Social and maternal factors affecting duckling survival in eiders *Somateria mollissima*

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Summary

1. With the aid of a novel survivorship model, an 8-year field study of social and maternal factors affecting duckling survival in eiders (*Somateria mollissima*) revealed that duckling survival probability varies in accordance with maternal brood-rearing strategy. This variability in survival provides compelling evidence of different annual fitness consequences between females that share brood-rearing and those that tend their broods alone. Consequently, as prebreeding survival is often a major source of individual variation in lifetime reproductive success, a female's annual, state-dependent (e.g. condition) choice of a brood-rearing strategy can be a critical fitness decision.
2. Variance in duckling survival among lone tender broods was best explained by a model with significant interannual variability in survival, and survivorship tending to increase with increasing clutch size at hatch. Clutch size was correlated positively with female condition. Hatch date and female body condition together affected duckling survival, but their contributions are confounded. We were unable to identify a relationship between female age or experience and duckling survival.
3. Variance in duckling survival among multifemale brood-rearing coalitions was best explained by a model that included the number of tenders, the number of ducklings and interannual variation in how their ratio affected survivorship. Hatch date did not significantly influence survival.
4. Expected duckling survival is higher in early life for lone tenders when compared with multifemale brood-rearing coalitions. However, as ducklings approach 2–3 weeks of age, two or three females was the optimal number of tenders to maximize daily duckling survival. The survivorship advantage of multifemale brood-rearing coalitions was most evident in years of average survival.
5. The observed frequency distribution of female group sizes corresponds with the distribution of offspring survival probabilities for these groups. Evidence for optimal group sizes in nature is rare, but the most likely candidates may be groups of unrelated animals where entry is controlled by the group members, such as for female eiders.
6. Our study demonstrates that differences in social factors can lead to different predictions of lifetime reproductive success in species with shared parental care of self-feeding young.

Key-words: brood survival, optimal group size, reproductive success, survival estimation

Introduction

Prebreeding survival is a major, albeit poorly understood, contributor of individual variation in lifetime reproductive success (Clutton-Brock 1991; Johnson, Nichols & Schwartz 1992; Lindström 1999). A considerable part of the variation in prebreeding survival is often environmentally induced and is thus outside individual control (e.g. Sedinger *et al.* 1997; van der Jeugd & Larsson 1998). On the other hand, maternal effects such as body condition, age, size, timing of breeding and clutch or brood size are found commonly to exert a strong effect on offspring survival when young are raised by their parent(s) (e.g. Clutton-Brock 1991). In addition, reproductive success may be influenced by social factors such as the number of adults and young in the brood, the ratio of juveniles to caring adults and the phenotypic characteristics of the adult members of social breeding groups. However, so far the importance of such effects has received little attention, with the exception of studies on cooperatively breeding vertebrates with helpers-at-the-nest (e.g. Russell *et al.* 2002) and social insects (e.g. Foster 2004).

Scrutiny of the social and maternal factors assumed to be important for prebreeding survival reveals inconsistent trends across species. For example, increasing brood size has been found to have deleterious or positive effects on offspring fitness in altricial (e.g. de Kogel 1997) and precocial species (Lepage, Gauthier & Desrochers 1998; Loonen *et al*. 1999), respectively. Early breeding, parental age, body condition, the number of caring adults and their ratio to the juveniles in social breeding groups have all been found to be either positively correlated with, or have no discernible effect upon, offspring survival probability (reviewed in Blums, Clark & Mednis 2002). A failure to simultaneously allow for all important factors influencing offspring fitness may lead us to accept spurious relationships between these factors and offspring survival and may explain, at least partly, the often equivocal trends of empirical work. It may also be very difficult to disentangle social and maternal influences on offspring survival even with carefully planned experiments, because these factors are often tightly coupled with each other (cf. Blums *et al*. 2002).

Knowing the shape of the function relating individual fitness to group size is paramount to understanding the evolution of social reproduction and predicted group sizes (Rannala & Brown 1994; Avilés & Tufiño 1998; Reeve & Emlen 2000; Öst *et al*. 2003b). Theory usually assumes that the benefits of grouping increase at a decelerating rate while the costs increase at an accelerating rate, leading to the prediction that a fitness optimum exists at intermediate group sizes (Sibly 1983; Giraldeau & Caraco 1993, 2000; Higashi & Yamamura 1993). While conceptually appealing, at present there is only limited empirical evidence for fitness functions with intermediate optimum group sizes (Avilés & Tufiño 1998; Russell *et al*. 2002; Williams, Lutz & Applegate 2003), and still fewer empirical studies have been able to show that the size distribution of naturally occurring groups reflects the consequences of different group sizes on individual fitness (but see Williams *et al*. 2003). Most groups in nature tend to be larger than optimal, as group members are often constrained from achieving the optimum group size by animals that attempt to join the group (Sibly 1983; Giraldeau & Caraco 1993, 2000; Brown & Brown 2000). Furthermore, in groups of related individuals, members may accrue inclusive fitness benefits, confounding the relationship between group size and group productivity (Giraldeau & Caraco 1993, 2000; Higashi & Yamamura 1993; Reeve & Emlen 2000). Consequently, the most probable candidates to exhibit a group size approaching the optimum are animals characterized by social dominance relationships such as socially breeding vertebrates, where entry into groups is typically group-controlled (Giraldeau & Caraco 1993), and where relatedness among group members does not add any additional complexity to the group size–group productivity relationship.

In the present study we investigated a suite of social and maternal factors affecting duckling survival in eiders *Somateria mollissima* (Linnaeus), based on repeated observations of offspring associated with individually known adults. Eider females may pool their broods and share brood-rearing, or they may tend their broods alone (Bustnes & Erikstad 1991; Kilpi *et al*. 2001; Öst *et al*. 2003a). This dichotomy of parental care strategies allowed us to conduct a set of analyses that evaluated the importance of maternal factors (e.g. body condition, female age, clutch size) on the survival of lone-tended broods in isolation from a second set of analyses investigating the effect of social factors (number of caring adults and ducklings and their ratio in amalgamated broods) on offspring survival in multifemale brood-rearing coalitions. The formation of such multifemale brood-rearing coalitions in eiders is characterized by aggression and the presence of female dominance hierarchies (e.g. Öst 1999), and the females forming enduring coalitions with each other are unrelated (Öst *et al*. 2005). We may therefore hypothesize that the observed distribution of female group sizes in a local population reflects the relationship between female group size and offspring survival probability in these groups. Additionally, the effect of hatch date on survival could be estimated for all broods irrespective of female care strategy. Data obtained over eight field seasons characterized by different weather and demographic conditions helped us to tease out year effects and their potential interaction with the variables of interest.

