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ORIGINAL ARTICLE

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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

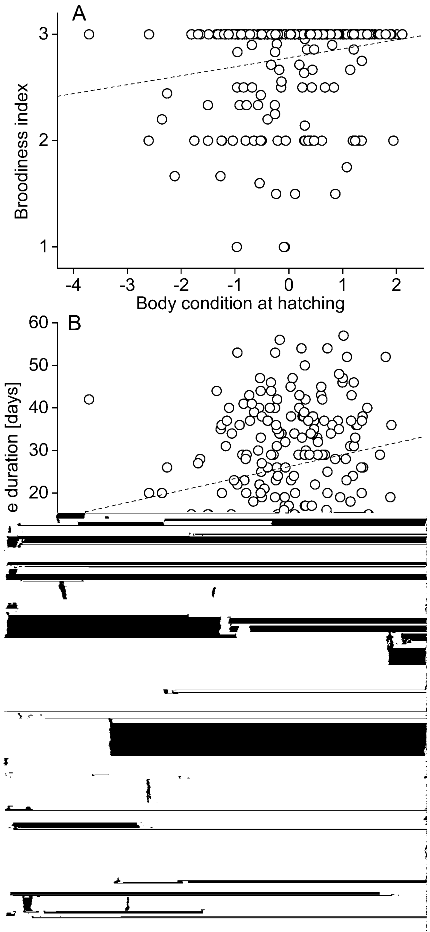

Fig. 1 The relationship between A an index of broodiness of a female (for definition, see Methods) and her body condition at hatching, B duration of care (for definition, see Methods) and body condition at hatching, and C duration of care and the index of broodiness. Shown are all data from 1997 to 2001; 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

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 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-ducklings=0.63+0.46 log-females; r^2= 0.07, $F_{1,156}$=11.96, P<0.001; minimum: log-ducklings= 0.36+0.55 log-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:

$F_{3,164}$=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, females (Munro and B dard 1977b; Minot 1980). How-

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