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Spatial structure and parental aggression in eider broods

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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,

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 & Erikstad 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 & Erikstad 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 × 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 × 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 ± 6.5 days (range 1–26 days, *N* 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 ± 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 ± 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 ± 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 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 (Norušis 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 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 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 □ 0.5).

Parental Aggression

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

Gorman, M. L. & Milne, H. 1972. Crèche behaviour in the common