Female characteristics and parental care mode in the crèching system of eiders, *Somateria mollissima*

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Eider females may abandon their young, care alone, or join in multifemale crèches. We studied the characteristics of female eiders adopting these strategies in 1996–1999. Female condition at hatching varied significantly between years. Over all years, 31% of all females abandoned, 23% tended alone and 46% crèched. In the year when average female condition at hatching was lowest, abandonment rate peaked (67%). Crèching birds were further identified as true crèchers staying more than 2 weeks with the original crèche, and transient crèchers leaving the crèche. The condition of females shortly before hatching showed a decreasing trend, with lone tenders being in best condition, followed by true crèchers, transient crèchers and abandoners. Clutch size, date of hatching relative to the population median, and female body size did not differ between groups. Individual females switched between care modes between years. Females weighed significantly less when abandoning than when tending, with no significant weight difference when the females remained as tenders between 2 years. This is consistent with the energetic salvage strategy hypothesis, which states that females in poor body condition should be more prone to abandon their brood. Our results support an adaptive approach to offspring care behaviour in eiders, driven by female condition.

Parents of long-lived species face a trade-off between current and future breeding attempts (Lindén & Møller 1989; Clutton-Brock 1991). These trade-offs may involve decisions at the brood-rearing stage, where parents have the option of rearing or not rearing. Intraspecific brood amalgamation is common in waterfowl with self-feeding young (Eadie et al. 1988; Beauchamp 1997). It provides a way of reducing the cost of abandonment, provided that some parents accept unrelated young. However, the determinants of intraspecific brood amalgamation in waterfowl remain poorly understood (Savard et al. 1998).

Crèching behaviour, where parents care for young from other individuals, is a classic example of apparently co-operative behaviour (Eadie et al. 1988). So far it has been studied almost exclusively from the perspective of social benefits to the donor and/or recipient parents, assuming that adoption is the behaviour under selection (Eadie & Lyon 1998). According to an alternative interpretation

(Eadie & Lyon 1998), crèching is driven by parental investment decisions of the donor parent, such that parents abandon young when the costs of continued care are high, or the benefits of care are low. Amalgamation of broods may then be a secondary outcome of selection acting on deserted offspring to find another brood to join. Furthermore, amalgamation also involves parental acceptance of unrelated young, and selection acting on avoidance or acceptance. Among the explanations for brood abandonment is the energetic salvage strategy hypothesis (Eadie et al. 1988), which predicts that females in poor body condition abandon their young to improve their own survival. Brood abandoning would therefore represent a situation in which an individual sacrifices its current reproductive success to improve its residual reproductive value.

Decisions about whether to continue brood care could also be based on expected benefits of care, for example the reproductive value of the brood itself (Carlisle 1985; Pöysä et al. 1997; Eadie & Lyon 1998; Pöysä & Milonoff 1999). The current fitness value of a brood can be divided into brood size and survival prospects. If these are low, then the cost of continued care may not be outweighed by the fitness return and parental care should terminate.

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In this case the proximate cue to brood abandonment may be brood size as such (Eadie & Lyon 1998) or it could be based on the survival prospects of the young, given that past mortality predicts future mortality of the brood (Carlisle 1982, 1985; Pöysä et al. 1997). Small clutch size or brood size increases the likelihood of desertion in many birds (Székely et al. 1996).

Eiders are long-lived sea ducks (Coulson 1999) and extreme capital breeders, subject to substantial costs prior to hatching (Korschgen 1977; Parker & Holm 1990; Kilpi & Lindström 1997). Females do not feed during incubation, leading under some circumstances to extreme postincubation anorexia, and much variation in female body condition both within and between breeding seasons (Öst 1999). Therefore, at hatching the survival prospects of some females could be severely reduced if they continued brood care. Bustnes & Erikstad (1991) found that abandoning and caring were not obligate individual strategies in the eider, but changed between years. They also presented evidence for the energetic salvage strategy hypothesis, showing that females in poor condition were more likely to abandon their brood. Our first aim was to test the validity of the energetic salvage strategy hypothesis.

