times$ census; year $\times$ census). This model was chosen because it accounted for most of the interactions among the factors, but still did not fit the data adequately, as opposed to the saturated model assuming a three-factor interaction, which had a perfect fit.

males showed a marked decline over the course of the breeding season ($r_s = -1.0$, $n = 6$, $P < 0.001$ in both 1997 and 1998), rapidly decreasing in number to a low level from the first to the second census (Fig. 1). Broods without females were found only in the last two censuses, so the break-up of family units began when ducklings were about 7 weeks old (Fig. 1).

The only model giving a reasonably good fit for within-year and between-year differences in tending strategy patterns was the saturated model assuming a three-factor interaction, indicating that all factors were dependent on each other (year $\times$ category $\times$ census; df = 0, Table 3). The model testing for two-factor effects did not acceptably fit the data (year $\times$ category; category $\times$ census; year $\times$ census; df = 3, Table 3). The standardized residuals of the model with two-factor effects were used to assess the direction of deviations from expected values. The deviations from expected values in different years were compared with data on female body condition at hatching. In the first census, lone tending was especially common in the poor year 1996, and, correspondingly, multi-female tending was most common in the two best years 1995 and 1998, followed by the intermediate year 1997 (Fig. 2). In the second census, multi-female tending was most common in the poor year 1996, least common in the best years 1995 and 1998, and again intermediate in 1997 (Fig. 2). It is noteworthy that multi-female broods de-

creased in frequency from the first to the second census in all years except the poorest year 1996.

FEMALE AGGRESSIVENESS

All aggression was directed against females either within the same brood or in adjacent groups, except for two females showing aggression towards ducklings. The frequency of aggression during both the early and late brood rearing season was determined for 26 individual females. The number of females per brood may influence the opportunity for aggression, but for this sample of females the mean number of females in the brood was similar during the periods (early period: 2.33 $\pm$ 1.79 females; late period: 2.08 $\pm$ 1.16 females; Wilcoxon's signed-ranks test: $z = 0.4$, $n = 26$, $P > 0.4$). The mean frequency of aggressive encounters tended to decrease over the course of the season (early period: 1.97 $\pm$ 6.15 hr^{-1}; late period: 0.49 $\pm$ 1.37 hr^{-1}; $z = 1.8$, $n = 26$, $P = 0.07$). Twenty-six birds out of a total of 90 brood-caring females in 1997–1998 initiated aggressions; 10 of these were lone tenders, 15 of broody status, and only 1 female of associate status in multi-female broods. I did not directly witness permanent exclusion of females during the focal watches. However, females in the same brood sometimes

fought violently with each other soon after hatch, and this was often followed by a break-up of the original family unit within a few days.

DISCUSSION

The structure of eider broods showed a regular pattern of within-season change, and a distinct pattern of between-year variation. The number of females in broods was most variable around peak hatching. Broods with more than two females soon decreased in frequency to a low level, the proportion of lone tenders increased, and the frequency of two-female broods remained fairly stable throughout the season. Aggression of brood-caring females tended to decrease with time, which may be related to the decline of broods with more than two females. Multi-female tending was initially most common in years when average female body condition was the highest, but it decreased in frequency within two weeks after peak hatching in all years except the poorest year.

The brood composition resembles that reported from the St Lawrence estuary, Canada (Bédard and Munro 1976), or the Gulf of Bothnia, Finland (Hildén 1964). Broods in St Lawrence were stable, the minimum duration of the parental bond being 40 days (Bédard and Munro 1976). Correspondingly, I found that the number of females in broods was roughly the same during the 2–7 weeks posthatch, indicating stability. Observations of marked individuals from the study area also suggest that broods are rather stable, apart from a short variable phase immediately following hatch (Kilpi et al., unpubl. data). This indicates that broods usually amalgamate soon after hatch, although transfer of young also occurs later in the rearing season (Kilpi et al., unpubl. data). Brood structure is very different in areas such as the Ythan estuary, Scotland (Gorman and Milne 1972) or the Dutch Wadden Sea (Hoogerheide 1950, Swennen 1989), where broods are large and very unstable, with a rotating female cohort tending the ducklings (Gorman and Milne 1972). A common feature is the large-scale spatial segregation between duckling and adult foods (Gorman and Milne 1972, Swennen 1989). Females may thus be forced to leave the young in order to feed (Gorman and Milne 1972), which may explain the large size and instability of broods. In the Baltic, the spatial segregation of habitat patches suitable for small ducklings and adults is only a few meters (Öst and Kilpi 1997). Females tending small young feed on nonpreferred prey, gammarids, but this phase lasts only a couple of weeks.