Statistical modelling of duckling survival is complicated by the fact that survival in broods results from a contemporary mixture of random and correlated (overdispersed) mortality processes (e.g. Ball *et al*. 1975; Simpson *et al*. 2005). Traditional methods of survival estimation lack the ability to statistically partition these two mortality processes, thereby limiting their ability to model survivorship processes accurately, and compromising the rigour that can be applied to hypothesis testing or model identification (Burnham & Anderson 2002) concerning duckling mortality (Smith, Boyd & Evans 2005). We therefore used a novel statistical method of survival estimation (Clutch and Brood Survivorship Model version 1·1·0; Smith *et al*. 2005) which partitions survivorship into random and correlated mortality profiles, each of which can be potentially related to putative covariates. This method accounts for overdispersion typical of survival data, and due to correlated mortality events, during the parameter estimation phase. Accommodation of overdispersion adjusts the statistical power appropriately for detecting factors affecting eider duckling survivorship and facilitates detection of underlying processes affecting eider duckling survival and its relationship to brood structure.

Methods

FIELD METHODS

Data on breeding eiders were collected in 1997–2004 near Tvärminne Zoological Station (59°50′ N, 23°15′ E), on the Baltic Sea in southwestern Finland. Adult eider females were captured on the nest on selected islands in the study area during the late stages of incubation to minimize nest desertion from trapping. The technique involved in the capture of females has been described by Kilpi *et al*. (2001). Females were given 3×3-cm wing flags with a unique colour combination (Öst & Kilpi 2000), and a unique combination of one to three permanent colour rings (2002–04). Altogether, 863 females

were marked with flags (1997: $n = 81$; 1998: $n = 81$; 1999: $n = 74$; 2000: $n = 134$; 2001: $n = 102$; 2002: $n = 124$; 2003: $n = 134$; 2004: $n = 133$).

Trapped females were weighed to the nearest 10 g on a spring balance, the length of the radius–ulna was measured to the nearest 1 mm and clutch size was recorded. One person (M. K.) conducted all the measurements to avoid interobserver variance. We also noted if the female had been previously ringed, as this gives us a relative age indicator for the birds. More than half of the successfully breeding females on our selected study islands [mean ± standard deviation (SD) island-wise capture success in 2003–05 = 52·7 ± 14·6%, range 24·2–83·3%, $n = 16$ islands] were trapped annually, and annual trapping effort has been similar since 1996 (Öst *et al.* 2003b). Because females show high breeding philopatry to their nesting island (Öst *et al.* 2005), previously unringed females will be, on average, younger than those ringed previously. We use a relative age indicator for females because females were not ringed as ducklings in our study population. We acknowledge bias in this variable, as it scores all unringed birds as unexperienced.

Females do not feed during incubation and therefore lose weight. To estimate a female's weight at hatching, we subtracted an estimate of the weight she would be expected to lose during the remaining incubation time from her measured incubation weight. Weight loss rate during incubation was estimated as the slope of a regression of log(body weight) on log(incubation time), taking into account year, type of nesting island and a slight non-linearity in their arithmetic relationship (Kilpi & Lindström 1997; Öst 1999). The incubation stage was estimated directly from known hatching dates or laying dates, or indirectly by egg floatation (Kilpi & Lindström 1997). Female condition indices were defined as the standardized residuals of actual estimated body weights at hatching from those predicted from regressions of log(body weight) on log(length of radius–ulna) (Ormerod & Tyler 1990). Standardized residual masses at hatching were derived separately for each year.

Hatching success of eider eggs is high (*c.* 90%) and shows low variability among clutches (Swennen 1989). Hatching is synchronous, with broods typically leaving the nest within a day of hatching (Öst & Bäck 2003). At each sighting of a marked female at sea, we recorded her identity, whether she was attending a brood, and the total number of females and ducklings in the brood. We were able to annually relocate *c.* 85–90% of all marked females, as in our study area both successfully breeding females and failed nesters stay in the vicinity of their nesting island for most of the brood-rearing period (Öst & Kilpi 2000). We monitored the number of duckling broods associated with marked females every few days (mean ± SD relocation interval 3·5 ± 3·3 days, $n = 2162$ intervals) until the temporary flags wore off or females had left the study area. Marker loss is expected to occur independently of the fate of the brood in which the female was observed. We assured the independence of censoring and brood fate by only including observations of known females still associated with ducklings in the survival analysis. Adhering to these stringent data selection criteria is especially important in eiders, as some females are known to attend brood-rearing coalitions transiently, leaving their young to be taken care of by other females (Kilpi *et al.* 2001; Öst *et al.* 2003a).

Females associated with broods were followed for up to 57 days after hatching of the young. Family units start to break up when ducklings are approximately 7 weeks old (Öst 1999), and fledging occurs at *c.* 70 days of age (Cramp & Simmons 1977). Each brood identifiable by at least one marked tending female was followed long enough to ensure correct assessment of the brood-rearing status of all females attending the brood (Öst *et al.* 2003a). This assessment is straightforward, as non-tending females are not tolerated within broods and are chased away promptly by the tending female(s) (Öst *et al.* 2003b). Disintegration of family units involves the departure of tending females, and our modelling approach can accommodate such changes (see Brood survivorship modelling below). Furthermore, only a small fraction of our brood observations concerned ducklings older than the age at which family units may start to disintegrate.

Females frequently pool their broods in the first few days after hatch, and those amalgamated broods that we observed typically, although not always, contained only one marked female. The age of ducklings in these broods at the time of observation was taken collectively to be the same as the age of the marked females' young. This is a reasonable decision, as our previous results have shown that in broods with more than one known female, there was no significant difference in the estimated hatching dates of the females (Öst *et al.* 2003a).

BROOD SURVIVORSHIP MODELLING

Our hypotheses concerning duckling survivorship are well suited for formal analysis using the Clutch and Brood Survivorship Model of Smith *et al.* (2005). This statistical model captures the deterministic and stochastic characterizations of duckling mortality and tests or ranks hypotheses pertaining to the potential influence of putative brood covariates on measured duckling survival. In our eider system, individual broods can be populated by more than 10 juveniles at hatch, providing a large sample for making survivorship inferences among broods. The model uses the Weibull probability density function as a tractable and flexible model of survivorship probabilities over time (Walpole *et al.* 1998). Survivorship is partitioned into random (R, duckling mortalities occur independently) and correlated (C, duckling mortalities do not occur independently) components by modelling survival as a mixture of two Weibull probability distributions, each representing either the random or the correlated components of mortality. Mortality events for the random mortality process are assumed to conform to a binomial probability distribution, while mortality events for a correlated mortality process are assumed to conform to a beta-binomial distribution. The beta-binomial distribution includes a parameter that explicitly accounts for overdispersion due to statistical non-independence of mortality events. Model output includes survival probabilities as functions of postulated covariates, calculated from maximum likelihood parameter estimates (coefficients) of the covariates, and their interactions, that operate on the parameters of the Weibull probability distributions.