In eiders female parental care options include abandonment, care for young by a single female which may also accept unrelated young, and joint care by two or more females in crèches, which may involve additional acceptance of unrelated young (Bédard & Munro 1976; Munro & Bédard 1977a; Bustnes & Erikstad 1991; Öst 1999). The last option is unique to eiders among waterfowl. There are few specific hypotheses as to which factors might affect lone tending or multifemale tending as alternative care modes. Our second aim was to see whether body condition and structural size of females might provide a cue to parental behaviour in tending females. Brood care in eiders consists of vigilance, brood defence and brooding of newly hatched young. It also entails indirect costs, because females are prevented from feeding on preferred prey (Öst & Kilpi 1999). As lone tenders probably pay the highest costs of brood care in terms of feeding constraints during early rearing (Öst & Kilpi 1999), lone tending may be a feasible option only for hens in good condition. Accordingly, Öst (1999) found that within 2 weeks of hatching, multifemale tending was more common than lone tending in years when the average condition of females was low. Based on this, we hypothesized that lone tenders should, on average, be in better body condition than crèching females. To our knowledge, this is the first study to address this central question.

The number of females in eider crèches decreases in the course of the season (Bédard & Munro 1976; Munro & Bédard 1977a; Öst 1999). These transient crèchers leave the offspring before parental care is typically terminated, and thus they should be regarded as abandoners, according to Székely et al.'s (1996) definition. We therefore hypothesized that such females should be in poorer body condition than permanently crèching birds, in accordance with the energetic salvage strategy hypothesis. Alternatively, they could base their decision to terminate care on brood value cues. Our third aim was to establish how long female crèche attendance lasts, and relate it to female characteristics.

METHODS

Data Collection

We carried out the study on the Hanko Peninsula, southwest-Finland (60°N, 23°E), in 1996–1999. The study area has been described by Kilpi & Lindström (1997) and Öst & Kilpi (2000). Eiders in the area breed colonially on small barren islets (average 1 ha) or larger wooded islands (average 9 ha), with certain islands being favoured (Öst & Kilpi 2000). The area holds annually ca. 1500 nesting females, and the population has been stable over the study years (unpublished data). The Baltic Sea is nontidal, and contains only few organisms that eiders can feed on (Öst 1999; Öst & Kilpi 1999).

We annually followed laying on a number of selected islands (9, 10, 12 and 11 in 1996, 1997, 1998 and 1999, respectively), establishing nest initiation dates for a large set of nests. Each year we then trapped females from these nests, using hand nets towards the end of the incubation period. Trapped females were ringed and weighed (to the nearest 10 g), and the length of the radius–ulna was measured (to the nearest 1 mm) and used as a structural size measurement. All weights and measurements were taken by the same person (M.K.) each year to reduce interobserver variance. We also attached a unique coloured flag of 3×3 cm to the third outermost primary. We checked the nest contents at trapping, and another one or two times (twice if we found the nest during laying) to record hatching success. Females known to have deserted the nest prior to hatching were not included in the analyses, because desertion was usually caused by predation.

We determined the timing of breeding of each female each year. Each female was then compared with the median for the entire annual sample. For many of the nests we knew true initiation or hatching dates, and for clutches with uncertain initiation date, we established the incubation stage with a water test. The difference between the estimated and the true incubation stage was not significant (Kilpi & Lindström 1997). We timed our trapping in such a way that we trapped females from the peak breeding cohort, avoiding early and late females. To the best of our knowledge, the females represent experienced breeders laying during the population laying peak. By including only females from the peak breeding cohort, we were able to avoid some confounding factors: egg predation is disproportionately high in the earliest breeders (unpublished data), and, in many birds, broods hatched late in the season are more often deserted than early broods (Székely et al. 1996). We used the incubation stage to estimate the remaining incubation time. We calculated the final weight of all females at the time of hatching by regressing body weight on incubation time (log-transformed data on weight and time, females that had incubated less than 10 days were excluded). A female's weight change during incubation depends on the year and the type of island she uses, weight loss

Table 1. Condition index, weight at hatching, daily weight loss on open (O) and wooded (W) islands, the R^2 of the regressions of log-transformed body mass on log-transformed incubation time, and the total number of fledged young for the entire population of ca. 1500 females

Year	Condition*	Weight (g)	N	Daily weight loss (g)	R^2	Fledged young
1996	−1.0±1.3	1358±176	46	O: 39.7±15.1 N=24	0.23	100
				W: 21.6±6.8 N=36	0.21	
1997	−0.1±1.0	1434±135	98	O: 31.0±3.7 N=54	0.53	1000
				W: 16.1±3.9 N=63	0.20	
1998	0.2±0.7	1490± 96	87	O: 12.1±4.9 N=44	0.13	600
				W: 13.4±3.2 N=64	0.21	
1999	0.4±0.7	1527±102	91	O: 12.5±6.7 N=44	0.08	1200
				W: 25.4±4.3 N=65	0.36	

