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Body condition and the grouping behavior of brood-caring female common eiders (*Somateria mollissima*)

Received: 28 November 2002 / Accepted: 5 May 2003 / Published online: 7 June 2003
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Abstract Both theoretical and empirical work has shown that group size increases with increasing ecological constraints on solitary breeding. Ecological constraints refer to extrinsic factors such as availability of breeding sites, food or mates. Common eider (*Somateria mollissima*) females pool their broods and share brood-rearing duties, or rear broods alone. Females are often in poor condition at hatching, as incubation is accomplished without feeding, and variation in body condition is largely environmentally induced and thus unpredictable. We found that the intensity of and duration of parental care that females provide is positively correlated with their body condition at hatching. This suggests that body condition is an ecological constraint on successful solitary breeding. We further observed that group productivity in common eider broods is a decelerating function of the number of tending females. As predicted, females in poorer condition (i.e., facing stronger ecological constraints) were found in larger groups. This result is straightforward if solitary tenders can enter any group at no cost. However, if entry is group-controlled, stable groups of non-relatives are predicted not to occur when per capita reproduction declines with group size. The N-person staying incentive model permits groups to form under these conditions, because reproduction is unevenly

divided between dominants and subordinates in the group. We discuss the plausibility of these alternative models of group size for understanding the grouping behavior of brood-caring female common eiders.

Keywords Body condition · Ecological constraints · Group size · N-person staying incentive model · *Somateria mollissima*

Introduction

Ecological constraints on solitary breeding have been identified as key factors affecting group size in breeding groups. Ample evidence from co-operatively breeding birds with helpers-at-the-nest, as well as from some social insects and mammals, suggests that group size increases with increasing ecological constraints on successful solitary breeding (e.g., Zack and Rabenold 1989; Pruett-Jones and Lewis 1990; Komdeur 1992; Walters et al. 1992; Bourke 1997; Faulkes et al. 1997). These empirical findings are corroborated by models of group size. Stronger ecological constraints on successful solitary breeding increase the difference between the fitness of individuals within groups as compared to solitary breeders, and thus larger group sizes are to be expected (Sibly 1983; Giraldeau and Caraco 1993; Higashi and Yamamura 1993).

In all previous studies, ‘ecological constraints’ refer to extrinsic factors such as availability of breeding sites, food and/or mates. However, for long-lived species such as seabirds, decisions about how much effort to expend on the current breeding effort can be constrained by the individual’s current body condition, such that individuals in poor condition may reduce their current effort to avoid jeopardizing survival and future breeding attempts (Clark and Ydenberg 1990; Bustnes and Erikstad 1991; Chastel et al. 1995; Erikstad et al. 1997; Olsson 1997; Kilpi et al. 2001). Considering that variation in body condition is often environmentally determined and thus unpredictable (e.g., Kilpi and Lindström 1997) and that poor body

Communicated by M. Webster

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condition is associated with low success in lone reproduction, body condition should be regarded as an 'ecological constraint' comparable with the ecological constraints typically referred to in studies of co-operative breeding.

A key factor affecting the attractiveness of grouping is the shape of the function relating group size and group productivity (e.g., Johnstone et al. 1999; Reeve and Emlen 2000). When the productivity function is decelerating, group members should oppose joiners, even though the joiners themselves may gain from group membership (e.g., Sibly 1983; Higashi and Yamamura 1993). Whether group entry is under the joiner's or the group members' control therefore has a profound influence on group formation and predicted group sizes (Giraldeau and Caraco 2000). In particular, in the absence of relatedness, stable groups are predicted not to occur when per capita reproduction declines with group size and entry is group-controlled.

Reeve and Emlen (2000) developed a framework for reproductive grouping that permits groups to form under these conditions. Their N-person staying incentive model also predicts that decreased expected output for solitary breeding increases the 'saturated' group size (i.e., the group size at which subordinates no longer find it worthwhile to join), but unlike in the group-controlled entry framework this can occur even when the productivity function decelerates. The reason is their assumption that dominants in the group control reproduction ('skew'), and leave joiners only enough gain to keep them in the group, reaping the rest for themselves.