We applied the model selection and inference paradigm of Burnham & Anderson (2002) to rank models for their ability to explain our duckling survivorship data. Under that paradigm, we used Akaike's information criterion (AIC), corrected for sample size and any residual overdispersion ($QAIC_C$) to rank competing models; residual overdispersion being indicated by a value of the variance inflation factor ($\hat{c}$) greater than unity calculated by using a parametric bootstrap for goodness-of-fit calculated as follows. Maximum likelihood parameter estimates from a model fitted to observed data were used to generate simulated data sets conforming to the deterministic and stochastic model structure of the fitted model. These statistically ideal data were then subjected to the model fitting procedure. Estimates and uncertainty for $\hat{c}$ were obtained from the ratio of the negative ln-likelihood for the observed data to the mean of the negative ln-likelihood for the simulated data.

We respected the principles of the information-theoretic approach to scientific inference by preselecting a set of putative covariates to explain our data based on a priori evidence from the literature supporting the potential influence of those covariates. Regarding relevant maternal factors, these covariates were selected among

those discussed by Blums *et al.* (2002), and relevant social factors were chosen based on previous literature on cooperatively breeding vertebrates with helpers-at-the-nest (Russell *et al.* 2002), among which multiple care-givers are common.

On the basis of our a priori hypotheses, for all analyses we posed that duckling survivorship could be determined in part by hatch date (HD, expressed as day of the year; day 1 = 1 April) and the class covariate year (Y). For lone tender broods, the annual body condition index of the single tending female (CI), clutch size at hatch (CS), the relative age of the tending female (MA) expressed as a class variable (0 if first year marked, 1 if previously marked) and known years (minimum estimate) of maternal experience (ME) were challenged with explaining our data. For multifemale brood-rearing coalitions, the number of tending females (NT), number of ducklings in the brood (ND) and the ratio of ND : NT are the covariates of interest. Given that our statistical model can partition mortality into random (R) and correlated (C) components, and that each putative covariate can operate potentially on R and C, and on the α and β parameters of the Weibull mortality function component (Smith *et al.* 2005), covariates can be subscripted to reflect the process and parameter upon which they operate (e.g. $HD_{R,a}$). Additionally we considered the possibility of covariate interactions, notably with year (e.g. $Y_{R,\alpha} \times NT_{R,\alpha}$). Because our putative covariates can enter our model independently, or interactively with other covariates in multiple ways, there is a large set of model covariate combinations that can potentially challenge our data. Preliminary model trials led us to focus upon a subset of covariate combinations and interactions and R or C model structures consistent with our hypotheses, and which showed meaningful and parsimonious statistical support for our data.

Two independent analyses were conducted. One analysis was applied to lone tenders only, the second to multifemale brood-rearing coalitions. The first set of analyses was concerned exclusively with broods that were tended by a single female throughout the entire brood-rearing season, while the data on multifemale brood-rearing coalitions could occasionally contain data records in which there might be only one female tending the brood at some part of the brood-rearing season. The data for both analyses meet important assumptions for the model of Smith *et al.* (2005). Specifically, (1) hatching of eggs within a clutch is essentially synchronous; (2) the number of surviving ducklings in a brood at any date is counted essentially without error; (3) the age of ducklings is known; and (4) an age of fledging (D) can be assigned. As we had few survivorship data for ducklings between 55 and 70 (age at fledging) days of age, we chose $D = 55$ for our analyses, past the age at which family units start to disintegrate (Öst 1999).

A key requirement of the Clutch and Brood Survivorship Model is that our putative brood covariates must apply to all data records for the brood. Thus, to apply the model in circumstances where the putative covariates change value within a 'brood', we must redefine that brood. This redefinition would need to occur if, for example, duckling survivorship were to be modelled as a function of a changing number of tending females or surviving ducklings in the brood. We accommodate this need for a redefinition in our analyses by defining 'pseudobroods' as subsets of observations for an original brood within which any values for pseudobrood covariates do not change, and where each pseudobrood exhibits a steady or declining number of individuals over time. Note that our pseudobrood concept results in no loss of brood mortality information, but a pseudobrood must consist of two consecutive data records to provide survivorship information. Informative pseudobroods varied in length from two to 20 data records, averaging [± standard error (SE)] 3·1 ± 1·8 data records.

Results

LONE TENDER BROODS

Variance in duckling survival among lone tender broods was best explained by a correlated (C) mortality model with significant interannual variation in survivorship (Table 1), as well as complex interactions among hatch date (HD), body condition of the tending female (CI), and clutch size at hatch (CS). Among these covariates, only CS had a non-interactive influence on duckling survival, with the probability at hatch date of a duckling surviving to 55 days tending to increase with clutch size at hatch in most years (Fig. 1). Indeed, the model lacking the two CS covariates (fourth-ranked model in Table 1) performed poorly. Our analysis also revealed that the
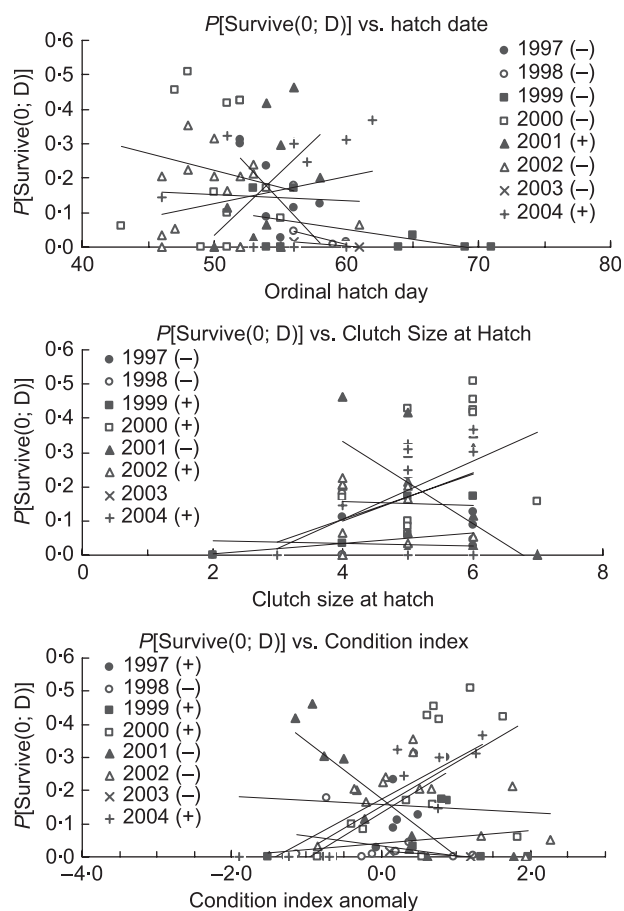