For details on data selection, see Methods. Means are given±SD.
*The condition index was derived as the standardized residuals of actual body masses from those predicted from regressions of log-transformed body mass on log-transformed length of radius–ulna.

usually being greater on open islands (Kilpi & Lindström 1997; Öst 1999). Therefore, our condition index was based on weight loss regressions for both types of islands (open versus wooded) for each year separately. Condition indices were derived as standardized residuals of actual body masses from those predicted from regressions of log-transformed body mass on log-transformed length of the radius–ulna (e.g. Ormerod & Tyler 1990).

We observed females and broods in the field with the aid of spotting scopes (32–60 ×). We tried to locate as many females as possible on their projected day of hatching, and subsequently tried to find them as often as possible during at least a 30-day period after hatching. We could not follow all females to the end of this period, because we lost track of the broods, or because broods were lost. Thus our data on female residence time in the area, and hence brooding duration, must be seen as only indicative.

When assigning a specific initial status as abandoner or tender, we adopted a stricter approach than Bustnes & Erikstad (1991), accepting only records made within 1 week of hatching instead of 14 days. This was done because our data suggested that 2 weeks was too long to detect short-term crèche attendance and high early mortality, concealing the true initial status of females. We assessed female care mode after having followed the female for at least 15 min. Subsequent observations were then used to verify the initial status, and we assessed female status again at 14 days posthatch. Tending females rarely leave their brood temporarily in search of, for example, new foraging areas. Therefore, the chance of classifying tenders wrongly as abandoners owing to short observation periods was small. Only two (1.2%) of 169 females observed at least twice in 1996–1999 were initially classified as abandoners and later found as

tenders. Many females remained in the area regardless of their status, and we had detailed records covering more than a month for a number of broods (see also Öst & Kilpi 2000).

We compared the brood sizes in broods and crèches with the original clutch size of the female(s) involved to determine if adoptions had occurred. Because ducklings were not individually marked, this gives a conservative estimate of adoption frequency from duckling mortality. We obtained data on the production of large young for the entire study population, with standardized censuses of ducklings (Öst 1999).

Data Selection Criteria

The data on daily weight loss during incubation for each year and island type included all females sampled in 1996–1999 that had incubated for at least 10 days (N=394, Table 1). This data set also included females observed in more than 1 year, because it was important to use a large annual sample to obtain an accurate estimate of daily weight loss; annual variation in daily weight loss was not analysed statistically. In all other analyses, except the descriptive data on subdivision of care mode (see below), data from only one randomly selected year was used if females had been seen in more than 1 year.

In the analyses of year quality and overall female weight and condition at hatching in 1996–1999 (Table 1), females that had been incubating for at least 10 days were selected (N=322). Only females for which we could assign an initial status were included in the data on care mode frequencies (N=155, Table 2), but the incubation time at capture of these females was not restricted. Owing to small sample sizes for specific care mode subcategories, we also included some observations of females seen in

Table 2. Frequencies of females abandoning their brood, tending it alone or joining in crèches

Female type	1996	1997	1998	1999	4 years combined
Abandoner	14 (66.7)	7 (18.4)	14 (28.0)	13 (28.3)	48 (31.0)
Lone tender	2 (9.5)	14 (36.8)	6 (12.0)	13 (28.3)	35 (22.6)
Crècher	5 (23.8)	17 (44.7)	30 (60.0)	20 (43.5)	72 (46.5)
Total	21	38	50	46	155

Only one observation per female is included. The percentage of yearly totals is shown in parentheses.

more than 1 year in the descriptive data on subdivision of care mode in 1997–1999 (see Results).

