# Spatial structure and parental aggression in eider broods

MARKUS ÖST* & ANETTE BÄCK†

*Department of Ecology and Systematics, University of Helsinki
†Environmental and Marine Biology, Åbo Akademi University

The spatial position of young animals within a brood affects their survival, so that marginal individuals are at greater risk of predation. Spatial brood structuring may be caused by differences in offspring size, age, hunger, or active parental manipulation through aggression. Nepotistic manipulation of brood structure would confer fitness benefits for parents accepting nondescendant young. However, insufficient kin recognition has often been considered to preclude such nepotism in birds, particularly in precocial waterfowl. We explored the spatial structure of ducklings within broods of eiders, *Somateria mollissima*, a seaduck with frequent brood amalgamation. We compared the distribution of ducklings of different origin relative to reference females whose kinship to the ducklings was known. We also observed female aggression towards ducklings, to evaluate the role of parental manipulation of brood structure. We found a nonrandom distribution of ducklings within broods; a female's own young were on average closer to her than unrelated young were. We also found evidence for parental nepotism: whether the brood contained unrelated young was the strongest predictor of female aggression towards ducklings. The spatial position, hatch weight and relative size of ducklings showed no significant correlations with each other, suggesting that active parental manipulation may be needed to explain the observed spatial structure. Our study conflicts with previous anecdotal evidence suggesting that brood amalgamation in eiders results in the disintegration of parent–offspring bonds, preventing parental exploitation of nondescendant young. It also opens up the possibility that the spatial position of ducklings depends on their mother's status in the female dominance hierarchy.

Parental antipredator behaviour is usually considered an 'unshared' resource that benefits all offspring equally and simultaneously (e.g. Lazarus & Inglis 1986; Ruusila & Pöysä 1998). However, predation risk may be unequally distributed among offspring if parents are not always successful in defending them against predators. Parents may be unable to defend all offspring simultaneously depending on the spatial configuration of the brood, so that marginal individuals, in absolute terms or relative to the parents, may be at greater risk.

Several mechanisms may contribute to brood structuring. Offspring may vary in size, with larger or older young being better at competing for access to safer, central positions (e.g. Wisenden & Keenleyside 1992, 1994; Mappes et al. 1997). Another simple mechanism is hunger; starving young are more active, so they may on average occupy a more peripheral position than well-fed ones (Swennen 1989; Romey 1996). Parents may also actively manipulate the position of offspring by means of aggression. For example, catfish, *Bagrus meridionalis*, parents actively exclude cichlid (*Haplochromis* spp.) young from the centre of mixed broods, leaving their own young in safer, central positions (McKaye & Oliver 1980; McKaye et al. 1992).

Parents may also nepotistically favour their own offspring over nondescendant young in amalgamated broods of conspecifics (reviewed by Wisenden 1999). Alloparental care will be favoured if the recipient is able to increase survival of its own young by accepting nondescendant young (e.g. Eadie et al. 1988). The fitness benefit accruing to the alloparent's own young may simply be a consequence of diluted predation risk in larger broods (e.g. Cooper & Miller 1992; Johnston 1994; Williams 1994), or the survival of their own young may be disproportionately high (e.g. Eadie & Lyon 1998). Nondescendant young may be located at the periphery of broods or further away from parents, surviving less well because of edge-biased predation (e.g. Nastase & Sherry 1997). If so, active parental manipulation of brood structure confers fitness benefits for alloparents (Eadie et al. 1988), since brood predation will fall disproportionately

*Correspondence: M. Öst, Department of Ecology and Systematics, P.O. Box 65 (Biocentre 3, Viikinkaari 1), FIN-00014 University of Helsinki, Finland (email markus.ost@helsinki.fi). A. Bäck is at the Åbo Akademi University, Environmental and Marine Biology, Akademigatan 1, FIN-20500 Turku, Finland.*

upon the nondescendant young confined to less favourable positions.