Common eiders (*Somateria mollissima*) provide an interesting system for evaluating the importance of ecological constraints on group size due to the variety of their parental care system. Some common eider females are 'lone tenders' and rear broods on their own, while other females rear young communally, and yet others are known to abandon their broods after a short period of care. Along the southwest Finnish coast, most females tend broods in coalitions, usually of 2–4 females (Öst 1999; Kilpi et al. 2001; Öst et al. 2003). The different parental care modes are associated with differences in body condition. Kilpi et al. (2001) found that lone tenders are on average in the best condition at hatching, followed by females in enduring multi-female coalitions, then transient crèchers, while non-tenders were in the poorest condition.

In a previous paper (Öst et al. 2003), we constructed a model in which common eider females, based on their body condition and the structure of the joint brood ('skew'), assess the fitness consequences of joining a coalition versus tending alone. Our model correctly predicted non-random patterns in the body conditions of females in enduring coalitions; females in good body condition only formed coalitions with females in poor condition and not with other females in good condition. Our previous model only considered partner choice as such, ignoring potential variation in the characteristics of females attending different sized groups. In the current

paper, we demonstrate that female body condition is synonymous with an ecological constraint on successful solitary breeding. Using data obtained during several field seasons, we test the prediction that females in poorer condition (i.e., facing stronger ecological constraints on successful lone reproduction) are willing to join larger groups. We also estimate the overall shape of the function relating expected group reproductive output to group size. Finally, we discuss the plausibility of alternative models of group size for understanding the grouping behavior of brood-caring female common eiders.

Methods

Field methods

This study was conducted in the archipelago surrounding Tvärminne Zoological Station (59°50'N, 23°15'E), on the Baltic Sea in southwestern Finland. Slightly less than 1,500 common eider females nest on small open islands and on larger wooded islands. Kilpi and Lindström (1997) and Öst and Kilpi (2000) describe the study area in more detail.

Incubating common eider females were captured on the nest with hand-nets on selected islands in the study area. We confined our trapping so as to coincide with the late stages of incubation for the peak breeding cohort, thereby minimizing nest desertion due to our trapping procedures (Kilpi et al. 2001). 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 that had been incubating for at least 10 days on target islands selected for behavioral observation were then given 3×3-cm flags with a unique color combination attached to the third-outermost primary (Öst and Kilpi 2000). Altogether 472 females were marked with flags during 1997–2001 (1997: $n=81$; 1998: $n=81$; 1999: $n=74$; 2000: $n=134$; 2001: $n=102$). One person (M.K.) conducted all the measurements to avoid inter-observer variance.

We derived estimates of the females' weight at hatching by using the methodology developed by Kilpi and Lindström (1997). Females do not eat during incubation and therefore lose weight. We subtracted from a female's measured incubation weight an estimate of the weight she had yet to lose during the remaining incubation time. The incubation stage was either estimated directly from known hatching dates or laying dates, or indirectly by an egg floatation test (Kilpi and Lindström 1997). Estimates of the incubation stage based on direct and indirect methods do not differ (Kilpi and Lindström 1997). The rate of body weight loss was estimated by regressions of log-transformed body weight on log-transformed incubation time, taking into account year and type of nesting island. 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). Standardized residual masses at hatching were derived for the pooled data from all 5 years under study.

We tried to locate individually known females for at least 30 days after hatching (observation period late-May to mid-July). All observations of a known female during 1 day constituted one observation. At each sighting of a female we recorded her identity and if she was attending a brood, and also the number of females and ducklings in the brood. Each focal brood was followed long enough to ensure correct assessment of the brood-rearing status of all females attending the brood (Öst et al. 2003). This assessment is straightforward in our study area, as non-tending females are not tolerated within broods and are promptly chased away by the tending female(s). Group size was defined as the number of tending females in a brood with at least one known female 3 weeks or more after the estimated hatching date of the marked female's young. By

Table 1 Frequencies of group sizes in common eider broods at Tvärminne in 1997–2001. Group size was defined as the number of tending females in a brood with at least one known female three 3 weeks or later after the estimated hatching date of the marked female's young. The percentage of yearly totals is shown in parentheses