Females included in the specific analysis of body characteristics were trapped on a mean $\pm$ SD of day 22 $\pm$ 1.5 days ($N=96$) of incubation, that is 4 days prior to hatching (Kilpi & Lindström 1997); all females that had incubated less than 20 days were excluded. This procedure left us with a set of females for which the incubation time was unambiguously known. There was no significant difference in the incubation stage at trapping between females that were subsequently defined as abandoning, crèching (two categories) or lone tending ($\bar{X} \pm$ SD; lone tenders: 21.6 $\pm$ 1.2 days, $N=28$; true crèchers: 21.8 $\pm$ 1.4 days, $N=28$; transient crèchers: 22.1 $\pm$ 1.7 days, $N=19$; abandoners: 21.8 $\pm$ 1.3 days; Kruskal–Wallis test: $H_3=1.5$, $P=0.68$). Therefore, we used the weight at trapping as the basis for analysing differences between these females. We also excluded the extreme year 1996 from this data set. This was done primarily because a viral infection (T. Hollmén, unpublished data) killed almost all ducklings within 2 weeks of hatching. This seriously affected our interpretation of female behaviour beyond the initial assessment of care mode.

Repeated observations on the same females were used to test characteristics of the same female with respect to changes in parental care decisions between years. In these data, we had to rely on projected weights at hatching because of deviance in the time females had been incubating at trapping.

Statistical Analysis

The means of the variables (clutch size, structural size, hatch date, trapping weight and condition index) in the four female categories were compared in an ANOVA framework. All the variables were checked for normality and homoscedasticity and transformations were not necessary.

As was hypothesized in the Introduction, the mean of the condition index should decrease with increasing intensity of care, that is, lone tenders should be in best condition, followed by true crèchers, transient crèchers and immediate abandoners. To test this trend hypothesis, we used contrasts within the ANOVA framework (Mandel 1964). The simplest specification of the trend hypothesis, that of a linear trend, was our starting point. Contrasts were also used to test nonlinearity of the trend. For the other variables (clutch size, structural size, hatch date, trapping weight), clear-cut hypotheses could not be

constructed. Hence, these variables were analysed with the standard F test.

We used two-tailed tests, except for a comparison between the body condition of females switching from care to abandoning between years. In this case, we had strong a priori reasons to predict that the direction of possible differences would be such that females are in poorer condition when abandoning, based on previous work by Bustnes & Erikstad (1991).

Means are given $\pm$ SD.

Ethical Note

All trapping of females was done under a national ringers' licence (to M.K.), and according to specific regulations of the Tvärminne Zoological Station. All possible care was taken to minimize nest desertion from our trapping procedures. We therefore timed our trapping to the late stages of incubation, when the overall fraction of deserting females is low (cf. Forbes et al. 1994). There is always a small risk of intervention by predators such as gulls and crows, and roughly 2% of target nests were destroyed. We have not noticed any other adverse effects of the procedures involved. Females ignore the flags up until 3–4 weeks after hatching; at some point they then try to preen them off. The flags fall off at the latest when moult begins. There is no evidence of long-term adverse effects of flagging; some females have been handled 4–5 years in a row, and still breed in the same nest cup year after year. Furthermore, the number of females breeding on the study islands has been increasing, in contrast to some other islands frequented by white-tailed sea eagles, *Haliaetus albicilla*.

RESULTS

Year Quality and Overall Female Condition

Total production of young in the study population varied from 100 in 1996 to 1200 in 1999 (Table 1). Female body condition and mean weight at hatching both varied significantly between years, being poorest in 1996 and best in 1999 (condition: Kruskal–Wallis test: $H_3=48.1$, $P<0.001$; weight: $H_3=43.4$, $P<0.001$). Female condition and mean weight at hatching improved sequentially over the years, so that the variances in weight and body condition also decreased (Bartlett's test: condition: $\chi^2_3=34.9$, $P<0.001$; weight: $\chi^2_3=24.4$, $P<0.001$). The production of fledged young, however, did not improve

Table 3. Clutch size, structural size (length of radius and ulna in mm), hatching date relative to the population median and trapping weight for females adopting different care behaviours in 1997–1999

Care type	Clutch	Size (mm)	Relative hatch date	Trapping weight (g)	N
Lone tender	4.9±1.1	107.2±2.9	−2.1±2.1	1620±99	28
True crècher	4.9±1.1	107.6±2.8	−1.6±2.7	1602±95	28
Transient crècher	4.6±0.8	108.6±3.3	−1.3±2.3	1589±107	19
Abandoner	5.1±1.2	106.9±2.5	−0.9±2.6	1541±124	21

Means are given±SD.

sequentially. The daily weight loss data indicate the quality of the year in terms of climate harshness during incubation, 1996 being the worst year, followed by 1997, 1999 and 1998 in improving order (Table 1).