Kin discrimination is considered less efficient in birds than in other taxa (e.g. Kempenaers & Sheldon 1996; Keller 1997). Precocial waterfowl have often been considered incapable of keeping track of their own young in amalgamated broods, with the result that some parents may accidentally lose their young to others, while other parents accept and care for unrelated young in what appears to be 'misdirected care' (e.g. Munro & Bédard 1977a, b; Weatherhead 1979; Patterson et al. 1982; Warhurst et al. 1983; Kehoe 1989; Afton 1993). According to this view, the absence of a 'central family unit' precludes nepotism and parental exploitation of nondescendant young in waterfowl (Kehoe 1989). However, some geese seem able to maintain central family units within amalgamated broods. Adopted Canada geese, *Branta canadensis*, goslings were found further away from tending parents, and survived less well than natural goslings (Nastase & Sherry 1997).

The eider, *Somateria mollissima*, is ideally suited for exploring whether family units exist within broods: communal brood care by several females predominates (e.g. Öst 1999; Kilpi et al. 2001), amalgamated broods can be very large (Gorman & Milne 1972), and broods tended by single females sometimes contain nondescendant young; the latter mode of brood amalgamation is typical of other ducks (Eadie et al. 1988). Brood-tending associations form during a few days of intense social interaction as females arrive at sea with their newly hatched broods (Öst & Kilpi 2000). Mothers and their broods may form large coalitions during this initial phase, but some females soon depart or groups break up, so usually two to four mothers then form enduring coalitions (Bédard & Munro 1976; Bustnes & Eriksad 1991; Öst 1999). According to anecdotal evidence, there is no selfish herd behaviour or differential treatment of young in eider broods, because brood amalgamation occurs before mother–offspring bonds develop, and hence a female is unable to distinguish nondescendant young from her own (Bustnes & Eriksad 1991).

Our objective was to explore whether ducklings are randomly distributed within eider broods, or whether the structure is nonrandom, thus allowing potential exploitation of nondescendant young. We compared the order of ducklings of different origin in broods relative to reference females whose kinship to the ducklings was known. We discuss mechanisms underlying the spatial configuration observed, including active parental manipulation through differential aggression. If there is parental nepotism, aggression should be more likely when the brood contains nondescendant young. We compared the explanatory power of this effect with other variables potentially influencing parental aggression.

## METHODS

### Duckling Spatial Structure

Data on spatial structure of ducklings in broods were collected during 15 May–25 June 2002 in the archipelago surrounding Tvärminne Zoological Station (59°50′N, 23°15′E), on the Baltic Sea in southwestern Finland. Kilpi & Lindström (1997) and Öst & Kilpi (2000) describe the area in detail.

Eider females were captured on the nest on selected islands in the study area during the late stages of incubation, to minimize nest desertion from trapping (Kilpi et al. 2001). Females were given $3 \times 3$-cm flags with a unique colour combination, attached to the third-outermost primary (Öst & Kilpi 2000), and a unique combination of one to three permanent colour rings. Altogether 124 females were marked with both flags and colour rings in 2002. Kilpi et al. (2001) describe the ethical aspects involved in the capture of females.

Dry ducklings of known females were marked with coloured $2 \times 1$-cm pieces of cross-stitch fabric, attached to the tips of down feathers with cyanoacrylate super glue, and weighed to the nearest 1 g on a Pesola spring balance. Ducklings received a nape tag with an individual colour, and a brood-specific colour attached to the back. Some ducklings were treated as their mother was captured; however, the majority of broods were handled as nests were revisited on their estimated hatching date determined by egg floatation (Kilpi & Lindström 1997). Our revisits to nests to mark the ducklings probably incurred little extra brood mortality, since females always stayed in sight, occasionally even vigorously defending the nest. The tags were observed to last a mean ± SD of $14.7 \pm 6.5$ days (range 1–26 days, $N=25$ broods). No adverse effects of tags on duckling behaviour or growth were detected. Altogether 195 ducklings from 51 different broods were marked and weighed.