Fig. 1. The probability, on hatch day (a = 0), that a duckling will survive to $D = 55$ days {P[survive(0; 55)]} for each of 74 lone tender broods for all years 1997–2004 as a function of ordinal hatch day (1 April = day 1), clutch size at hatch, and the body condition of the tending female expressed as an anomaly of the mean annual body condition of trapped females. Although all three covariates contribute to the top-ranked model presented in Table 1 for lone tender broods, their individual influence on P[survive(0; 55)] is difficult to interpret. Generally, the effect of each covariate tends to differ depending upon the year, although increased clutch size at hatch seems to be a reliable predictor of a higher P[survive(0; 55)]. When a trend could be calculated, (+) or (–) after each year indicates the tendency of the trend as the value of the independent variable increases.

Table 1. Model rankings and associated statistics for the independent analyses of lone tender broods and multifemale brood-rearing coalitions. For the lone tender broods, a baseline NULL model identifies a constant mortality rate for a correlated mortality (*C*, duckling mortalities not statistically independent) only process, based on the results of preliminary analyses. For the multifemale brood-rearing coalitions, a baseline NULL model is defined as mixture of constant random (*R*, duckling mortalities are statistically independent) and correlated (*C*) mortality rate processes. A NULL model includes no postulated covariates affecting duckling survivorship. More complex models (hypotheses) incorporating our covariates are expressed relative to the NULL models. Parameterization of the NULL models is explained in Smith *et al.* (2005). Y: class variable for the eight years analysed; NT: number of tending females; ND: number of surviving ducklings; ME: known number of years (minimum estimate) of maternal experience for the tending female; MA: relative age of the tending hen; HD: ordinal hatch day of the year (day 1 = April 1); CI: body condition index for the tending female; CS: clutch size at hatch. The symbol *K* represents the number of estimated parameters, ΔQAIC$_C$ is the ĉ corrected ΔAIC$_C$, *w* the QAIC$_C$ weights, while QnlnL is the ĉ corrected model negative ln-likelihood

Rank	Model description	?QAIC$_C$	K	w	QnlnL	R^2
	Lone tender broods					
1	NULL + CS$_{C,\alpha}$ + CS$_{C,\beta}$ + (CS × CI)$_{C,\alpha}$ + (CS × CI)$_{C,\beta}$ + (HD × CI)$_{C,\alpha}$ + (HD × CS)$_{C,\alpha}$ + (Y × CI)$_{C,\alpha}$	0·00	16	0·94	251·12	0·60
2	NULL + CS$_{C,\alpha}$ + CS$_{C,\beta}$ + MA$_{C,\alpha}$ + MA$_{C,\beta}$ + ME$_{C,\alpha}$ + ME$_{C,\beta}$ + (CS × CI)$_{C,\alpha}$ + (CS × CI)$_{C,\beta}$ + (HD × CI)$_{C,\alpha}$ + (HD × CS)$_{C,\alpha}$ + (Y × CI)$_{C,\alpha}$	5·85	20	0·05	249·96	0·60
3	NULL + HD$_{C,\alpha}$ + HD$_{C,\beta}$ + CS$_{C,\alpha}$ + CS$_{C,\beta}$ + (Y × CI)$_{C,\alpha}$ + (Y × CI)$_{C,\beta}$ + (CS × CI)$_{C,\alpha}$ + (CS × CI)$_{C,\beta}$ + (HD × CI)$_{C,\beta}$ + (HD × CI)$_{C,\alpha}$ + (HD × CS)$_{C,\alpha}$ + (HD × CS)$_{C,\beta}$	8·60	27	0·01	244·14	0·64
4	NULL + (CS × CI)$_{C,\alpha}$ + (CS × CI)$_{C,\beta}$ + (HD × CI)$_{C,\alpha}$ + (HD × CS)$_{C,\alpha}$ + (Y × CI)$_{C,\alpha}$	18·81	14	0·00	262·56	0·46
5	NULL (α_C, β_C, θ_C)	26·29	3	0·00	277·42	0·36
6	NULL + Y$_{C,\alpha}$ + Y$_{C,\beta}$	35·17	17	0·00	267·69	0·48
	Multifemale brood-rearing coalitions					
1	NULL + NT$_{R,\alpha}$ + NT$_{C,\alpha}$ + NT$_{R,\beta}$ + NT$_{C,\beta}$ + ND$_{R,\alpha}$ + ND$_{C,\alpha}$ + ND$_{R,\beta}$ + ND$_{C,\beta}$ + (ND:NT × Y)$_{R,\alpha}$ + (ND:NT × Y)$_{C,\alpha}$	0·00	31	0·55	1849·60	0·69
2	NULL + NT$_{R,\alpha}$ + NT$_{C,\alpha}$ + NT$_{R,\beta}$ + NT$_{C,\beta}$ + ND$_{R,\alpha}$ + ND$_{C,\alpha}$ + ND$_{R,\beta}$ + ND$_{C,\beta}$ + HD$_{R,\alpha}$ + HD$_{C,\alpha}$ + HD$_{R,\beta}$ + HD$_{C,\beta}$ + (ND:NT × Y)$_{R,\alpha}$ + (ND:NT × Y)$_{C,\alpha}$	0·42	35	0·45	1845·80	0·70
3	NULL + NT$_{R,\alpha}$ + NT$_{C,\alpha}$ + NT$_{R,\beta}$ + NT$_{C,\beta}$ + HD$_{R,\alpha}$ + HD$_{C,\alpha}$ + HD$_{R,\beta}$ + HD$_{C,\beta}$ + (ND:NT × Y)$_{R,\alpha}$ + (ND:NT × Y)$_{C,\alpha}$	27·53	31	0·00	1863·37	0·64
4	NULL + NT$_{R,\alpha}$ + NT$_{C,\alpha}$ + NT$_{R,\beta}$ + NT$_{C,\beta}$	107·13	11	0·00	1934·24	0·61
5	NULL (α_R, β_R, θ_R, α_C, β_C, θ_C, f)	210·43	7	0·00	1978·88	0·48

Lone tender broods: *n* = 74; ducklings: *n* = 1929; number of brood predictions made and evaluated: 353; effective independent sample size: 1123·06. The bootstrapped estimates of c ± 1 standard error (SE) for the top-ranked model is 1·18 ± 0·05. The top-ranked model [quasi-Aikake's information criterion$_C$ (QAIC$_C$) = 534·56] passed the parametric bootstrap diagnostic for goodness-of-fit.