Frequency of Care Mode

Crèchers, lone tenders and abandoners were on average observed 3.6 days from hatching, with no difference between the categories (crèchers: 3.4 ± 2.7 days, $N=72$; lone tenders: 3.4 ± 2.8 days, $N=35$; abandoners: 4.2 ± 3.4 days, $N=48$; Kruskal–Wallis test: $H_2=1.28$, $P=0.53$). Multi-female tending was the prevalent initial mode of brood care in the entire data set with an overall frequency of 46.5% in all study years (Table 2). Lone tenders accounted for 22.6%, and abandoners for 31% of the observed females. The majority of brood-caring females (i.e. excluding abandoners) joined crèches (71.4, 54.8, 83.3 and 60.6% in 1996–1999, respectively). The frequencies of abandoners, lone tenders and crèching females varied significantly between years (goodness of fit test of 3×4 contingency table: $\chi^2_6=23.4$, $P = 0.0007$). Examination of cell-specific χ^2 values revealed that the proportion of abandoners was exceptionally high in 1996 ($\chi^2_{cell}=8.6$; Table 2). Subdividing the contingency table (Zar 1999) indicated that the difference between years in care mode frequencies was largely due to the high frequency of abandoners in 1996. Thus, excluding the year 1996 and considering the remaining 3×3 table resulted in a non-significant χ^2 (goodness of fit test: $\chi^2_4=8.4$, $P=0.08$), whereas a comparison of care mode frequencies in 1996 against the combined frequencies for all the other years revealed a highly significant difference (goodness of fit test of 3×2 table: $\chi^2_2=14.5$, $P=0.0007$).

Subdivision of Care Mode

After the first week of brood care, we were able to divide lone tending and crèching females into subclasses according to their behaviour (1997–1999 data). Single females that were likely to be tending their own brood were termed true lone tenders, and those adopting additional ducklings as adopting lone tenders. The other two categories of females were crèchers remaining in their crèche (true crèchers) and crèchers subsequently leaving their crèche, later observed as not associated with broods

(transient crèchers). Among these brood-caring females ($N=84$), true crèchers were most abundant (38.1%), followed by transient crèchers (27.4%), true lone tenders (26.2%) and adopting lone tenders (8.3%).

Transient crèchers were observed outside their initial crèche without a brood on average within 7.2 ± 2.4 days ($N=23$) of hatching, having been first observed in it on average 2.9 ± 1.6 days after hatching. This means that some lone tender females might have initially been categorized wrongly.

The total lengths of the observation period (if more than 2 weeks) for all lone tenders combined, abandoners and crèchers were similar (lone tenders: 23 ± 10 days, $N=11$; abandoners: 27 ± 9 days, $N=14$; true crèchers: 27 ± 9 days, $N=12$; transient crèchers: 25 ± 8 days, $N=16$; Kruskal–Wallis test: $H_2=0.68$, $N=53$, $P=0.57$).

Characteristics of Females According to Care Mode

Table 3 gives the mean clutch size, length of the radius and ulna (structural size) and hatching date relative to the population median. There were no differences between female groups with respect to these variables (ANOVA: clutch size: $F_{3,92}=0.64$, $P=0.59$; size: $F_{3,92}=1.32$, $P=0.27$; relative hatching date; $F_{3,92}=0.48$, $P=0.70$). The trapping weights differed almost significantly (ANOVA: $F_{3,92}=2.30$, $P=0.08$).

The average difference in condition index between adjacent care intensity categories was $- 0.26$ (linear trend contrast: $F_{1,92}=8.44$, $P=0.005$; Fig. 1). Nonlinearity was not found ($F_{2,92}=0.037$, $P=0.95$), in accordance with Fig. 1.