Broods typically left the nest within a day of hatching. We observed eider broods daily from suitable vantage points with the aid of spotting scopes ($\times 20–60$). When a brood with at least one marked duckling was observed, we recorded (1) the total number of marked and unmarked ducklings and females, and their identity, (2) the relative size of all ducklings, by visually relating the length of the duckling's body to the length of the female's head while swimming, to an accuracy of 0.25 female head lengths (Öst & Kilpi 1999; Öst et al. 2002), (3) duckling activities (feeding, moving, resting on land or water), and (4) female aggression towards young.

To document the spatial distribution of ducklings, we conducted scan samples (Altmann 1974) of the position of marked and unmarked ducklings in the same brood with respect to a reference female at 30-s intervals. Whenever possible, we chose as a reference the mother of the marked young in the brood. However, occasionally the mother of the marked young had lost her flag, or she was no longer associated with her young. In such cases, we chose as a reference another marked female, or, in a few cases, an unmarked female, provided that she was either tending the brood alone, or unambiguously distinguishable owing to distinct external features. In addition to scanning the positions of different categories of young (marked versus unmarked), we also obtained data on the positions of individually recognizable young relative to a reference female. Typically these data consisted of marked ducklings from the same clutch. We compared

the positions of individual young to evaluate the role of weight and size as predictors of position in the brood. The interrelations of hatch weights were known for ducklings from the same clutch. The relative sizes of ducklings were estimated at the time of observation.

All observations of a reference female (brood) on 1 day constituted one observation. We combined all observations of the same reference female before analysis, to maximize observation time per brood. Pooling of data over several days was justified, as most observations of marked ducklings were distributed over a short period in the early brood-rearing period (mean ± SD time span = $5.9 \pm 5.8$ days, range 0–20 days, $N=33$ broods). To minimize serial correlation of consecutive scans and to give a fair representation of duckling spatial structure, we excluded (1) repeated scans of ducklings resting (sleeping) on land in fixed positions (sampling was resumed when the spatial structure changed) and (2) broods scanned fewer than 10 times (5 min) in total. Analyses of duckling spatial structure were based on data collected during a mean ± SD of $0.97 \pm 0.76$ h (range 0.1–2.6 h, $N=33$) of scan sampling per brood; the mean age of marked ducklings whose mother was known ± SD was $11.9 \pm 5.9$ days (range 1–24 days, $N=25$).

## Parental Aggression

Data on female aggression directed at ducklings in the same brood were collected during 2000–2002. We recorded time–activity budgets of known females as described by Öst et al. (2002), continuously monitoring agonistic interactions within the brood. A comprehensive set of variables potentially influencing the incidence of parental aggression by focal females was determined: (1) total observation time (h); (2) clutch size; (3) female category (lone tender/multifemale tender); (4) number of ducklings in the brood; (5) female size (length of the radius–ulna, mm); (6) female condition index (residual mass at hatching, defined below); (7) age of focal female's young (days); and (8) 'confirmed adoption' (defined below).

All data collected on a known female on 1 day constituted one observation. The observations of a focal female from 1 year were pooled before analysis, to maximize observation time per bird. For females with more than one observation per season and no documented aggression towards ducklings, we used the median number of ducklings and females (nonrandomly distributed variables) and the mean age of ducklings (normally distributed variable) in the analysis. If aggression was observed, we used the age of ducklings and brood structure at the time of aggression in the analysis. If aggression was observed more than once, we used the median number of ducklings and females, and the mean age of ducklings, of the observations involving aggression. We excluded females with a total observation time of less than 10 min. We made 201 observations of focal birds during 2000–2002 (2000: $N=70$; 2001: $N=57$; 2002: $N=74$), representing 176 individual females, and the mean observation time per bird ± SD was $1.72 \pm 1.27$ h (range 0.17–5.43 h). Although 20 females were observed

in more than 1 year, parental aggression did not seem to be linked to particular individuals (all observations of aggression involved different birds) and thus bias caused by an inflated sample size is likely to be negligible.

Incubating females were captured on the nest, weighed to the nearest 10 g on a Pesola spring balance, measured (radius–ulna length to the nearest 1 mm) and marked with coloured flags (2000–2002) and colour rings (2001–2002). We also recorded clutch size. The approved methods developed by Kilpi & Lindström (1997) were used to derive estimates of the female's weight at hatching. Female condition indices were derived as the standardized residuals of actual estimated body masses at hatching from those predicted from regressions of log-transformed body mass on log-transformed radius–ulna length (Ormerod & Tyler 1990). Standardized residual masses at hatching were derived for the pooled data from 2000–2002.