Multifemale coalitions, pseudobroods: *n* = 1424; ducklings: *n* = 25 673; number of pseudobrood predictions made and evaluated: 1819; effective independent sample size: 9032·12. The bootstrapped estimates of c ± 1 SE for the top-ranked is 1·13 ± 0·02. The top-ranked model (QAIC$_C$ = 3761·76) passed the parametric bootstrap diagnostic for goodness-of-fit.

effect of CI varied interannually, with the probability at hatch date of a duckling surviving to 55 days increasing substantially with better female condition in some years (Fig. 1). Overall, our results imply that HD, CS and CI interact biologically in a manner difficult to discern, and we found no statistically significant relationships in the six pairwise comparisons among values for CS, HD and CI for the 74 broods that were observed during eight breeding seasons. We were also unable to find statistical support for any influence of the relative age of the tending female (MA) or her known maternal experience (ME) as a predictor of duckling survival (second-ranked model of Table 1). Because MA and ME can potentially be correlated strongly with CS, CI and HD, we investigated this possibility for our data. We found no statistical evidence for the six pairwise correlations between MA or ME and CS, CI or HD, recognizing that our power to detect an effect of MA or ME on survivorship is reduced because these variables are imperfect metrics of female experience (see Field methods). Competitors of our top-ranked model, but excluding either of

HD, CS or CI, consistently failed to garner enough statistical support to compete with our best supported model (i.e. the ΔQAIC$_C$ values yielded model weights approaching zero).

MULTIFEMALE BROOD-REARING COALITIONS

Variance in ducking survival among multifemale brood-rearing coalitions was best explained by a model with a mixture of random (*R*) and correlated (*C*) mortality (Table 1) that includes an important influence of the number of tending females (NT), the number of surviving ducklings (ND) and interannual variation in how the ratio of these two factors (ND : NT) affected survivorship. Data on body condition of the tending females (CI) and their clutch size at hatch (CS) were unavailable for the majority of females in amalgamated broods (as they are unmarked), so these covariates could not be investigated. However, as ducklings in amalgamated broods are approximately the same age, we were able to investigate any effect of a common hatch date (HD) on
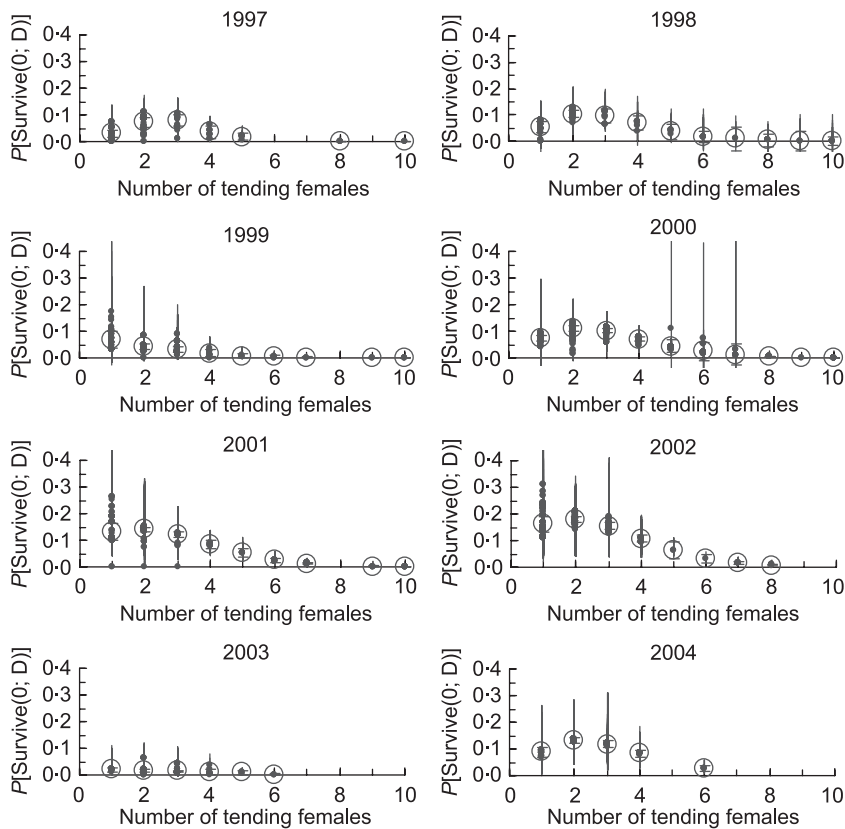
Fig. 2. The probability, on hatch date (a = 0), that a duckling will survive to D = 55 days {P[survive(0; 55)]} as a function of the number of tending females for each of 3242 pseudobroods for all years 1997–2004 (solid circles, with 95% confidence limits represented by vertical bars). Also portrayed is the mean P[survive(0; 55)] for each year (large open circles, with 95% confidence limits represented by T-bars, generally within the open circle). This portrayal is based on the top-ranked model of Table 1 for multifemale brood-rearing coalitions.

duckling survivorship. Our results (second- and third-ranked models in Table 1) show that models with HD were supported more poorly statistically than was our best model that lacked information on HD as a covariate, thereby diminishing support for HD as a probable predictor of duckling survival. Other models posed as subsets of our top-ranked model consistently failed to garner enough support to compete with our best supported model.

