Behavioral Ecology Vol. 14 No. 3: 311–317

Condition and coalition formation by brood-rearing common eider females

Markus Öst,[a] Ron Ydenberg,[b] Mikael Kilpi,[c] and Kai Lindström[a]
[a]Department of Ecology and Systematics, P.O. Box 65, FIN-00014 University of Helsinki,
Finland, [b]Behavioral Ecology Research Group, Department of Biological Sciences,
Simon Fraser University, Burnaby, BC V5A 1S6, Canada, and [c]Aronia Research Centre,
Åbo Akademi University & Sydväst Polytechnic, Raseborgsvägen 6–8, FIN-10600 Ekenäs, Finland

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 (*Somateria mollissima*) 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, *Somateria mollissima.* *[Behav Ecol 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 (*Somateria mollissima*) 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 crècher, 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 crèchers, and nontenders.

In this study we investigated the decisions of individual females about joining a brood-rearing association (a coalition). Specifically, we tested predictions of a model in which, based on their body condition and the structure of the joint brood, females assess the opportunities afforded by joining the coalition versus lone tending. Our model is related to transactional models of social evolution (Reeve, 2000). Data obtained during several field seasons allowed us to compare known-condition females in enduring and transient coalitions.

Address correspondence to M. Öst. E-mail: markus.ost@helsinki.fi.
Received 8 August 2001; revised 30 January 2002; accepted 25 June 2002.

© 2003 International Society for Behavioral Ecology

Downloaded from http://beheco.oxfordjournals.org/ at Simon Fraser University on May 20, 2015

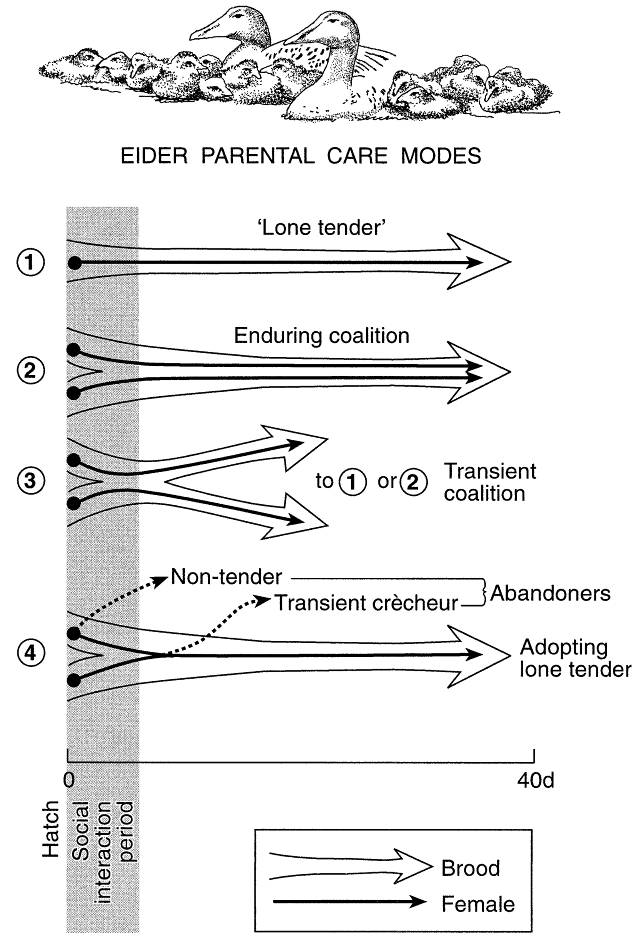

Figure 1

A representation of four processes underlying eider brood-rearing patterns. Females may tend a brood alone (1), or (2) in association with one or more other females (an enduring coalition). Females may form a temporary association (3) that breaks up during the first few days (transient coalition); these females may become lone tenders or enter into other coalitions. Females may enter an association (4) and abandon after a short period (transient crèchers), leaving the young behind with the other female(s). Mothers who have adopted young in this way are not distinguishable from lone tenders unless the maximum brood size of six is exceeded. Finally, some females were known to have incubated to a very late stage but were never observed with any young. They are termed abandoners, though some may be transient crèchers whose period of care was shorter than the interval between observations.

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 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 (bbbaaa). 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 $([N_a + N_b]!)/(N_a!N_b!)$. Therefore, 2 females with 3 ducklings each have 20 possible arrays, 2 females with 4 ducklings each have 72 possible arrays, and 2 females with 5 ducklings each have 252 possible arrays. A female with 3 and a female with 4 ducklings have 35 possible arrays, and so on. The exact array should be of considerable interest to a female when deciding whether to join a coalition.