In our data set, seven females switched from care (five crèchers, two lone tenders) to abandoning between years. A further four females switched between lone tending and crèching. The hatching weight of females that did not change their care mode was similar in the 2 years in which they were encountered (two-tailed paired t test: $t_9=1.7$, $P=0.13$, weight change on average 43 ± 25 g). Females changing from care (either as lone tenders or crèchers) to abandoning weighed significantly less when they were encountered as abandoners (one-tailed paired t test: $t_6=2.3$, $P=0.03$, weight change on average $(-106 \pm 45$ g).
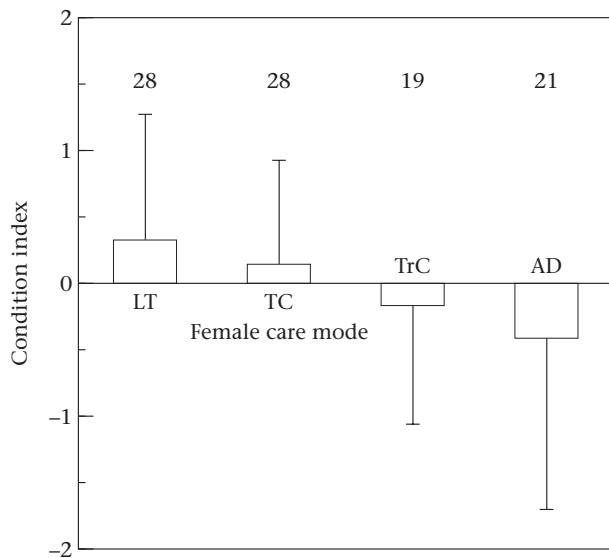
Figure 1. Condition index for lone tenders (LT), true crèchers (TC), transient crèchers (TrC) and abandoners (AD) in 1997–1999. Means+SD are shown. Sample sizes are given above the bars. For definition of condition index see Table 1.

DISCUSSION

Females in poor body condition abandoned their broods more frequently than females in better condition. This is indicated both by the general result that abandonment was more frequent in a year when average female condition was low, and the specific analysis, which showed that individual females were in poorer condition when abandoning than when tending broods. These results fit the predictions of the energetic salvage strategy hypothesis (Eadie et al. 1988). Bustnes & Erikstad (1991) found a significant body weight difference between abandoners and tenders in only 1 (poor) year out of 3, and a higher frequency of abandoners in that year. The overall frequency of abandoners in our study was lower than in theirs but equally variable between years. A direct comparison of these frequencies is not possible, however, because Bustnes & Erikstad (1991) used a 14-day interval to identify initial status. This time frame would have been too long to detect transient crèching in our data set.

Our results indicate that the intensity of care females are able to give is condition dependent. Thus, we showed a trend for crèching females to be, on average, in poorer condition than lone tenders, a factor that may promote crèching. Öst & Kilpi (1999) found that brood-caring females must adopt a feeding technique similar to ducklings, that is, short dives precluding feeding on favoured blue mussels, *Mytilus edulis*. Crèching may allow females to use a more flexible foraging mode (Öst & Kilpi 1999), and increase the time available for feeding (L. Mantila & M. Öst, unpublished data). Within the crèching category of females, transient crèchers tended to be in poorer condition than permanently crèching females. This finding supports our hypothesis that transient crèchers should be regarded as abandoners (cf. Székely et al. 1996).

Similarly, Monaghan et al. (1992) found that Arctic tern, *Sterna paradisea*, parents in poor condition deserted their young earlier than parents in good condition. The investment in current reproduction probably differs between all four care mode categories we identified, with lone tenders and immediate abandoners representing the endpoints of a continuum (Fig. 1).

The purpose of abandoning could be to replenish body reserves more efficiently and to ensure future breeding attempts (Bustnes & Erikstad 1991). Öst & Kilpi (1999) found that abandoners used sites with an abundance of blue mussels, while females tending small young were forced to feed on organisms in the shallow littoral, such as amphipods, *Gammarus* spp. Abandoners immediately shifted to blue mussels after losing the brood. Desertion may therefore confer advantages for future breeding, such as faster preparation for moult, documented in great reed warblers, *Acrocephalus arundinaceus* (Ezaki 1988).

We found no difference in clutch size between abandoners and brood-caring females, so brood size per se does not appear to influence the decision to continue brood care. Bustnes & Erikstad (1991, 1995), however, found that eider females that abandoned their broods had smaller clutches than females tending broods. The likelihood of desertion also increases in other waterfowl, as a consequence of experimental reductions in clutch size (Armstrong & Robertson 1988), or brood size (Eadie & Lyon 1998). Our result may seem surprising, considering that female body reserves should be positively correlated with clutch size in capital breeders (Ankney & MacInnes 1978; Erikstad et al. 1993). We would therefore expect that abandoners, because they are demonstrably in poor condition, would also lay smaller clutches than tenders. However, we estimated female body condition at hatching, which may be unrelated to female body reserves prior to laying, owing to individual variation in mass loss during incubation (Kilpi & Lindström 1997). Furthermore, eiders may be more prone than other birds to base their abandonment decision on body reserves rather than brood size: clutch size variation is small, and thus the value of the brood will not vary much, considering the long lifetime and number of breeding opportunities in this species (Coulson 1984, 1999).