The ratio of ducklings to females in eider broods shows little geographic variation (Bédard and Munro 1976). The initial ratio in my study area (5:1) is higher than those previously reported—3.5:1 in Scotland (Gorman and Milne 1972), 3.15:1 in St Lawrence (Bédard and Munro 1976), and 2.1–3.3:1 in the Netherlands (Swennen 1989). Severe gull predation leads to high initial duckling mortality, and the number of females is initially higher in these populations, lowering the ratio (Munro and Bédard 1977b, Mendenhall and Milne 1985, Swennen 1989). Geographic clutch size variation is small, so clutch size hardly affects the ratio. The number of ducklings per female has been considered stable or increasing during the rearing season (Ahlén and Andersson 1970, Gorman and Milne 1972, Bédard and Munro 1976). Duckling numbers decrease with time due to mortality, but this loss is offset by a simultaneous decrease in the number of tending females (Ahlén and Andersson 1970, Bédard and Munro 1976). However, I found that the number of ducklings per female decreased with time. The primary reason is duckling mortality, but in my study area the simultaneous departure of females from broods does not seem to equal duckling losses, because broods initially have fewer females. Mendenhall (1979) found that the ratio of ducklings to females was lower in the smallest broods, but for larger broods it did not correlate with duckling number. I found that the number of ducklings per female increased with duckling number. Exclusion of the smallest broods gave the same result. The risk of chilling may be larger in large broods. Nonetheless, chilling seems to be a minor cause of mortality, because only 5% of newly hatched young are exposed to it. Mendenhall (1979) obtained similar results.

The females departing from multi-female broods are probably of subordinate status (Bédard and Munro 1976, Swennen 1989). I found that one or two females tended the majority of broods soon after peak hatching. Groups with two broody females often form stable coalitions with little aggression between the females (Bédard and Munro 1976, Bustnes and Erikstad 1995). The departure of low-ranking females may result from aggressiveness from broodier

females, weakening maternal motivation, or a behavioral conflict between weakening maternal motivation and increasing hunger (Ahlén and Andersson 1970, Munro and Bédard 1977a, Swennen 1989). My results indicate that aggressiveness of broody females might play a part in driving away subordinates. Alternatively, temporary brood attendance may be a reproductive tactic of the female. For example, her own brood may have suffered high initial brood loss, making continued parental care unprofitable (the brood success hypothesis; Pöysä et al. 1997). By temporarily attending the group, her young may receive continued care, while she may soon be freed from parental duties.

Initially, multi-female broods were especially common in years when female body condition was the highest, but in the next census these were more common in poor years. According to another study from the same area, females using a multi-female tending strategy are, on average, in slightly better body condition at hatching than lone tenders, which in turn are in better condition than brood abandoners (Kilpi et al., unpubl. data). This is in line with the observation that lone tending was initially more common in years when overall female body condition was poor. According to the energetic salvage strategy hypothesis, lone tenders might thus be more prone to abandon their brood than multi-female tenders. This in turn might explain the observed decline in the frequency of lone tending from the first to the second census in a poor year. The decision to abandon is probably made soon after hatch, because the chances of finding parents willing to adopt may be lower after strong parental bonds develop (Bustnes and Erikstad 1995). In a favorable year, more females would be capable of rearing broods successfully, including lone tenders. The proportion of lone tenders would then increase after the break-up of broods with more than two females. Two-female broods also decrease slightly in frequency when family units start to break up, further increasing the proportion of lone tenders. The factors possibly causing differences in condition between lone tenders and females using a multi-female tending strategy are currently under investigation.

Nest density is a key determinant of pre-hatch brood amalgamation in waterfowl (Beauchamp 1997, Robertson 1998), and may also affect the opportunities for post-hatch brood amalgamation, given that high nest-density may increase the likelihood of brood encounters after hatching (Beauchamp 1997). However, because the breeding population at Tvärminne has been stable during the study period, it is unlikely that the observed between-year patterns in the frequency of tending strategies are primarily caused by annual differences in nest density.

The proportion of lone-tender broods with excess young was similar among years despite considerable annual variation in the proportion of brood abandoners, and thus variation in the number of potential adoptees. This may indicate selection acting on parents to prevent the adoption of unrelated young (Eadie and Lyon 1998). Adoption has been argued to be of little or no cost to adults in precocial species (Pierotti 1988, Williams 1994), yet females often treat foreign young with marked hostility indicating some potential cost of adoption (Eadie and Lyon 1998, pers. observ.).

Because this study does not present data on individual females, it is difficult to separate between alternative hypotheses explaining brood-caring decisions. For example, it may be difficult to distinguish between the brood success and energetic salvage strategy hypotheses if early brood mortality varies in unison with overall female body condition. However, the year 1998 is exceptional because females were in good condition at hatching, and yet fledgling production was low. The structure of broods in 1998 closely resembles the structure of the best year 1995 (Fig. 2), although duckling mortality was nearly as high as in the poorest year 1996. This indirectly supports the conclusion that female body condition *per se* influences brood-caring decisions.

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