Tend alone or form coalition?

To decide between lone tending and joining a coalition, a female compares the fitness value of the two alternatives. (For now we do not need to specify fitness exactly.) Assume that the possible brood arrays can be ordered from highest to lowest fitness value for each female, and for simplicity assume that the relationship is linear (Figure 2). The fitness value of lone tending is represented as a horizontal line, the height of which depends on a female's body condition. Brood arrays that offer a female a higher fitness value than lone tending are attractive, whereas those that offer a lower fitness value are not (Figure 2). A coalition is formed when there are brood arrays that offer both females higher fitness than lone tending. The example in Figure 2A shows a case for which this is false, and the example in Figure 2B shows a case for which this is true.

This simple model helps explain the relation between body condition and parental care mode described above. Good body condition females are less likely to enter coalitions because the range of brood arrays that give higher fitness than lone tending is narrower and skewed to one end of the range, for which fewer suitable partners can be found. It can further be shown theoretically that the range of acceptable brood arrays expands with brood size (Öst et al., unpublished data).

Which hens are suitable coalition partners? Figure 3 illustrates the effect of condition on joining a coalition. The diagonal line is the critical fitness value of a brood array that makes crèching worthwhile for female A, in relation to her condition. She should form a coalition with another female if the brood array lies to the left of (below) this line. The vertical lines are the critical fitness values of the brood array that make crèching worthwhile for low, medium, and good condition B females. They should join a coalition with brood arrays to the right of the vertical line representing their condition. Note that the range of acceptable brood arrays increases as condition decreases.

Figure 3 shows that high-condition females should form coalitions only with poor-condition females and not with other high- or even medium-condition females. Intermediate-condition females are willing to form coalitions with each other or with hens in poor condition. But a poor-condition female has a broad range of acceptable brood arrays and will accept a coalition with any female. We predicted a positive relationship between the body condition of a female and the difference between her body condition and that of her (potential) coalition partner. We tested this prediction by

Downloaded from http://beheco.oxfordjournals.org/ at Simon Fraser University on May 20, 2015

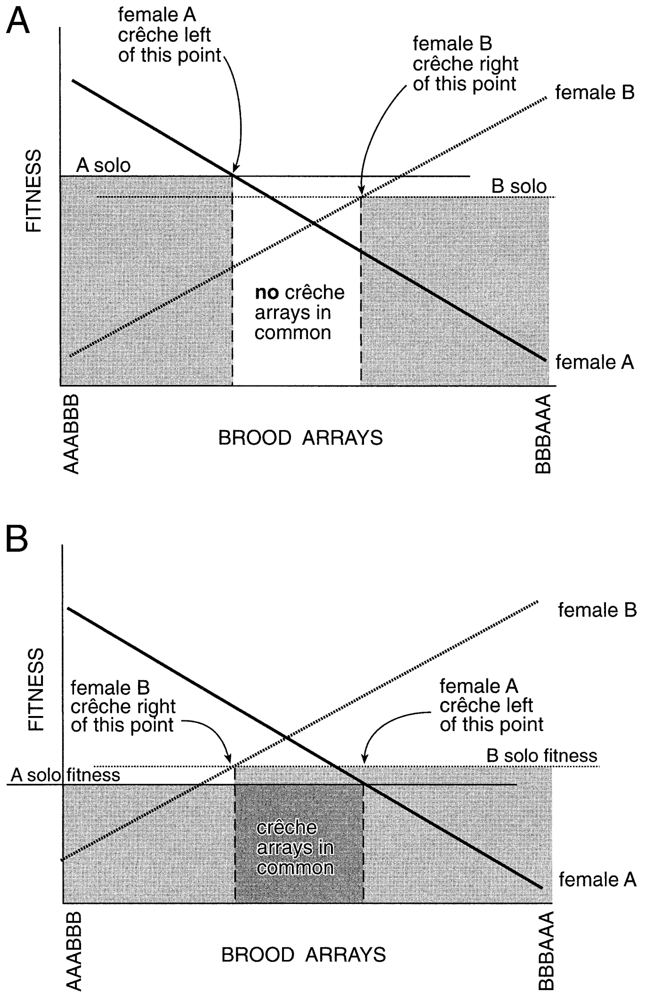

Figure 2

A model of coalition formation by brood-rearing female eiders. The *x*-axis shows the sequence of brood arrays from AAABBB (best for female A) to BBBAAA (best for female B). Mother's fitness is shown by the diagonals, and the fitness of lone-tending by the horizontal lines, the height of which depends on the mother's condition. A coalition is favored when the brood array gives both mothers higher fitness than lone tending. This requirement does not hold in the example shown in panel A, but is satisfied in panel B.