For lone tenders, adoption was confirmed if the number of observed ducklings exceeded the focal female's clutch size at least once. For multifemale tenders, adoption was confirmed if the total number of ducklings in the amalgamated brood at least once exceeded the summed clutch size of all marked females in the brood, plus six ducklings for each unknown female. The maximum clutch size in unparasitized nests is six (Öst 1999).

## Statistical Analysis

If family units exist within eider broods, we predicted that a reference female's own young should on average be closer to her than nondescendant young, that is, the position rank of her own young should be lower. Our data fell into three categories: (1) marked versus unmarked ducklings; reference female mother of marked ducklings; (2) marked versus unmarked ducklings; reference female unrelated to the marked ducklings; and (3) marked ducklings of different origin; reference female mother of only one of them. For category 1 we predicted that rank would be lower for marked ducklings; for category 2 rank should be higher for marked ducklings; and for category 3 rank should be lower for marked-own than for marked-other ducklings. The median position of ducklings of different origin with respect to the reference female was compared by Wilcoxon signed-ranks tests. If ducklings were equidistant to the reference female, the rank assigned to these tied observations was the mean of the ranks to which each of these ducklings would have been assigned had they not been tied (Sokal & Rohlf 1995; Zar 1999). Although scans within each brood inevitably showed some serial correlation, the dependence of consecutive observations was likely to be small. This is because ducklings are typically highly mobile, the maximum dispersion of broods was usually a few metres or less, and individual ducklings could thus traverse the entire brood repeatedly during the 30-s scan interval. Using Fisher's method of combining $P$ values (Sokal & Rohlf 1995), we combined results from individual broods in a simple meta-analysis to yield an overall statistic.

We did separate meta-analyses for the three data categories, since they encompass different aspects of the

problem. The last data category provides the most accurate test of our 'family unit' hypothesis, while the first two provide a conservative test (Sokal & Rohlf 1995): unmarked ducklings may in reality include an unknown number of ducklings with lost markings. This extraneous noise in our data might render it harder to falsify the null hypothesis. The second data category provides a good test for potential bias inherent in the data collection. During scanning, our focus was typically on the reference female and her immediate surroundings, so we might have failed to observe marked ducklings far from her. As a consequence, we might find a bias towards lower position rank for marked young. Data of type 2 allow us to discover any such bias, since we predicted marked ducklings would have a higher rank than unmarked ones.

We compared the positions of individually recognizable young relative to a reference female either by Wilcoxon signed-ranks tests (2 ducklings) or Friedman tests (>2 ducklings); in the latter case, pairwise comparisons were done with Tukey's tests applied on ranks (Zar 1999). To compare broods, we did a brood-wise ranking of the hatch weights and the spatial positions of individually recognizable young relative to each other. We explored the relations between hatch weight rank, position rank and relative size rank with Spearman rank correlations. Position ranks were further subdivided into 'raw' ranks, that is, individual young were ranked relative to each other based on mean position rank, regardless of whether these ranks differed significantly from each other, and 'significant' ranks; in this case, ducklings were assigned different ranks relative to each other only when mean position ranks showed statistically significant differences.

We used a backward stepwise multiple logistic regression to evaluate the relative influence of the predictor variables (see above) on female aggression towards ducklings (binary variable: aggressive or not). All eight predictor variables, as well as an interaction term female category × confirmed adoption, entered the initial model. Female category and confirmed adoption were categorical variables; the remaining variables were regarded as continuous. The criterion for removal of a variable from the model was $\alpha=0.10$ for the log-likelihood ratio statistic and, for entry into the model, $\alpha=0.05$ for the score statistic (Norusĭs 1994).