Group size	1997	1998	1999	2000	2001	5 years combined
1	10 (47.6)	6 (35.3)	8 (28.6)	13 (25.0)	10 (20.0)	47 (28.0)
2	7 (33.3)	9 (52.9)	12 (42.9)	23 (44.2)	32 (64)	83 (49.4)
3	4 (19.0)	2 (11.8)	8 (28.6)	15 (28.8)	8 (16)	37 (22.0)
4	0 (0)	0 (0)	0 (0)	1 (1.9)	0 (0)	1 (0.6)
Total	21	17	28	52	50	168

using this restrictive definition of group size we avoided including females that are transient in broods; transient crèchers are present in the broods during the social interaction period spanning roughly the first 2 weeks after hatch (Öst 1999; Kilpi et al. 2001; Öst et al. 2003). Thus, the female group size defined by us was always as small as or smaller than the maximum number of females observed in broods during early brood-rearing, and stability with respect to female numbers was almost invariably the rule after this group size had been reached. To explore the relationship between the number of females and ducklings in broods, we compared the maximum and minimum number of ducklings observed in broods after the 'saturated' female group size (described above) had been reached. Only one observation per brood was included, so as to exclude multiple observations of known females tending the same brood. The bias caused by duckling mortality is likely to be similar for all broods regardless of female group size, because the time interval between the date for observing both the maximum and minimum number of ducklings and the focal female's hatching date in the brood was similar for all group sizes (group size 1: maximum 7.21 ± 0.89 days, minimum 26.23 ± 2.26 days, $n=47$; group size 2: max. 9.88 ± 0.78 days, min. 27.38 ± 1.28 days, $n=76$; group size 3: max. 10.38 ± 1.18 days, min. 29.30 ± 1.90 days, $n=34$; group size 4: max. 6 days, min. 35 days, $n=1$; maximum number, one way ANOVA: $F_{3,154}=2.12$, $P=0.10$; minimum number, Kruskal-Wallis ANOVA: $H_3=2.16$; $P=0.54$).

We measured two attributes related to parental care intensity (parental effort) of common eider females, the level of 'broodiness' and duration of care. We based our estimate of female broodiness on the conventional classification used by Bédard and Munro (1976). According to their classification, broody females lead the brood during movements, do most of the vocalization and vigilance behavior, and brood the young. Associate females are less active, but nevertheless stay almost as close to the ducklings as broody females. Visiting females stay at the fringe of the brood, and they temporarily leave the brood at moderate human disturbance (Bédard and Munro 1976). Given that the observation time of a brood is sufficient, it is usually straightforward to determine the level of broodiness of a focal bird. Nonetheless, the classification by Bédard and Munro (1976) is still sensitive to subjective interpretation. We took the following measures to minimize any subjective bias and to make our estimate of broodiness as robust as possible: (1) the level of broodiness was measured on a coarse-grained decreasing scale from 3 to 1 (3 = broody females and broody/associate females; 2 = associate females and associate/visiting females; 1 = visiting females), (2) the index of broodiness was derived as the average score of all observations of a focal female, and (3) observations where broodiness could not be unequivocally determined were omitted. Our broodiness index was based on 5.6 ± 0.29 (mean \pm SE) determinations of broodiness per bird (range 1–23 determinations, $n=259$ females).

The duration of care of a focal female was determined as the time interval between the last observation of the female and the hatching date of her clutch, provided that she was still attending a brood when last sighted, or, alternatively, as the time interval between the first observation of the female without young and the hatching date. To improve the accuracy of our estimate of care duration we excluded cases in which (1) the duration of care was less than 14 days and the bird was still caring for young when last sighted (marking may have been lost prematurely); (2) brood size

was one in the observation preceding the first observation of the focal female without young (duration of care constrained by complete brood loss); and (3) the interval between the observation of the focal female with and without young exceeded 7 days (estimate too inaccurate).

Statistical methods

A two-sample Kolmogorov-Smirnov test showed that the frequency distribution of condition indices at hatching of marked females observed at sea ($n=386$) during 1997–2001 was similar to that of all females weighed ($n=640$) during 1997–2001 ($D=0.025$, $P=0.99$). Consequently, the marked females we observed at sea fairly represent the entire breeding population at Tvärminne.