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

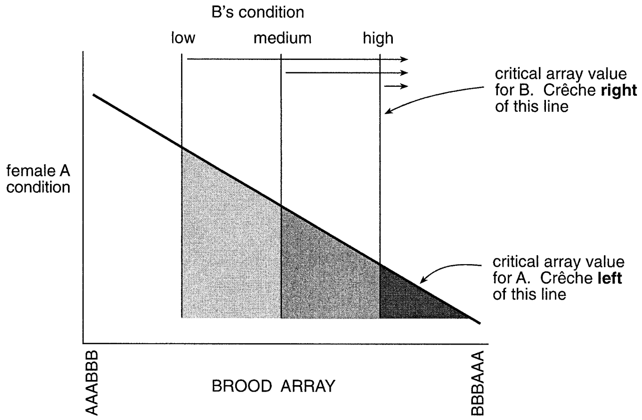

Figure 3

The effect of mothers' conditions on coalition formation. The vertical lines give brood arrays above which a mother favors coalitions when in good, average, or poor condition. The prospective partner with given condition favors a coalition at brood arrays to the left of the diagonal. A coalition can form when it improves fitness for both mothers.

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 and on larger, wooded islands. A comprehensive description of the study area is given by Kilpi and Lindström (1997) and Öst (2000).

Incubating common eider hens were caught on the nest with hand-nets on selected islands in the study area. We confined our trapping to the late stages of incubation to minimize nest desertion due to trapping procedures (cf. Forbes et al., 1994). In addition, we trapped females only from the peak breeding cohort because egg predation is disproportionately high in the earliest breeders, and broods hatched late in the season are more often deserted than broods hatched early in the season (Székely et al., 1996). Trapped females were weighed to the nearest 10 g on a Pesola spring balance, the length of the radius-ulna was measured to the nearest 1 mm, and clutch size was recorded. Females were then given 3 × 3 cm flags with a unique color combination attached to the third-outermost primary (Öst and Kilpi, 2000). Altogether we marked 370 females with flags during 1997–2000 (1997: $n = 81$, 1998: $n = 81$, 1999: $n = 74$, 2000: $n = 134$). All measurements were taken by the same person (M.K.) to reduce interobserver variance.

Females do not eat during incubation, and therefore they lose weight. To estimate a hen's weight at hatching, we subtracted from her measured incubation weight an estimate of the weight she would lose during the remaining incubation time. We estimated her stage of incubation directly from known hatching date or laying dates or indirectly by an egg floatation test (see Kilpi and Lindström, 1997), and regressions of body weight on incubation time, taking into account year and type of nesting island, gave an estimate of the rate of body weight loss (Kilpi and Lindström, 1997; Öst, 1999). 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 length of radius-ulna (Ormerod and Tyler, 1990). We derived standardized residual masses at hatching separately for each year.

During daily observations made with the aid of spotting scopes (20–60×), we tried to locate individually known females during at least 30 days after hatching (observation period late-May until mid-July). At each sighting of a flagged female, we recorded her identity, and, if she was attending a brood, we recorded the number of other females and ducklings in the brood.

A coalition was defined as enduring if two individually known females and their ducklings had consistently associated over a period of at least 2 weeks. Although nontending females share the same foraging area and temporarily mingle with broods (see, e.g., Beauchamp, 2000; Bustnes, 1993), it is straightforward to separate these females from brood-caring females in our study area. Nontending females are not tolerated within broods and are chasen away by the tending females; all broods were followed long enough to ensure

Downloaded from http://beheco.oxfordjournals.org/ at Simon Fraser University on May 20, 2015