A revealing result is the identification of a relationship between the probability, on hatch date, that a duckling will survive to 55 days of age, and the number of tending females (Fig. 2). This result shows a tendency for two to three females being optimal, on average, over the brood-rearing period, in 6 of 8 years. Examining this relationship over time, Fig. 3 identifies the number of females tending a brood that maximizes the probability of duckling survival as a function of brood age. For multifemale brood-rearing coalitions, Fig. 3 is based on the fourth-ranked model in Table 1, which focuses particularly on the relationship between the number of tending females and duckling survival. Although the other significant factors that are captured in the best-supported model are excluded in this model, the model still explains a substantial proportion of the total variance ($R^2 = 0.61$) when compared to the null model ($R^2 = 0.48$). The portrayal in Fig. 3 argues that single tender broods are optimal during the earliest days posthatch, but that two or more tending females become preferable after ducklings reach about 19 days of age. This conclusion also holds true when the data on multifemale brood-rearing coalitions are compared with the data on
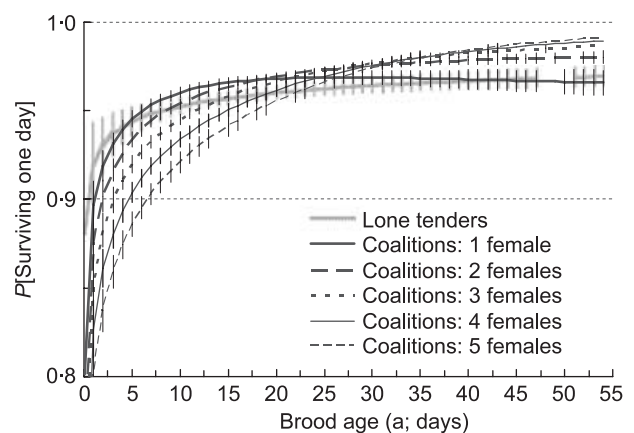

Fig. 3. The probability of surviving one day, as a function of brood age (a) and the number of tending females (± 1 standard error), of ducklings in multifemale coalition broods based on the fourth-ranked model in the lower panel of Table 1, and in lone tender broods based on the fifth-ranked model in the upper panel of Table 1. 'Lone tenders' refers to broods that were tended by a single female throughout the entire brood-rearing season, while 'Coalitions: 1 female' refers to multifemale brood-rearing coalitions in which the number of tending females in the brood, during some part of the brood-rearing season, was one. Ducklings older than about 19 days in multitender broods tend to have improved survival when there is more than a single tender.

'exclusive' lone tenders (Fig. 3). When the annual portrayals in Fig. 2 are superimposed (Fig. 4), we notice that broods with two or three tenders seem to improve the probability of duckling survival to 55 days most during those years when
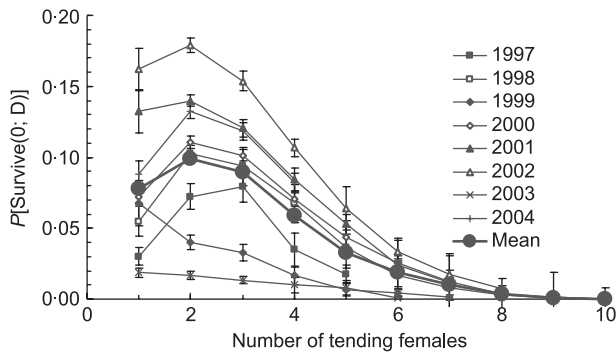
Fig. 4. For each year, the probability on hatch date (a = 0) that a duckling will survive to D = 55 days {P[survive(0; 55)] ± 1 (standard error)} as a function of the number of tending females. The mean P[survive(0; 55)] is the unweighted average over all 8 years 1997–2004. This portrayal is based on the top-ranked model of Table 1 for multifemale brood-rearing coalitions.
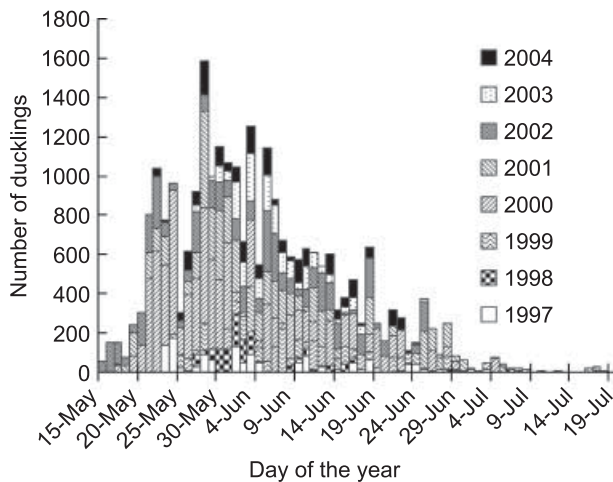

Fig. 6. Frequency distribution of 3242 pseudobroods of multifemale brood-rearing coalitions according to brood age (days) and the number of tending females (1997–2004).

Fig. 5. Frequency distribution of the number of ducklings associated with 3242 pseudobroods of multifemale brood-rearing coalitions according to day of the year (1997–2004).

argument that coalitions with two or more tending females maximize duckling survival once they reach an age of about 19 days should be robust to instabilities in brood composition in the first week or so after hatching. The great majority of the survivorship predictions evaluated statistically (1569 of 1819 records, 86·3%) concerned pseudobroods in which ducklings were more than 1 week old, and our observed frequency of multitender broods in our study area increases in concert with the value of those multitender broods for improving duckling survival (Fig. 6).

Discussion

By analysing simultaneously a suite of factors influencing offspring survival in eider broods using a novel statistical method, we were able to advance our understanding of this poorly understood component of the life cycle in waterfowl (Johnson *et al*. 1992). Our study focused upon social and maternal influences on offspring survival, but the pronounced interannual variation we found is indicative of the additional impact of environmental factors on offspring survival (see below). Our analysis of data limited to lone-tended broods led us to conclude that neither female body condition nor hatch date had a detectable independent effect on offspring survival probability (Table 1). Alternatively, clutch size was associated positively with offspring survival in most years and interacted in a complex way with hatch date, indices of body condition and interannually. As a suite, these covariates predict duckling survivorship satisfactorily, but the role of each covariate in predicting duckling survivorship is refractory to conclusive interpretation in the absence of controlled experiments (Fig. 1). Unfortunately, such experiments are very difficult to design and execute in a natural setting such as our eider system.

We could find no statistical support that female age or maternal experience was an important predictor of offspring survival, although we recognize that our indicators of age and experience are imperfect. Not detecting a direct effect of body condition on duckling survival may seem surprising, considering that both the intensity and duration of parental care that female eiders provide has previously been shown to be

overall survival probability is near the mean for the study period. Single tender broods seem to maximize the probability of surviving to 55 days during those years with overall unusually low survivorship probabilities. In years of particularly high survival, two or three tenders provide less of a duckling survival benefit than during years of average overall duckling survival.