### RESULTS

#### Duckling Spatial Structure

The three meta-analyses upheld the predictions of our family unit hypothesis. The mean position rank of marked ducklings was consistently lower than that of unmarked ducklings, when the reference female was the mother of the marked ducklings (data category 1: $\chi^2_{38}=471.5$, $P<0.001$; Fig. 1a). Correspondingly, the overall position rank of marked ducklings was higher than that of unmarked ducklings, when the reference female was not the mother of the marked young (data category 2: $\chi^2_{14}=26.75$, $P=0.02$); however, the data are clearly more heterogeneous in this case, and one observation
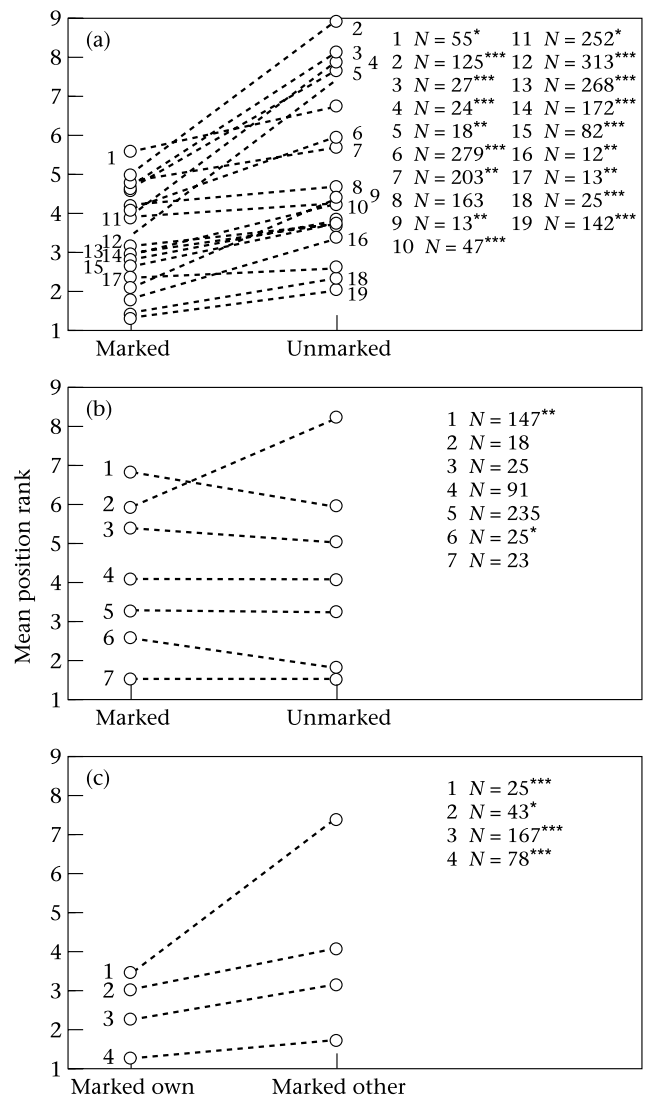


**Figure 1.** The mean position rank of ducklings of different origin with respect to a reference female. The lower the rank, the closer the ducklings were to the female. (a) Broods with marked and unmarked ducklings, where the reference female was the mother of the marked young; (b) broods with marked and unmarked ducklings, where the reference female was unrelated to the marked ducklings; (c) marked ducklings of different origin, only one of them belonging to the reference female. Data from the same brood are connected with a dashed line. Number of scans and significance levels from Wilcoxon signed-ranks tests are shown (*$P<0.05$; **$P<0.01$; ***$P<0.001$).

contradicted the general trend of higher ranks for marked ducklings (Fig. 1b). For marked ducklings of different origin, the reference female's own young were consistently closer to her (data category 3: $\chi^2_8=109.5$, $P<0.001$; Fig. 1c). Of the 30 reference females included in these analyses, 24 (80%) were multifemale tenders, and six (20%) were lone-tending females.