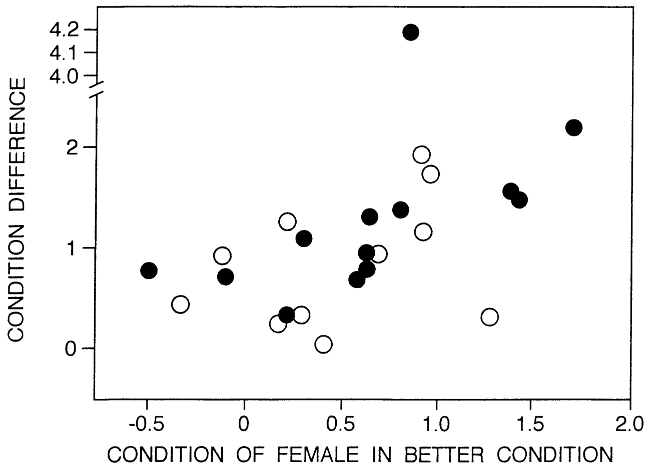

Figure 4
Enduring (filled circles) coalitions of brood-rearing mother eiders. The *x*-axis is the condition of the better of the (prospective) coalition partners, and the *y*-axis the difference between her condition and that of the partner. The Spearman rank correlation coefficient expected on a random draw of 13 pairs of partners is .427. That observed here is .868, which has a probability of <0.01 of occurring by chance. Excluding the outlier does not affect this result. As predicted, mothers in transient coalitions (open circles) have condition more similar than those in enduring coalitions. The observed correlation coefficient is .296, not significantly different from that expected on a random draw of 11 pairs of partners, .387. The sample of transient coalitions contains some females observed more than once, however, including each female only once does not affect the outcome.

correct assessment of the brood-rearing status of focal individuals. We identified 13 enduring coalitions during 1997–2000 (1997: $n = 1$, 1998: $n = 5$, 1999: $n = 3$, 2000: $n = 4$).

A coalition was defined as transient if two marked birds were observed in the same brood once early in the brood-rearing period but both were subsequently observed attending in association with other females and ducklings. We did not include cases in which one of the females was subsequently seen without young because we could not rule out the possibility that all her ducklings had died. We observed 11 transient coalitions during 1997–2000 (1997: $n = 1$, 1998: $n = 2$, 1999: $n = 2$, 2000: $n = 6$). The estimated hatching dates of females in both enduring and transient coalitions were similar (paired-sample t test: $t = 1.41$, df $= 23$, $p = .17$).

Statistical methods

Our model predicts that as female condition increases, a female should form stable coalitions only with females of relatively poor condition. Hence we expected a positive correlation between the condition of the female in better condition and the difference in condition between the females. However, because the theoretical maximum difference in condition between two females increases with an increase in the better female's condition, a positive correlation may be expected purely by drawing random pairs from the population. To account for this, we used a randomization procedure to test whether our observed correlation exceeded that expected by chance. We obtained a representative sample of the condition of breeding females at hatching at the Tvärminne study site by including all trapped females in 1997–2000, which were either seen associated with young or which had incubated at least 20 days at the time of trapping (incubation time in Tvärminne is about 26 days). Altogether 371 females trapped in 1997–2000 fulfilled these criteria (1997: $n = 90$, 1998: $n = 76$, 1999: $n = 93$, 2000: $n = 112$). Thirteen pairs of females were drawn at random without replacement from this representative population; one pair was drawn from 1997, five pairs from 1998, three pairs from 1999, and four pairs from 2000, just as in the data. We calculated the Spearman rank correlation between the condition of the better female in the pair and the condition difference between the two females for these 13 pairs, and the process was repeated 100,000 times. We used a rank correlation because body condition was not normally distributed in the actual sample. The proportion of cases in which the simulated r_s value was at least as large as the actual r_s value was calculated, estimating the probability of obtaining the observed or a more extreme outcome under the null hypothesis of females forming coalitions with each other at random.

We also used the randomization procedure described above to test the Spearman rank correlation for the 11 transient coalitions by drawing 11 pairs of females at random from the population. These random samples were again distributed among years in proportion to the actual data. The process was repeated 100,000 times. We then calculated the probability of obtaining the observed or a more extreme outcome under the null hypothesis of random pairing. However, the same females were in some cases seen forming transient coalitions with more than one known female in the same season. To account for the resulting dependence of data, we calculated the correlation coefficient repeatedly by computing all possible unique cases with each female represented only once. The probability of obtaining the most extreme of these unique correlation coefficients was subsequently estimated with the randomization procedure described above after reducing the number of randomly drawn pairs to correspond to the number of pairs in the data, with each female represented only once. This procedure gave us a conservative probability estimate.

RESULTS

The condition of the female in better condition in an enduring coalition and the difference in condition between the two females in a coalition showed a strong positive correlation ($r_s = .868$, $n = 13$; Figure 4). Our randomization test showed that the probability of observing a Spearman correlation coefficient value as $\geq .868$ by randomly drawing 13 pairs from the population of breeding females was <0.01. The mean simulated correlation was .427.