Any correlation between condition and group size in our sample may be influenced by factors such as sample size and the frequency distribution of group sizes in the sample. To account for this, we used a randomization procedure to test whether our observed correlation exceeds that expected by chance. The frequency distribution of female numbers in broods shows between-year variation related to overall female condition (Öst 1999). Therefore, the test was done by drawing a year-specific random sample of females equal in size to the actual annual sample from the population without replacement ('population' equals all weighted females: 1997: $n=117$; 1998: $n=109$; 1999: $n=112$; 2000: $n=171$; 2001: $n=131$), and randomly assigning these females to a group size in exact proportion to the year-specific distribution of group sizes in the actual sample (Table 1). The Pearson correlation coefficient between the condition at hatching and the group size assigned to each female was calculated after pooling the five randomly drawn annual samples of females (1997: $n=21$; 1998: $n=17$; 1999: $n=28$; 2000: $n=52$; 2001: $n=50$; Table 1), and the process was repeated 100,000 times. The proportion of cases in which the simulated r value was lower than the actual r value was tabulated, estimating the probability of obtaining a more extreme outcome under the null hypothesis of group size and body condition being independent of each other. Although some females occur in more than 1 year in the data, problems with lack of statistical independence are likely to be small because body conditions and group sizes were year-specifically combined in the analysis.

Parametric tests are used whenever the data fulfilled the assumptions of these tests, and statistical tests are two-tailed unless otherwise stated. To normalize distributions, we log-transformed the number of ducklings and females in broods when investigating the relationship between reproductive output and female group size. We report means and standard errors in the text.

Results

Body condition and care intensity

There was a significant positive correlation between the mean score of broodiness of a female and her body condition at hatching, including all data from 1997 to 2001 in the analysis (Spearman rank correlation:

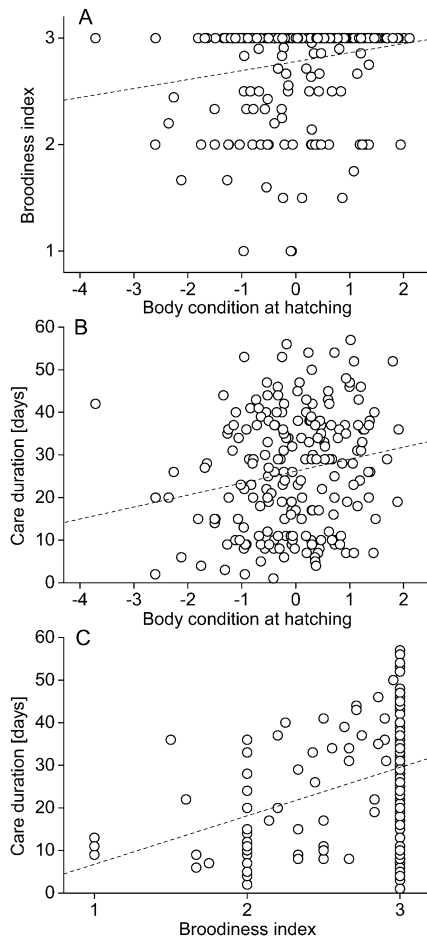


Fig. 1 The relationship between **A** an index of broodiness of a female (for definition, see Methods) and her body condition at hatching, **B** duration of care (for definition, see Methods) and body condition at hatching, and **C** duration of care and the index of broodiness. Shown are all data from 1997 to 2001; female body condition refers to standardized residual masses at hatching derived for pooled data from all study years. *Broken lines* indicate linear regression equations fitted to the data for illustrative purposes only

$r_s=0.182$, $n=259$, $P=0.003$; Fig. 1A). The duration of care of a female and her body condition at hatching were also positively correlated in the data from 1997 to 2001 (Pearson correlation: $r=0.188$, $n=203$, $P=0.007$; Fig. 1B). Finally, the two measured attributes related to parental care intensity, level of broodiness and care duration, also showed a positive correlation with each other ($r_s=0.30$, $n=195$, $P<0.001$; Fig. 1C).

Body condition and group size

A female's body condition at hatching and the number of females in the brood she was subsequently attending showed a negative correlation in the pooled data from 1997 to 2001 ($r=-0.207$, $n=168$; Fig. 2). Our randomization test showed that the probability of observing a correlation coefficient value lower than -0.207 by randomly drawing 168 females from the population of

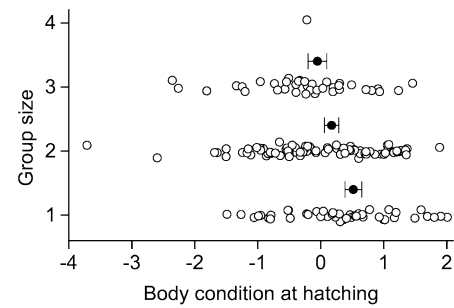


Fig. 2 The relationship between female group size (for definition, see Table 1) and body condition at hatching in 1997–2001. Slight random jitter has been added to the variable group size to make overlapping data points easier to distinguish. Mean (\pm SE) body condition of females in groups of different sizes is also shown

breeding females was 0.004. The mean simulated correlation was -0.0064 . We conclude that the null hypothesis of female group size and body condition being independent of each other can be refuted. Females in poorer condition joined larger groups.