The position of ducklings relative to each other was not correlated with their hatch weights or relative size at the time of observation. Thus, 'raw' position ranks (see Statistical Analysis) were not correlated with hatch weight ranks (Spearman: $r_s=0.20$, $N=43$ ducklings/16

**Table 1.** The final backward stepwise multiple logistic regression model of female aggression towards ducklings in the same brood

| Variable | β | Wald $\chi^2_1$ | P | OR | 95% CI |
|---|---|---|---|---|---|
| Confirmed adoption | 2.51 | 15.14 | <0.001 | 12.3 | 3.5–43.4 |
| Observation time (h) | 0.44 | 8.23 | 0.004 | 1.56 | 1.15–2.11 |
| Number of ducklings | 0.06 | 4.41 | 0.04 | 1.06 | 1.00–1.12 |
| Female category×confirmed adoption | −1.28 | 3.21 | 0.07 | 0.28 | 0.07–1.13 |

Regression coefficients, significance, odds ratios (OR) and 95% confidence intervals (CI) of the odds ratios of the variables included are shown.

broods, $P=0.20$) or relative size ranks ($r_S= -0.08$, $N=53$ ducklings/20 broods, $P=0.58$), and there was no relation between hatch weight ranks and relative size ranks ($r_S= -0.02$, $N=43$ ducklings/16 broods, $P=0.88$). Similarly, all combinations of 'significant' position rank (see Statistical Analysis) and the aforementioned variables yielded nonsignificant correlations (all $Ps \geq 0.5$).

## Parental Aggression

Of 201 focal females, 39 (19.4%) behaved aggressively towards young in their own brood. After removing nonsignificant predictor variables one by one, we found that a model composed of the variables confirmed adoption, observation time, number of ducklings and the interaction female category × confirmed adoption produced the best fit of parental aggression towards ducklings ($\chi^2_4=42.69$, $P<0.001$; $-2$ log likelihood$=155.10$; Table 1). Confirmed adoption was by far the strongest predictor of whether a female was aggressive towards ducklings: the odds of behaving aggressively increased 12.3-fold when the brood presumably contained unrelated young (Table 1). Not unexpectedly, there was a 1.6-fold increase in the odds of observing parental aggression for every additional hour of observation of the focal female, as well as a 1.1-fold increase for each additional duckling in the brood (Table 1). Finally, there was also a weak tendency for parental aggression to be more strongly linked with confirmed adoption in lone tenders than in multifemale tenders; however, the interaction between female category and confirmed adoption was not quite significant in the final model (Table 1).

## DISCUSSION

Contrary to previous belief, eider females in this study seemed able to discriminate against foreign young. A female's own young were on average closer to her than unrelated young. Although observer bias towards lower position rank for marked ducklings probably exists (cf. Fig. 1a, b), the overall trend in all of our three comparisons agreed with our predictions, supporting the family unit hypothesis. Ephemeral markings precluded estimating duckling survival, but edge-biased predation has previously been shown in eiders (Swennen 1989), Canada geese (Nastase & Sherry 1997) and various other taxa (e.g. Wisenden 1994; Mappes et al. 1997; Cocroft

2002). Consequently, at least in broods tended by a single female, her own young should on average survive better than nondescendant young. The situation is more complicated in multifemale broods; here the survival prospects of a female's offspring may depend on the mutual dominance relationships of females in the crèche. Subordinate females are usually confined to the fringe of crèches (Bédard & Munro 1976; Öst 1999), so their young may survive less well, either because they are more peripheral, or because involuntary separation limits the ability of those females to affect the survival of their young.

We also found evidence for differential treatment of ducklings within broods. Whether the brood presumably contained young unrelated to the female(s) was the strongest predictor of female aggression towards ducklings. We have never observed a mother with marked ducklings treat them with hostility; correspondingly, marked females whose young were unmarked because we failed to mark them have been observed to attack marked young in their brood containing a mixture of ducklings of different origin. These observations suggest that parental aggression, besides being generally more common in broods with nondescendant young, almost exclusively involves these unrelated offspring.

'Confirmed adoption' was inferred from simple counts of females and young. Some multifemale coalitions probably fulfilled the criteria for 'confirmed adoption', but this was masked by duckling mortality. Furthermore, multifemale broods by definition contain some ducklings and females unrelated to each other (Bédard & Munro 1976). The incidence of parental aggression was unrelated to whether the female cared alone or jointly with other females; this may indicate a social constraint on female selfishness, imposed by the presence of other females.