Pöysä & Milonoff (1999) and Pöysä et al. (1997) argued that goldeneyes, *Bucephala clangula*, use the success of the brood as the primary cue for desertion. Also gadwall, *Anas strepera*, broods with the greatest duckling mortality, independent of brood size, were more likely to be abandoned (Gendron & Clark 2000). We cannot directly address the brood success hypothesis on the basis of our data. However, the abandoning–adoption process in eiders is often rapid, broods seem to amalgamate almost immediately when reaching the water, and amalgamated broods mostly contain ducklings of equal sizes (Bustnes & Erikstad 1995). Furthermore, Bustnes & Erikstad (1995), referring to unpublished data from Svalbard, pointed out that 40% of females hatching young had abandoned them within a day of the young leaving the nest. Therefore, the time frame for assessing brood survival rates may be too short to be effective in eiders. We also have frequent observations on marked females who cared for

their, often in the end, sole duckling the entire rearing season (Öst 2000). In some of these cases the female continued to care for her much reduced brood, despite the heavy and rapid (within a few days) initial mortality. We find the brood success hypothesis less likely than the energetic salvage strategy hypothesis as the mechanism underlying abandonment in eiders. However, the brood success hypothesis may be involved in abandonment decisions made by initially crèching females. The transient crèchers we identified made their decision in about a week, during which time a firm parent–offspring bond should have developed (Bustnes & Erikstad 1991).

Savard et al. (1998) have questioned the existence of voluntary brood abandonment in waterfowl. In the case of the eider, abandoning would thus translate into poor rearing ability, with subsequent involuntary loss of ducklings to other females. Presumably, such losses should result from aggressive encounters between brooding females, or simply because ducklings are attracted to certain females (Bédard & Munro 1976; Munro & Bédard 1977a). This point, recently raised by Savard et al. (1998), would merit further attention. As reviewed by Savard et al. (1998), predation events that make broods scatter are the primary force promoting initial brood amalgamation. We have repeatedly seen crèches form under conditions not influenced by any interference, and we therefore do not think that disturbance is needed to explain why broods amalgamate.

Why do some females remain as lone tenders? We cannot find any obvious advantage to this behaviour, yet we have shown that females in good condition tended alone. In addition, Öst (1999) provided data indicating that, as the season progresses, lone tending becomes the prevalent mode of care. Munro & Bédard (1977b) hypothesized that large broods may be vulnerable to 'group attacks' by gulls, which would constitute a cost especially to adopting lone-tending females. On the other hand, many females together may be more successful at deterring predators (Munro & Bédard 1977b; Minot 1980). If feeding sites are limiting, lone tenders may also be at a competitive disadvantage in clashes with feeding groups tended by several females. Social dominance in many species of waterfowl is associated with group size, larger family units being dominant (Loonen et al. 1999). The attractiveness of lone tending for females in good condition nevertheless implies some as yet unknown benefit of monopolizing brood care. Females may be able to control the division of parental care between their own and others' offspring in a crèche, as has been shown for Canada geese, *Branta canadensis* (Nastase & Sherry 1997). Females in good condition may be able to care alone, without joining crèches, within which the female dominance hierarchy (Bédard & Munro 1976; Munro & Bédard 1977a) might determine the partitioning of care between individual females' young.

Two contrasting views of offspring desertion have been prevalent: one approach considers desertion as a behavioural abnormality or accident, and the other regards it as the result of an adaptive life history decision (Székely et al. 1996). Our study strongly favours the latter approach. We have shown that desertion is a flexible strategy in eider females, conditional on the body condition of the parent. Aborting the current breeding attempt may increase the female's survival prospects, and thus future reproductive success, if she is in poor condition, given that investment in the current brood is correlated with expected future benefits from subsequent broods in long-lived animals (Maynard Smith 1977; Sargent & Gross 1985). However, long-term data are required to verify if females really are able to enhance their lifetime reproductive success by deserting.

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