Group size and group productivity

A group size of two females was the most prevalent one in the entire data set with an overall frequency of 49.4% in all 5 years under study (Table 1). Lone tenders accounted for 28% of all groups, and females in groups of three birds for 22% of the observed females in 1997–2001 (Table 1). The average group size was 1.95 females and the typical group size (Jarman 1974) was 2.22 females. Groups with more than three females are rare; only one marked female out of 168 was later found in a group of four females (Table 1).

There was a significant positive relationship between both the maximum and minimum numbers of ducklings and the number of females per brood (maximum: linear regression: $\log\text{-ducklings}=0.63+0.46\times\log\text{-females}$; $r^2=0.07$, $F_{1,156}=11.96$, $P<0.001$; minimum: $\log\text{-ducklings}=0.36+0.55\times\log\text{-females}$; $r^2=0.10$, $F_{1,156}=16.58$, $P<0.001$). The slopes of both relationships were less than one (maximum: one-tailed t test: $t_{156}=4.08$, $P<0.001$; minimum: $t_{156}=3.28$, $P<0.001$), confirming that the ratio of ducklings to females decreased as female group size increased.

Since female body condition is not independent of female group size (see above), body condition might confound the relationship between reproductive output and female group size. We did two separate tests to evaluate whether the lower ratio of ducklings to females in larger groups is affected by group size per se, or simply caused by variation in individual reproductive quality. First, we compared the clutch size of females associating in different sized groups, and found no differences between female categories (group size 1: 5.13 ± 1.12 , $n=47$; group size 2: 4.73 ± 1.30 , $n=83$; group size 3: 4.76 ± 1.50 , $n=37$; group size 4: 6, $n=1$; one way ANOVA:

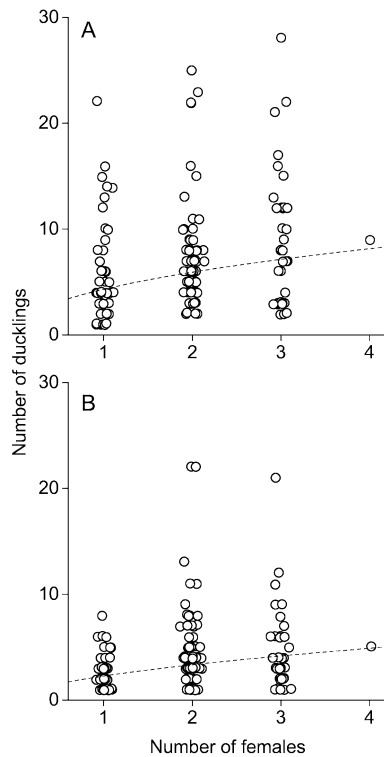


Fig. 3a-b The relationship between the number of ducklings and females (i.e. female group size, defined in Table 1) in broods in 1997–2001. **A** maximum number of ducklings observed in broods after the ‘saturated’ female group size had been reached; **B** minimum number of ducklings observed in broods and ‘saturated’ female group size. Slight random jitter has been added to the variables to make overlapping data points easier to distinguish. Broken lines show the regression equations for the relationship between log-duckling number and log-female number (see text)

$F_{3,164}=1.26$, $P=0.29$). Second, we tested the independent effects of female group size and body condition on the number of ducklings with generalized linear models, controlling for each other effect using Type III sum of squares. The overall model for the maximum number of ducklings was $\log\text{-ducklings}=0.63+0.49\times\log\text{-females}+0.028\times\text{condition}$ ($R^2=0.08$, $F_{2,155}=6.58$, $P=0.002$), and for the minimum number of ducklings $\log\text{-ducklings}=0.35+0.57\times\log\text{-females}+0.017\times\text{condition}$ ($R^2=0.10$, $F_{2,155}=8.43$, $P<0.001$). There was no significant effect of female body condition on either the maximum ($t_{155}=1.09$, $P=0.28$) or minimum ($t_{155}=0.59$, $P=0.56$) number of ducklings observed. By contrast, female group size had a statistically significant effect on both the maximum and minimum number of ducklings (maximum: $t_{155}=3.62$, $P<0.001$; minimum: $t_{155}=4.10$, $P<0.001$). In addition, we checked for an interaction between group size and body condition, by including group size as a factor in the analyses. Neither body condition nor the interaction were significant in any of these models, only female group size had a significant effect. Taken together, this evidence suggests that the number of ducklings in a brood is a decelerating function of female group size as such (Fig. 3).