Figure 4 indicates the presence of a potential outlier in the data on enduring coalitions. Omitting this observation and rerunning the randomization test so that 12 pairs were randomly drawn from the population of breeding females (3 pairs of females were randomly drawn from the year 2000 instead of 4 pairs in the original analysis) did not affect the outcome. There was still a strong positive correlation between the female in better condition in an enduring coalition and the difference in condition between the two females ($r_s = .874$, $n = 12$). The probability of observing a Spearman rank correlation as $\geq .874$ by randomly drawing 12 pairs of females was 0.01. The mean simulated correlation was .431. We conclude that the null hypothesis of females forming coalitions with each other at random can be refuted. In accordance with the model's prediction, females in good condition formed coalitions with females of poor or average condition.

In transient coalitions, the condition of the better female and the difference in condition between the two females also showed a positive correlation ($r_s = .296$, $n = 11$, Figure 4). However, our randomization test showed that the probability of observing a Spearman rank correlation as $\geq .296$ by

Downloaded from http://beheco.oxfordjournals.org/ at Simon Fraser University on May 20, 2015

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 correlations for these possible unique cases ranged from –.179 ($n = 7$ pairs) to .548 ($n = 8$ pairs). The randomization test showed that the probability of obtaining the observed or a more extreme correlation ranged from 0.380 to 0.920. The mean simulated correlation value for all possible unique cases was either .364 ($n = 7$ pairs) or .367 ($n = 8$ pairs). Unlike that of pairs of females that formed enduring coalitions, the distribution of condition differences in pairs of females that formed transient coalitions could not be distinguished from a random draw of the population.

DISCUSSION

Our coalition-joining model showed that the range of acceptable brood arrays decreases with increasing condition of the female, leading to the prediction that lone tenders should, on average, be in better condition than crèching females. This prediction is in agreement with previous data (Kilpi et al., 2001; Figure 1). The model also predicts that females in good condition should preferentially join coalitions with females in relatively poor condition and not with other females in good condition. This prediction is supported by our data. In enduring two-female coalitions, the positive correlation between the better female's condition and the difference in condition between the females was stronger than would be expected by random grouping of females. We were also able to show that in transient coalitions of females, this correlation did not differ from the correlation we would expect under random pairing in the breeding population. This indicates that our sample of transient coalitions contains some female–female combinations in which two females in relatively good condition may have been too evenly matched regarding their body condition to benefit from a permanent coalition. This observation supports the model prediction that a combination of two good-condition females does not promote formation of stable coalitions. However, females in transient coalitions are by no means prevented from finding other suitable coalition partners in the course of the social interaction period. Thus, in our sample of 18 females in transient coalitions, only 3 (16.7%) females continued care as lone tenders, 7 females (38.9%) ended up in two-female coalitions, and 8 females (44.4%) formed a coalition with more than two females after the split with the transient coalition partner.

Female eiders thus seem to use body condition as one cue to discriminate among potential coalition partners. A parallel can be drawn between coalitions in female eiders and cooperation among reproducing female invertebrates. Pleometrosis, in which several queens cooperate to raise a first brood, is a common alternative breeding strategy to solitary nesting in many ants (Bernasconi and Strassmann, 1999). Kinship is unimportant in pleometrosis; rather, females seem to use female body condition (measured as body weight) as a cue in partner choice, in a manner consistent with increasing their competitive advantage. In laboratory experiments, Nonacs (1990, 1992) found that heavy queens were more likely to join another queen instead of nesting solitarily, and, when given a choice between joining either a light or a heavy queen, queens always preferred the lighter resident. Moreover, these preferences could be changed by experimental manipulation of queen condition. One difference between eider females and ant cofoundresses is that when the first workers mature, ant queens fight until almost invariably only one female survives. Accordingly, lighter queens are more likely to leave nest sites when joined by others (Nonacs, 1992). Therefore, ant queens may be expected to favor individuals of similar condition in the field, although this assumption remains untested (Bernasconi and Strassmann, 1999). In eiders, competition is less fierce, and the coalitions may be more reciprocal in nature: coalitions among higher vertebrates are usually assumed to be beneficial to both parties, and both individuals potentially choose their partners (Dugatkin and Sih, 1998).

The assumptions of the model seem to fit with eider natural history. Female eiders incubate continuously for 26 days, without eating at all (Korschgen, 1977; Parker and Holm, 1990). As a consequence, they fall from a preincubation mass of about 2200 g to about 1400 g (Gabrielsen, 1994), and in exceptional cases females are known to have starved on their nests (Öst and Kilpi, 1999). Recovery after hatch thus seems likely to be an important fitness consideration.