Could the nonrandom distribution of ducklings simply be a consequence of size- or age-stratification, or variation in hunger levels? Correlations between duckling position ranks, hatch weight ranks and relative size ranks suggest that these factors may not play a major role in explaining our results. There was no correlation between position rank and hatch weight rank. If hatch weights correlate with body condition, we would expect far positions to be associated with low hatch weights, since starving ducklings tend to be near the periphery of broods (Swennen 1989). There was also no tendency for the reference

female's own young to be consistently larger or smaller than the ducklings of different origin in the data included in the meta-analyses. Of the 30 broods observed, 23 (76.7%) had same-sized ducklings, the reference female's own young were larger in three cases (10%), and the ducklings of four (13.3%) were smaller than the foreign young. Taken together, this evidence suggests that active parental manipulation may be necessary to account for our results. Our prime motivation for undertaking this study was the observation of females persistently chasing a particular duckling within the brood, forcing the victim to occupy a peripheral position. The power of parental aggression as a driving force structuring broods is demonstrated by coots (*Fulica* spp.); here, parents actively maintain a strict linear hierarchy of young within broods through parental aggression, with positions close to the tending parents of highest value (Horsfall 1984; Lyon et al. 1994).

Given that eider parents are able to discriminate against foreign young, why is brood mixing so common? A substantial proportion of females terminate parental care prematurely, leaving their brood to be taken care of by others (e.g. Bustnes & Erikstad 1991; Kilpi et al. 2001). Abandoned ducklings are likely to survive less well than ducklings that stay with their mother (cf. Nastase & Sherry 1997; Eadie & Lyon 1998); however, females transiently attending broods are in poor body condition, so they avoid jeopardizing survival and future breeding attempts by reducing their current parental effort (Bustnes & Erikstad 1991; Hario & Kekkinen 2000; Kilpi et al. 2001; Bustnes et al. 2002). Bird parents often treat foreign young attempting to join a brood with marked hostility, sometimes even killing them (e.g. Brown 1998; Eadie & Lyon 1998; Savard et al. 1998). This aggression has often been taken as evidence that accepting extra young is costly or maladaptive (e.g. Redondo et al. 1995; Brown 1998; Savard et al. 1998). However, we suggest that parents accept foreign young in expectation of enhanced survival prospects of their own young, but this benefit may be realizable only if parents force nondescendant young to accept a less favourable position. If the foreign young are considerably larger or older than the parent's own offspring, accepting them will not be favoured (Brown 1998); consequently, e.g. in Barrow's goldeneyes, *Bucephala islandica*, 10 days seems to be an age threshold for accepting unrelated young (Eadie & Lyon 1998). The age of ducklings did not significantly influence the frequency of parental aggression in our study, nor do we regularly observe abandoned ducklings in the field. Since eider ducklings are subject to higher predation pressure (Mendenhall & Milne 1985; Åhlund & Götmark 1989; Swennen 1989) than goldeneyes (Pöysä et al. 1997; Eadie & Lyon 1998), acceptance of foreign young may be favoured over a broader range of size or age differences between young, simply because of the dilution of predation risk. In line with this reasoning, geese parents reaping an additional benefit of improved social dominance through augmented group size (e.g. Lepage et al. 1998; Loonen et al. 1999) readily accept foreign goslings over several months (Choudhury et al. 1993).

To conclude, our results are in conflict with previous anecdotal evidence suggesting that brood amalgamation in ducks results in the disintegration of parent–offspring bonds, preventing parental exploitation of nondescendant young (e.g. Bustnes & Erikstad 1991). They demonstrate the importance of systematic exploration of phenomena that are easily taken for granted, such as accidental brood mixing in ducks. Our finding of nonrandomness in the spatial structure of eider broods should be seen only as a necessary first step to understanding how direct reproduction is divided among cobreeding eiders. The logical next steps would be to relate duckling spatial position to survival, and to explore the relation between the spatial position of ducklings and their mother's status in the female dominance hierarchy.

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