Discussion

The body condition of common eider females was negatively related to the level of broodiness and duration of care, strongly suggesting that it is a constraint on successful solitary breeding. Females in poor condition are also more likely to abandon their newly hatched broods (Bustnes and Erikstad 1991; Hario and Kekkinen 2000; Kilpi et al. 2001; Bustnes et al. 2002). The fundamental importance of body condition in regulating care duration and care intensity is well established among seabirds (reviewed by Tveraa et al. 1998; Tveraa and Christensen 2002). Body condition in eiders seems largely determined by environmental factors such as severity of weather during incubation and food abundance affecting the level of stored reserves (Kilpi and Lindström 1997). In particular the fact that individual females show large annual variation in body condition which in turn affects their tending decisions (Bustnes and Erikstad 1991; Kilpi et al. 2001), suggests that the constraints imposed by body condition are primarily ecological rather than being determined by, e.g., genetic quality.

We observed that group productivity in eider broods is a decelerating function of the number of participating females. The available evidence suggests that this is a function of group size, and not merely a consequence of females in poorer condition associating in larger groups. Thus, the clutch size of females in different sized groups was similar, and we detected a significant effect of female group size, but not of body condition, on the total number of ducklings in broods. Even though the body condition of only one female per brood was included in our models, this should not cause bias as it is reasonable to assume that the known female represents a true random sample of the females in the group. Furthermore, the long duration of ‘saturated’ groups, spanning a considerable part of the rearing season (average time interval between observing the maximum and minimum number of ducklings 17.76 ± 1.08 days, $n=158$) by itself adds credence to our interpretation that female group size plays an important role in shaping the overall reproductive output. However, experimental manipulations would be needed to verify this interpretation conclusively.

A variety of factors may influence the observed decline in per capita productivity with group size. For small ducklings the major agent of mortality is depredation by gulls, and larger broods may be more attractive targets (Munro and Bédard 1977b). Common eider females can defend the brood effectively against attacks once the ducklings are close to the tending female (Mendenhall and Milne 1985; Swennen 1989). Most victims are ducklings that stray too far from the tending female(s), and therefore fail to react to the alarm calls in time (Swennen 1989). Larger broods are likely to be spatially more spread out than smaller ones, and thus a predator may have a better chance of finding suitable targets at the edge of large broods. This potential disadvantage of larger groups may partly be offset by more efficient predator detection and defense by several

females (Munro and Bédard 1977b; Minot 1980). However, detection probability of a predator generally increases at a decreasing rate with group size (Pöysä 1987; Roberts 1996), and a similar relationship might be expected for group size and efficiency of brood defense. Group productivity may also decline with group size owing to more intense competition for food or enhanced disease transmission.

We verified that females in poor condition were on average found in larger groups. If entry into groups is under the joiner's control, our finding is straightforward regardless of the shape of the group productivity function (Sibly 1983; Giraldeau and Caraco 1993; Higashi and Yamamura 1993). But, under the 'group-controlled entry' model of group size (Giraldeau and Caraco 1993, 2000), new joiners should not be accepted by the group members since they lower per capita reproductive output, unless group insiders and outsiders are related and inclusive fitness considerations are at stake. By contrast, groups can form under these conditions in the N-person staying incentive model of group size (Reeve and Emlen 2000). Our preliminary analysis of the relatedness of common eider females in enduring coalitions indicates that relatedness is close to zero (unpublished data). Thus, according to Reeve and Emlen (2000), the existence of cooperative associations of non-relatives when the group output function is decelerating by itself suggests that the staying incentive (transactional) model of group size is supported.

