

Condition and coalition formation by brood-rearing common eider females

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Partner choice is important in nature, and partnerships or coalitions within which reproduction is shared are the subject of growing interest. However, little attention has been given to questions of which individuals are suitable partners and why. Common eider (*S dia i i a*) females sometimes pool their broods and share brood-rearing duties, and body condition affects care decisions. We constructed a model in which females, based on their body condition and the structure of the joint brood, assess the fitness consequences of joining a coalition versus tending for young alone. We tested the model's predictions by comparing data on the condition of females in enduring and transient coalitions. Our model showed that the range of acceptable brood arrays in a female coalition decreases with increasing condition of the female, so females tending alone should be in better condition than multifemale tenders. This prediction is in agreement with previous data. The model also predicts that females in good condition should join coalitions with females in poor condition and not with other females in good condition. This prediction was also supported by data: in enduring two-female coalitions, the positive correlation between the better female's condition and the difference in condition between the two females was stronger than would be expected by random grouping of females. In contrast, in transient coalitions of females, this correlation did not differ from the correlation expected under random grouping. Model assumptions seem to fit with eider natural history, and the model may prove to be a useful way to study brood amalgamation behavior of waterfowl in general. *Key words*: body condition, brood amalgamation, coalitions, common eider, parental care, partner choice, solitary tending, *S dia i i a*. [*B a Ec 14:311 317 (2003)*]

Animals are frequently faced with choosing partner(s) with whom to share a task. Partner choice by definition denotes a nonrandom tendency for an individual to associate with some individuals over other potential partners (Dugatkin and Sih, 1998). Although partner choice is likely to be important in various social contexts, most of the attention has been devoted to the study of mate choice, especially by females (see Dugatkin and Sih, 1998). Partnerships (also called "alliances" or "coalitions") within which reproduction is shared are the subject of growing interest, though here the emphasis has been on inequalities (skew) in reproductive share among group members and the mechanisms whereby the shares are decided. These are seen as key factors in social evolution (Clutton-Brock, 1998; Johnstone, 2000). Little direct theoretical attention has been given to questions of which individuals might be suitable partners or why.

Even when one can experimentally document partner choice, the precise rules used may remain unknown. The mechanisms for partner choice among kin are somewhat better understood; familiarity may often be important (Dugatkin and Sih, 1998). However, partner choice regularly occurs also among unrelated individuals (Bernasconi and Strassmann, 1999). Here, the criteria used in partner choice may be some phenotypic cue such as body size (e.g., Ranta et al., 1992; Willmer, 1985) or body mass and/or body condition (e.g., Nonacs, 1990, 1992). Most work on partner choice criteria has been performed in the laboratory (Bernasconi and Strassmann, 1999), and few studies to date

have examined partner choice criteria other than relatedness in the field, especially in higher vertebrates.

Common eider (*S dia i i a*) females are known to pool their broods (a brood coalition is called "crèche") and sometimes share brood-rearing duties. In the archipelago along the southwest Finnish coast, some females are lone tenders and rear broods on their own, while other females are known to abandon their broods after a short period of care, but most females tend broods in associations, usually of two hens (Öst, 1999).

Brood-tending associations form during a few days of intense social interaction as females depart the nesting islands and arrive at sea with their recently hatched broods (Öst and Kilpi, 2000). Mothers may be observed in groups of up to 13 females and with their broods during this period. Aggression and even vicious fighting are common (Öst, 1999). Two and sometimes three or even four hens may form an association that persists for the full brood-rearing period, or the females may separate after a few days, sometimes later joining with other females. The observable outcomes of this complex system (lone tender, multifemale tender, transient crèche, nontender; see Figure 1) are associated with body condition. Kilpi et al. (2001) showed that lone tenders are in the best condition, followed by permanent multifemale tenders, transient crèches, and nontenders.

In this study we investigated the decisions of individual females about joining

value (e.g., Horsfall, 1984; Lyon et al., 1994). Alternatively, there could be a number of high-quality close positions and lower quality far positions (Nastase and Sherry, 1997). In either case 2 females with 3 ducklings each could array them in 20 different ways, from one in which the 3 ducklings of female A occupy the best 3 spots (aaabbb) to the reverse (bbbbaa). The possible number of different arrays is found by calculating the number of combinations (how many combinations of three positions can be drawn from the total of six available?), which in this case equals $[6!/(3!3!)]$. More generally, if female A has N_a ducklings and female B has N_b ducklings, the number of combinations is $[(N_a + N_b)!]/(N_a! N_b!)$.

A coalition-joining model

Our model rests on four main assumptions: (1) body condition affects the intensity of care that females are able to give; (2) two females are able to care better than one; but (3) females cannot care equally well for all the offspring in a brood; so (4) the fitness gain from entering a coalition for any individual female depends on the brood array. We assumed that, in general, those closer to the mother receive better care (Mappes et al., 1997), either because they have better access to food, are better defended, or both. We assumed that ducklings are somehow arrayed within a (joint) brood, with the result that the prospects of some are better than those of others.

Ducklings could be arrayed within a brood in a variety of ways. For example, a strict linear hierarchy could be maintained with positions close to tending females of highest

comparing the body conditions of associating eider females that formed enduring and transient brood-rearing coalitions.

METHODS

We observed breeding eiders during 1997–2000 in the archipelago surrounding Tvärminne Zoological Station (59°50' N, 23°15' E), on the Baltic Sea in southwestern Finland. Approximately 1500 hens nest on small, open islands

correct assessment of the brood-rearing status of focal individuals. We identified 13 enduring coalitions during 1997–2000 (1997:

randomly drawing 11 pairs from the population of breeding females was >0.65 . The mean simulated correlation was .387. By including each female only once in the data, the computed

females were significantly more successful at defending their clutches against invertebrate predators than single females. Multifemale tending may also be advantageous if there is competition for feeding sites; larger families dominate over smaller ones in many geese (e.g., Loonen et al., 1999), although competition for feeding sites is probably less important among eiders (Bustnes and Erikstad, 1991). A parallel can be found among invertebrates: the main benefit of pleometrosis in ants is higher success at brood raiding (Bernasconi and Strassmann, 1999).

Are ducklings maintained in consistent arrays by tending females, and is the survivorship of a duckling affected by its position in the brood? In coots, females actively maintain a strict linear hierarchy of young within broods through parental aggression, with positions close to the tending females of highest value (Horsfall, 1984; Lyon et al., 1994).

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