After hatching, ducklings must be closely guarded, particularly from predatory gulls (Mendenhall and Milne, 1985; Swennen, 1989). Eiders feed mainly by diving, so intense feeding necessarily interferes with a mother's ability to guard her brood. Brood care also puts an additional strain on mothers because females and small ducklings preferentially use different foods, which in the Baltic are located several meters apart (Öst and Kilpi, 1999). Tending females forage like their young, whereas nontending females are able to feed on preferred food, blue mussels, throughout the rearing season. Individually marked females immediately switched to a mussel diet after losing their brood (Öst and Kilpi, 1999). The fact that females in poor condition abandon their broods (Bustnes and Erikstad, 1991; Hario and Kekkinen, 2000; Kilpi et al., 2001) also suggests that brood care and efficient condition recovery are incompatible. The option of brood desertion is likely to lower the attractiveness of enduring coalition formation for females in poor condition; however, including this option adds complexity that goes beyond what our current model can encompass.

Shared brood care may lessen the conflict between condition recovery and brood care. Multifemale tenders take an intermediate position between lone tenders and nontenders concerning feeding methods and choice of feeding habitat (Öst and Kilpi, 1999). Lone tenders show the highest frequency of dabbling, forage closest to the shoreline, and make the shortest dives, indicating that they are more restricted to duckling foods than are multifemale tenders. Lone tenders also devote a larger proportion of time to vigilance at the expense of feeding than do individual females in multifemale coalitions (Öst et al., 2002). The time-budgeting benefits of grouping even extend to nontending females feeding in close vicinity to broods; these females spent significantly more time feeding and less time being alert than nontending females feeding away from broods (Bustnes, 1993). In contrast, Beauchamp (2000) found that the time allocated to feeding and vigilance did not vary with the number of females in the brood. One reason that grouping did not appear to affect female time budgets in this study may have been the short observation time of unmarked individuals, which may potentially make it difficult to separate tending and nontending individuals from each other.

Two females are presumably better able to guard and care for a (joint) brood than is a lone tender. Minot (1980) and Munro and Bédard (1977) argued that several eider females together are more efficient at deterring predators, and Munro and Bédard (1977) also reported higher survival in larger broods. Multifemale tending also potentially improves predator detection: Öst et al. (2002) found that the collective vigilance of mulitifemale broods was at least 20% higher than that of lone tenders. Correspondingly, Mappes et al. (1995) showed experimentally that two shield bug (*Elasmucha grisea*)

Downloaded from http://beheco.oxfordjournals.org/ at Simon Fraser University on May 20, 2015

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). Alternatively, there could be a number of high-quality close positions and lower quality far positions. In either case, the arrangement of a female's ducklings across available sites of a joint brood will influence the value of forming a joint brood with another female. In Canada geese, Nastase and Sherry (1997) showed that adopted goslings were located farther away from female adults than natural goslings. This disadvantageous positioning of adopted goslings also lowered their survival compared to natural goslings. In goldeneyes, Eadie and Lyon (1998) showed that adopted young had lower survival than ducklings of the host female, although the reason for this difference is unclear because the positioning of ducklings was not specifically reported. It seems reasonable to assume that the distance to the mother affects survival, as evidence from a variety of taxa suggests that offspring at edge positions are exposed to higher predation risk than offspring in central positions (birds: Nastase and Sherry, 1997; insects: Mappes et al., 1997; fish: Wisenden, 1994).

Aerial attacks by gulls are a major mortality factor of small eider ducklings, but eider females can defend the brood effectively against attacks if the ducklings are close to the tending female (Mendenhall and Milne, 1985; Swennen, 1989). The ducklings congregate into a compact group when the female gives alarm calls. Most victims are ducklings that stray too far from the tending female and therefore fail to react to the alarm calls in time (Swennen, 1989). Starving ducklings are more likely to disperse farther away from the female (Swennen, 1989). In addition, the size and/or age of a duckling could be expected to influence its position in a brood; duckling age clearly affects a female's decision to accept extra young in some waterfowl (e.g., Eadie and Lyon 1998). Taken together, these facts make it plausible that there may exist some structure in joint eider broods. However, detailed investigations into the exact nature of the brood array in eiders are needed.