To discriminate between these alternative models of group size, we need to establish the rules of entry in common eider brood-rearing coalitions, and to determine whether reproductive shares are unevenly divided in these associations. Early coalition formation is characterized by frequent aggression between females, both within- and particularly between eider broods (Munro and Bédard 1977a; Öst 1999). Another distinctive character is the formation of female dominance hierarchies, with females assuming different roles in the brood (Bédard and Munro 1976; Öst 1999). The females departing from multi-female broods are probably of subordinate status (Bédard and Munro 1976; Swennen 1989); our finding that low 'broodiness' is associated with short care duration (Fig. 1C) supports this view. The frequent observations of intense fighting at the outset of brood-rearing suggests that group membership is contested. In general, group-controlled entry is the rule in animals characterized by social dominance relationships (Giraldeau and Caraco 1993). The differing roles of eider females also indirectly suggests that reproduction may not be equally divided within brood-rearing coalitions. These arguments seem to be in line with the N-person staying incentive model of group size (Reeve and Emlen 2000), but detailed investigations into the entry rules of common eider coalitions and the relationship between social dominance and reproductive skew are needed to rule out alternative group size models.

Although female body condition is significantly negatively correlated with group size, this relationship shows

wide variation (Fig. 2). We believe that this variation is not merely measurement error; at least a part of this variation can be explained by the partner choice criteria used by females forming enduring coalitions. In our previous paper, we showed theoretically and empirically that females in good body condition should only form coalitions with poor condition females, and not with other females in good condition (Öst et al. 2003). A good condition female is less likely to enter a coalition because reproductive output of the coalition should be strongly skewed in her favor to afford her higher fitness than lone-tending, and thus fewer suitable coalition partners can be found. In contrast, a female in poor condition is more likely to enter a coalition because she has a low expected reproductive output if she were to rear the brood on her own (i.e., ecological constraints are severe), and thus she will be willing to accept even a low share of reproduction in a coalition (Öst et al. 2003). Hence we may expect to find combinations of females where the difference (i.e., variance) in body condition between partners is large, and can potentially accommodate the large variation shown in Fig. 2.

Our data strongly support the idea that a female's condition constrains her ability to rear offspring as a lone tender, and it may be expected that her condition also influences her ability to contribute to communal rearing. We have not directly considered this issue here, but the group productivity function (Fig. 3) would include this factor, as it was estimated from coalitions observed in the field within which females were presumably giving the level of care appropriate for their condition. The great variability observed suggests that there may be adjustments in the intensity of care that females of a given condition are willing to give when in coalitions, perhaps in exchange for a more favorable brood arrangement. The intense social interactions (Öst 1999) at the outset of the brood-rearing period may perhaps be viewed as negotiations (McNamara et al. 1999) between potential coalition partners about brood arrangement and effort.

Emlen (1997) suggests that future researchers of animal social dynamics should place particular emphasis on studying species exhibiting shared reproduction, and which do not show biparental care. Common eiders nicely fit this description. The potential of common eiders for testing models of social dynamics may have gone unnoticed because crèching behavior in waterfowl has previously been regarded as a form of reproductive parasitism (e.g., Eadie and Lyon 1998), rather than within a reproductive skew framework. By showing that body condition equates to an ecological constraint on successful solitary reproduction, we were able to confirm that the group size that a female is willing to accept increases as her body condition falls. Group productivity decreases with group size and group members are probably unrelated — these facts suggest that skew adjustments by dominant group member(s) are necessary to explain grouping behavior of brood-caring female common eiders — but we still need more data to exclude alternative explanations.

Acknowledgements We thank Katja Helle, Patrik Karell, Lili Mantila, Henry Pihlström, Tobias Tamelander, Peter Waldeck and Mats Westerbom for help in the field. Tvärminne Zoological Station provided excellent working facilities. We thank Elizabeth Tibbetts and two anonymous reviewers for their helpful comments on the manuscript, and the Academy of Finland (grant no. 51895 to M.Ö. and grant no. 163390 to M.K.) and the Ella och Georg Ehrnrooth foundation for funding. Common eiders were trapped under a Finnish ringer's license, according to Finnish legislation and specific regulations of the Tvärminne Zoological Station.