It is important to acknowledge that, by conducting our multifemale brood-rearing coalition analysis on pseudobroods, we are disguising the fact that the number of ducklings in the study area increases during the earlier part of the brood-rearing season (Fig. 5), while simultaneously the larger broods may be disintegrating into several smaller broods (Öst 1999). During this reassortment (cf. Flint, Sedinger & Pollock 1995), female eiders apparently recognize their young as they form family units within mixed broods (Öst & Bäck 2003), exchanging at most a few ducklings (Bustnes & Erikstad 1991). Nevertheless, as our brood survival analysis extended over the greater part of the brood-rearing period, our
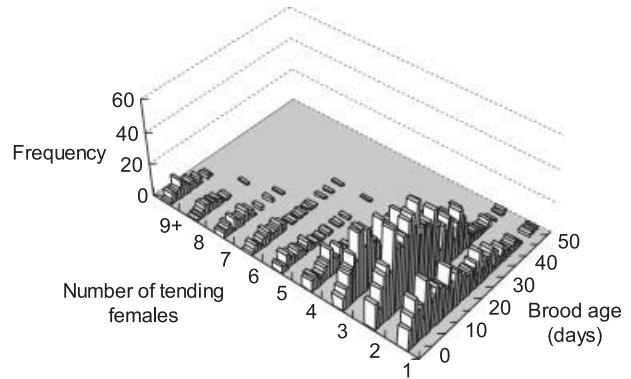
positively correlated with body condition (Bustnes & Erikstad 1991; Kilpi *et al*. 2001; Öst *et al*. 2003b). However, there are at least three potential explanations for this result. First, each female opting for the lone tender care strategy may be above some critical level of body reserves that allows effective protection of her young by vigorous antipredatory vigilance and defence. Lone tenders are, on average, in best body condition at hatching of all nesting females (Kilpi *et al*. 2001). Secondly, the clutch size of lone tenders was correlated positively with their body condition. If strong enough, this collinearity may mask any positive effects of condition on offspring survival probability or, alternatively, better condition is expressed primarily through increased clutch size. Finally, female body condition may have limited influence on offspring survival, although this admittedly seems unlikely in a capital breeder such as the eider. By contrast, our finding that larger clutch sizes tended to improve the probability of surviving to 55 days, notwithstanding the collinearity with female body condition, is expected. Most studies conducted on precocial species have found an increased prefledging survival of offspring in larger broods (Lepage *et al*. 1998; Loonen *et al*. 1999; Smith *et al*. 2005), including the eider (Munro & Bédard 1977). On the other hand, data by Bustnes & Erikstad (1991) indicated that the proportion of an eider brood surviving per day was similar irrespective of brood size; however, their study was based on a small sample.

We found that both the number of tending females and the ratio of ducklings to tending females were powerful predictors of duckling survivorship (Table 1). Duckling survivorship showed a remarkably consistent domed distribution in relation to the number of tending females in 6 of the 8 years under study (Fig. 2), with groups of two or three females being optimal for increasing duckling survival, especially in years of average duckling survival (Fig. 4). That there were distinct year effects for the influence of the number of tenders on duckling survivorship suggests that multiple tenders may have little, or even negative, fitness value in some, perhaps atypical, years. After controlling for covariates tightly coupled with the ratio of ducklings to tenders such as brood size and brood age, the overall pattern was for more tending hens per brood to be associated with higher duckling survivorship as ducklings approached 20 days of age (Fig. 3). The ratio of ducklings to tending females shows little geographical variation in eider populations (Öst 1999), which lends further credence to our result that the number of tending hens per brood is, overall, an important fitness consideration. Our finding that more tending hens per brood improves survival in broods with multiple tenders seemingly contradicts our results from the lone tender analysis, suggesting that brood size is correlated positively with duckling survival. However, one plausible explanation for this discrepancy is that the factors shaping parental investment in antipredatory behaviour are not directly comparable among these two groups of tenders. Whereas social factors shape female investment in antipredatory vigilance, lone tenders may adjust their investment in vigilance based more directly on brood value. In multifemale brood-rearing coalitions, the proportion of time spent vigilant by a focal female is correlated positively with the proportion of her clutch to the total number of ducklings (Öst *et al*. 2007a), and hence investment in vigilance is expected to decrease in large amalgamated broods. In contrast, lone tenders are expected to increase their current parental vigilance when their own brood size increases, in accordance with parental investment theory (Trivers 1972).

In cooperatively breeding vertebrates with helpers-at-the-nest, there is growing evidence that the number of helpers (reviewed in Jennions & Macdonald 1994) and the number of care-givers per juvenile (e.g. Russell *et al*. 2002) are positively related to reproductive success. Our results provide compelling evidence that social factors may also be important predictors of offspring survival in species characterized by shared parental care where the care-givers do not feed the young. We found evidence that both female group size and the ratio of ducklings to tenders affected duckling survivorship (survivorship diminishing with unfavourably high ratios). A plausible hypothesis for this finding is that both female group size *per se* and the female's ability to protect all ducklings in the face of an attack may play a role in duckling survival.

Why, then, is duckling daily survival probability lower in the earlier days (younger than 20 days) posthatch for multifemale brood-rearing coalitions? Both the number of ducklings and females, and their ratio, peak during this period (Öst 1999). Although an increased number of tenders for the brood should allow quicker responses on attack (reviewed in Lind & Cresswell 2005), and should improve the efficiency of defence (e.g. Munro & Bédard 1977; Mappes, Kaitala & Alatalo 1995), there are several factors that tend to counteract these benefits in groups containing large numbers of newly hatched, vulnerable young. Because group dispersion typically increases with group size (e.g. Russell *et al*. 2002), and the success rate of gull *Larus* spp. aerial attacks on eider ducklings increases with the dispersion of ducklings from tending adults (Mendenhall & Milne 1985; Swennen 1989), the efficiency of brood defence is expected to show diminishing returns with increasing group size. Lone tenders may more easily manage to keep together their own brood of maximally six ducklings (disregarding relatively infrequent adoptions). This increasing group dispersion in larger broods may also limit the ability to effectively convey information about potential threats among multiple tenders (Pöysä 1994; Fernández-Juricic, Siller & Kacelnik 2004). Larger groups are, presumably, also easier to detect, so predators may attack them preferentially (Munro & Bédard 1977; Botham *et al*. 2005). Finally, the reproductive share of individual females in brood-rearing coalitions is the lowest in the early brood-rearing period characterized by large clusters of females and young, reducing the investment in individual antipredatory vigilance by the females (Öst *et al*. 2007a).