The coalition-formation model outlined here is related to models of reproductive skew (Clutton-Brock, 1998; Johnstone, 2000). In skew models, a dominant individual is assumed to partition gains (usually reproduction, but it could be food or other resources; Hamilton, 2000), conceding enough that subordinates stay in the group. The assumption of strong dominance is not essential, however. The allocation of gains (skew) could also arise by incomplete control of any one individual (Clutton-Brock, 1998; Johnstone and Cant, 1999). We cannot distinguish between these alternatives. The aggression and fighting between eider hens at the outset of brood rearing suggests that no single individual has control, and the hens may be contesting the brood array, but later observations of hens in apparently dominant and subordinate roles is consistent with concession models.

Brood amalgamation is common in waterfowl (Beauchamp, 1997, 1998; Eadie et al., 1988), but perhaps due to the large interspecific variation, there are no unifying hypotheses explaining its function in this group (Eadie and Lyon, 1998; Öst, 1999, 2000). Theoretical work has until now made a clear distinction between the processes of adoption and abandonment, neglecting the fact that these decisions always involve the interests of at least two parties. The coalition-joining model proposed in here may prove to be a useful way to look at the diversity of care among waterfowl in general. It may be particularly rewarding to try to identify the factors leading to instability of female coalitions in some waterfowl, such as scoters and goldeneyes (e.g., Kehoe, 1989; Pöysä et al., 1997), but to stability in others, such as eiders. Large intraspecific variation in parental care patterns exists even within eiders (Schmutz et al., 1982), so the first step in approaching these questions may be to compare common eider populations to reveal the factors that cause the attractiveness of lone tending versus coalition formation to vary so widely among different populations.

Tvärminne Zoological Station provided excellent board and lodging. We thank Yannis Deligiannis, Katja Helle, Patrik Karell, Lili Mantila, Henry Pihlström, Tobias Tamelander, and Mats Westerbom for help with fieldwork. We thank Reuven Dukas and Bernie Crespi for pointing out the relevance of the partner choice framework, and two anonymous referees for helpful comments on the manuscript. This study was financed by the Academy of Finland (grant no. 51895 to MÖ and grant no. 163390 to M.K.), the Ella och Georg Ehrnrooth Foundation, the Nessling Foundation, the Walter and Andrée de Nottbeck Foundation, and the EC Interreg IIa-program.

REFERENCES

Beauchamp G, 1997. Determinants of intraspecific brood amalgamation in waterfowl. Auk 114:11–21.

Beauchamp G, 1998. The relationship between intra- and interspecific brood amalgamation. Condor 100:153–162.

Beauchamp G, 2000. Parental behaviour and brood integrity in amalgamated broods of the common eider. Wildfowl 51:169–179.

Bernasconi G, Strassmann JE, 1999. Cooperation among unrelated individuals: the ant foundress case. Trends Ecol Evol 14:477–482.

Bustnes JO, 1993. Exploitation of others' vigilance by the common eider *Somateria mollissima*. Wildfowl 44:108–110.

Bustnes JO, Erikstad KE, 1991. Parental care in the common eider (*Somateria mollissima*): factors affecting abandonment and adoption of young. Can J Zool 69:1538–1545.

Clutton-Brock T, 1998. Reproductive skew, concessions, and limited control. Trends Ecol Evol 13:288–292.

Dugatkin LA, Sih A, 1998. Evolutionary ecology of partner choice. In: Cognitive ecology (Dukas R, ed). Chicago: University of Chicago Press; 379–403.

Eadie JM, Lyon BE, 1998. Cooperation, conflict and crèching behavior in goldeneye ducks. Am Nat 151:397–408.

Eadie JM, Kehoe FP, Nudds TD, 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. Can J Zool 66:1709–1721.

Forbes MRL, Clark RG, Weatherhead PJ, Armstrong T, 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. Behav Ecol Sociobiol 34:79–85.

Gabrielsen GW, 1994. Energy expenditure in arctic seabirds (PhD dissertation). Tromsø, Norway: University of Tromsø.

Hamilton IM, 2000. Recruiters and joiners: using optimal skew theory to predict group size and the division of resources within groups of social foragers. Am Nat 155:684–695.

Hario M, Kekkinen J, 2000. Parentage choice in common eider females [in Finnish with English summary]. Suomen Riista 46: 37–47.

Horsfall JA, 1984. Brood reduction and brood division in coots (*Fulica atra*). Anim Behav 32:216–225.

Johnstone RA, 2000. Models of reproductive skew: a review and synthesis. Ethology 106:5–26.

Johnstone RA, Cant MA, 1999. Reproductive skew and the threat of eviction: a new perspective. Proc R Soc Lond B 266:275–279.