References

- Bédard J, Munro J (1976) Brood and crèche stability in the common eider of the St. Lawrence Estuary. *Behaviour* 60:221–236
- Bourke AFG (1997) Sociality and kin selection in insects. In: Krebs JR, Davies NB (eds) *Behavioural ecology. An evolutionary approach*, 4th edn. Blackwell, Oxford, pp 203–227
- 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
- Bustnes JO, Erikstad KE, Bjørn TH (2002) Body condition and brood abandonment in common eiders breeding in the high arctic. *Waterbirds* 25:63–66
- Chastel O, Weimerskirch H, Jouventin P (1995) Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76:2240–2246
- Clark CW, Ydenberg RC (1990) The risks of parenthood. I General theory and applications. *Evol Ecol* 4:21–34
- Eadie JM, Lyon BE (1998) Cooperation, conflict and crèching behavior in goldeneye ducks. *Am Nat* 151:397–408
- Emlen ST (1997) Predicting family dynamics in social vertebrates. In: Krebs JR, Davies NB (eds) *Behavioural ecology. An evolutionary approach*, 4th edn. Blackwell, Oxford, pp 228–253
- Erikstad KE, Asheim M, Fauchald P, Dahlhaug L, Tveraa T (1997) Adjustments of parental effort in the puffin: the roles of adult body condition and chick size. *Behav Ecol Sociobiol* 40:95–100
- Faulkes CG, Bennett NC, Bruford MW, O'Brien HP, Aguilar GH, Jarvis JUM (1997) Ecological constraints drive social evolution in the African mole-rats. *Proc R Soc Lond B* 264:1619–1627
- Giraldeau L-A, Caraco T (1993) Genetic relatedness and group size in an aggregation economy. *Evol Ecol* 7:429–438
- Giraldeau L-A, Caraco T (2000) *Social foraging theory*. Princeton University Press, Princeton, N.J.
- Hario M, Kekkinen J (2000) Jälkeläishoidon jakautuminen haahkalla. *Suom Riista* 46:37–47
- Higashi M, Yamamura N (1993) What determines animal group size? Insider-outsider conflict and its resolution. *Am Nat* 142:553–563
- Jarman PJ (1974) The social organization of antelope in relation to their ecology. *Behaviour* 48:215–267
- Johnstone RA, Woodroffe R, Cant MA, Wright J (1999) Reproductive skew in multimember groups. *Am Nat* 153:315–331
- 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
- Komdeur J (1992) Importance of habitat-saturation and territory quality for the evolution of cooperative breeding in the Seychelles warbler. *Nature* 358:493–495
- McNamara JM, Gasson CE, Houston AI (1999) Incorporating rules for responding into evolutionary games. *Nature* 401:368–371
- 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 brood rearing activities. *Ornis Scand* 11:165–172
- Munro J, Bédard J (1977a) Crèche formation in the common eider. *Auk* 94:759–771
- Munro J, Bédard J (1977b) Gull predation and crèching behavior in the common eider. *J Anim Ecol* 46:799–810
- Olsson O (1997) Clutch abandonment: a state-dependent decision in king penguins. *J Avian Biol* 28:264–267
- 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. *Ring 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, Kilpi M (2000) Eider females and broods from neighboring colonies use segregated local feeding areas. *Waterbirds* 23:24–32
- Öst M, Ydenberg R, Kilpi M, Lindström K (2003) Condition and coalition formation by brood rearing common eider females. *Behav Ecol* 14:311–317
- Pöysä H (1987) Feeding-vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. *Behaviour* 103:108–122
- Pruett-Jones SG, Lewis MJ (1990) Sex ratio and habitat limitation promote delayed dispersal in superb fairy wrens. *Nature* 348:541–542
- Reeve HK, Emlen ST (2000) Reproductive skew and group size: an N-person staying incentive model. *Behav Ecol* 11:640–647
- Roberts G (1996) Why individual vigilance declines as group size increases. *Anim Behav* 51:1077–1086
- Sibly RM (1983) Optimal group size is unstable. *Anim Behav* 31:947–948
- Swennen C (1989) Gull predation upon eider *Somateria mollissima* ducklings: destruction or elimination of the unfit? *Ardea* 77:21–45
- Tveraa T, Christensen GN (2002) Body condition and parental decisions in the snow petrel (*Pagodroma nivea*). *Auk* 119:266–270
- Tveraa T, Saether B-E, Aanes R, Erikstad KE (1998) Body mass and parental decisions in the Antarctic petrel *Thalassoica antarctica*: how long should the parents guard the chick? *Behav Ecol Sociobiol* 43:73–79
- Walters JR, Copeyon CK, Carter IJH (1992) Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk* 109:90–97
- Zack S, Rabenold K (1989) Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. *Anim Behav* 38:235–247