Apart from these considerations of the expected relationship between group size and group vulnerability, there may be differences in the individual quality of females associating in different-sized groups. Öst *et al*. (2003b) showed that the preference for group size was a conditional strategy in eider females, such that females in poorer body condition at

hatching were found in groups with more tending females. A female's body condition is expected to contribute to her ability to contribute to communal rearing. Thus, a female eider's investment in antipredatory vigilance in a brood-rearing coalition declines with declining body condition (Öst *et al.* 2007a). Due to these individual differences in parental quality (Öst *et al.* 2003b) and dominance (Öst, Jaatinen & Steele 2007b), it is conceivable that the survival prospects of offspring of different origin may differ even within the same mixed brood. Group living also entails other costs such as competition for food, disease and parasite transmission (e.g. Hass & Valenzuela 2002), and these costs are expected to increase with group size. This could, potentially, explain why single females tending on average smaller broods seemed to do better in years with unusually low duckling survival (Fig. 4), when ducklings in our eider population are often afflicted by disease (Hollmén *et al.* 2002). While we have suggested before that the female group size–group productivity function is decelerating (Öst *et al.* 2003b), based on the total number of ducklings in broods as a function of female group size, the present study is the first rigorous validation of this relationship (Fig. 4).

Inspection of the observed distribution of female group sizes among broods in our study area (data from 1997 to 2001; Öst *et al.* 2003b) reveals a striking correspondence with the distribution of offspring survival probabilities in these groups. Öst *et al.* (2003b) considered 'saturated' female group sizes, i.e. the number of tending females in broods with at least one known female 3 weeks or more after the estimated hatch date of the marked female's young (this group size was always as small as or smaller than the maximum number of observed tenders, and female group sizes were almost invariably stable after this group size had been reached). When average 'saturated' female group sizes are considered, a group size of two females is the most prevalent one (frequency 49·4%), while lone tenders and females in groups of three comprised 28% and 22% of all marked birds, respectively. The preponderance of groups with two and three females is even more obvious when 'typical' group sizes are considered (Jarman 1974; 'typical' being the average number of animals in the group of a randomly chosen animal), resulting in an average 'saturated' group size of 2·22 females (Öst *et al.* 2003b). 'Saturated' groups with four or more females are rare, allowing us to conclude that brood-caring female eiders group themselves in a way that approaches the optimum regarding offspring survival probability. Although cases where the distribution of naturally occurring groups reflects the consequences of different group sizes on individual fitness are rare (but see Williams *et al.* 2003), our results are perhaps not altogether surprising, considering that entry into groups is assumed to be controlled by the group in eiders (Öst *et al.* 2003b), and the females are unrelated (Öst *et al.* 2005).

We found only a weak and non-significant effect of hatch date on duckling survival probability. While several other studies on birds have found a positive effect of early breeding on offspring survival probability (reviewed in Brinkhof *et al.*

1993), such a relationship is by no means universal (Milonoff, Pöysä & Virtanen 1995; van der Jeugd & Larsson 1998; Simpson *et al.* 2005). It is noteworthy that the study by Simpson *et al.* (2005), also using the Clutch and Brood Survivorship Model, found a similar lack of effect of hatch date on duckling survivorship in mallards *Anas platyrhynchos*. This may indicate that traditional methods of survival estimation may fail to account for all covariates that potentially interact with hatch date, resulting in spurious causal links between hatch date and offspring survival. None the less, as shown by Blums *et al.* (2002), restricting the observation period to encompass only the prefledging period may underestimate the fitness benefits of early breeding, as strong directional selection favouring recruitment of the earliest hatching female ducks may override the negative effects of early hatching on prefledging survival, which had a mid-season maximum.

How likely is it that differences in offspring prefledging survival translate into differences in lifetime reproductive success of females? Because adult eiders are long-lived with an estimated yearly survival close to 85% (Yoccoz *et al.* 2002), even minute differences in expected yearly survival rates among individuals in such species might have large evolutionary consequences (Clutton-Brock 1988; Clark & Ydenberg 1990). Thus we would expect eiders to exhibit reproductive costs in terms of future reproduction rather than survival (cf. Stearns & Kawecki 1994). Indeed, eider females laying larger than average-sized clutches in a given year have been found to lay smaller than average-sized clutches in the subsequent year (Yoccoz *et al.* 2002). However, the main trend in studies of waterfowl is that the expected life-history trade-offs for these precocial breeders are either weak or non-existent (e.g. Williams, Loonen & Cooke 1994; Christensen 2002), or that fitness components are correlated positively within individuals (Lepage *et al.* 1998; Loonen *et al.* 1999; Yoccoz *et al.* 2002), suggesting that the measured traits are correlates of individual quality (Blums *et al.* 2005). For example, female eiders laying large clutches have been found to have a slightly higher survival rate than females laying small clutches (Yoccoz *et al.* 2002). Consequently, it seems reasonable to assume that the social and maternal factors identified by this study as important for offspring survival in eiders are correlated with individual differences between females in lifetime reproductive success. As the quality of rearing conditions of parents and their offspring may be correlated, determining the contribution of short-term effects of early conditions to overall fitness differences may, in fact, underestimate the long-term fitness consequences, especially in long-lived species (van de Pol *et al.* 2006).

While our study does not address specifically environmental effects on duckling survival, the statistical evidence for correlated mortality events found in both analyses is consistent with the hypothesized *modus operandi* of environmental effects such as disease and weather events on offspring survival (Simpson *et al.* 2005). In contrast, aerial attacks by gulls are targeted typically at single ducklings (Mendenhall & Milne 1985; Swennen 1989). We should bear in mind that the social and maternal factors affecting offspring fitness always

interplay with, and are modified by, environmental effects in the population. In fact, other studies have also provided empirical evidence that suggests environmental factors may, in some years, be more important than female-specific traits for reproductive success in waterfowl (van der Jeugd & Larsson 1998; Blums *et al.* 2002).

For example, in eiders, factors such as winter climate (Lehikoinen, Kilpi & Öst 2006) and spring climate (Swennen 1991) have been found to be correlated with subsequent fledging success in the population. Also epidemics caused by viral agents may potentially have a profound influence on offspring survival in some years in our study population, causing as high as 99% mortality of ducklings in epidemic years (Hollmén *et al.* 2002). Environmental factors may also show interesting and sometimes unanticipated interactions with predation risk on ducklings. For example, Swennen (1989) observed that whereas gull predation pressure on eider ducklings showed little annual variation, predation success was strongly correlated with greater dispersion of ducklings when food availability was low. To conclude, as a logical next step, we encourage comprehensive long-term studies that partition the coincident effects of social, maternal and environmental factors on offspring survival in a statistically rigorous manner (cf. Blums *et al.* 2002; Russell *et al.* 2002). It would also be rewarding to focus more future attention upon interannual variability in predation risk (*sensu* Lank & Ydenberg 2003) and prey targeting behaviour, as this may change our perceptions of how effective prey decision-making is in reducing predation (Lima 2002; Lind & Cresswell 2005) and how eiders behave to mitigate contemporary predation risk.

Acknowledgements

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