Downloaded from http://beheco.oxfordjournals.org/ at Simon Fraser University on May 20, 2015

Kehoe FP, 1989. The adaptive significance of crèching behaviour in the white-winged scoter (*Melanitta fusca deglandi*). Can J Zool 67: 406–411.

Kilpi M, Lindström K, 1997. Habitat-specific clutch size and cost of incubation in common eiders, *Somateria mollissima*. Oecologia 111:297–301.

Kilpi M, Öst M, Lindström K, Rita H, 2001. Female characteristics and parental care mode in the crèching system of eiders, *Somateria mollissima*. Anim Behav 62:527–534.

Korschgen CE, 1977. Breeding stress of female eiders in Maine. J Wildl Manage 41:360–373.

Loonen MJJE, Bruinzeel LW, Black JM, Drent RH, 1999. The benefit of large broods in barnacle geese: a study using natural and experimental manipulations. J Anim Ecol 68:753–768.

Lyon BE, Eadie JM, Hamilton LD, 1994. Parental choice selects for ornamental plumage in American coot chicks. Nature 371:240–243.

Mappes J, Kaitala A, Alatalo RV, 1995. Joint brood guarding in parent bugs—an experiment on defence against predation. Behav Ecol Sociobiol 36:343–347.

Mappes J, Mappes T, Lappalainen T, 1997. Unequal maternal investment in offspring quality in relation to predation risk. Evol Ecol 11:237–243.

Mendenhall VM, Milne H, 1985. Factors affecting duckling survival of eiders *Somateria mollissima* in northeast Scotland. Ibis 127:148–158.

Minot EO, 1980. Tidal, diurnal and habitat influences on common eider rearing activities. Ornis Scand 11:165–172.

Munro J, Bédard J, 1977. Gull predation and crèching behavior in the common eider. J Anim Ecol 46:799–810.

Nastase AJ, Sherry DA, 1997. Effect of brood mixing on location and survivorship of juvenile Canada geese. Anim Behav 54:503–507.

Nonacs P, 1990. Size and kinship affect success of co-founding *Lasius pallitarsis* queens. Psyche 97:217–228.

Nonacs P, 1992. Queen condition and alate density affect pleometrosis in the ant *Lasius pallitarsis*. Insect Soc 39:3–13.

Ormerod SJ, Tyler SJ, 1990. Assessments of body condition in dippers *Cinclus cinclus*: potential pitfalls in the derivation and use of condition indices based on body proportions. Ringing Migr 11: 31–41.

Öst M, 1999. Within-season and between-year variation in the structure of common eider broods. Condor 101:598–606.

Öst M, 2000. Feeding constraints and parental care in female eiders (PhD dissertation). Helsinki, Finland: University of Helsinki.

Öst M, Kilpi M, 1999. Parental care influences the feeding behaviour of female eiders, *Somateria mollissima*. Ann Zool Fenn 36:195–204.

Öst M, Kilpi M, 2000. Eider females and broods from neighboring colonies use segregated local feeding areas. Waterbirds 23:24–32.

Öst M, Mantila L, Kilpi M, 2002. Shared care provides time-budgeting advantages for female eiders. Anim Behav 64:223–231.

Parker H, Holm H, 1990. Patterns of nutrient and energy expenditure in female common eiders nesting in the high arctic. Auk 107: 660–668.

Pöysä H, Virtanen J, Milonoff M, 1997. Common goldeneyes adjust maternal effort in relation to prior brood success and not current brood size. Behav Ecol Sociobiol 40:101–106.

Ranta E, Lindström K, Peuhkuri N, 1992. Size matters when three-spined sticklebacks go to school. Anim Behav 43:160–162.

Reeve HK, 2000. A transactional theory of within-group conflict. Am Nat 155:365–382.

Schmutz JK, Robertson RJ, Cooke F, 1982. Female sociality in the common eider duck during brood rearing. Can J Zool 60:3326–3331.

Swennen C, 1989. Gull predation upon eider *Somateria mollissima* ducklings: destruction or elimination of the unfit? Ardea 77:21–45.

Székely T, Webb JN, Houston AI, McNamara JM, 1996. An evolutionary approach to offspring desertion in birds. Curr Ornithol 13:271–330.

Willmer C, 1985. Thermal biology, size effects, and the origin of communal behaviour in *Cerceris* wasps. Behav Ecol Sociobiol 17: 151–160.

Wisenden BD, 1994. The dilution effect and differential predation following brood adoption in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). Ethology 96:203–212.

Downloaded from http://beheco.oxfordjournals.org/ at Simon Fraser University on May 20, 2015