

# Costs of reproduction in common eiders (*Somateria mollissima*): an assessment of relationships between reproductive effort and future survival and reproduction based on observational and experimental studies

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**ABSTRACT** *The two traditional approaches to the study of costs of reproduction, correlational and experimental, have been used in parallel in a breeding colony of common eiders (*Somateria mollissima*) and were compared in this paper. The analysis of the observational data was based on a two-strata capture-recapture model, the strata being defined on the basis of the clutch size laid by individual females in a given year. The best model according to  $AIC_C$  indicated substantial variation in survival, recapture and transition rates, but overall a pattern emerged: females laying large clutches have a somewhat higher survival and much higher capture rate than females laying small clutches, and transition from large to small clutch size occurs much more frequently than the reverse transition. The analysis of the experimental data (adding/removing one egg) showed that no clear effect was found on either survival or transition rates. We conclude by suggesting (1) that condition should be included in multi-strata models in addition to reproductive effort; (2) that a specific study design for estimating the proportion of non-breeding females should be implemented, and (3) that non-breeding (a non-observable state in this study) may be influenced by previous reproduction events.*

## 1 Introduction

Observational field studies on costs of reproduction often correlate reproductive success in one year to the reproduction and survival in subsequent years. The

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negative correlation expected under the hypothesis that increased reproductive effort leads to a lower future reproductive success is often confounded by individual variation in, for example, quality ('good' birds reproduce and survive well; e.g. Reznick, 1985; Roff, 1992). Experimental studies, by manipulating reproductive effort and randomizing the assignment of treatment in order to remove bias (e.g. Cox, 1958), are therefore not confounded by the effects of covariates such as individual quality, but because they involve manipulation of individual birds, may introduce artefacts due to the complex behaviour of individual birds (for example changes in dispersal rates; see Doligez *et al.*, this issue).

Common eiders are large sea ducks with precocial young, and with an extreme incubation strategy, as they do not feed during the entire incubation period (Parker & Holm, 1990; Erikstad & Tveraa, 1995). The body mass of females increases prior to egg laying, and then decreases by up to 50% during incubation through the loss of stored lipid and protein (Parker & Holm, 1990; Erikstad & Tveraa, 1995). This strategy is likely to have evolved as an anti-predator strategy (predation occurring mostly when females leave the nest; Erikstad & Tveraa, 1995). Furthermore, females incubating large clutches lose more weight than females incubating small clutches (Erikstad & Tveraa, 1995), and therefore may pay a cost in terms of future reproduction and survival (Erikstad *et al.*, 1993). We analyse in this paper (1) observational data obtained through a long-term (1986 to present) capture-mark-recapture study, and (2) experimental data resulting from the manipulation of clutch size (Hanssen *et al.*, forthcoming). We specifically ask if survival and reproduction the following year vary as a function of reproductive effort in the current year. Using clutch size as a measure of reproductive effort allows us to use multi-strata models (Nichols *et al.*, 1992; Brownie *et al.*, 1993; Nichols *et al.*, 1994) to explore these relationships between reproduction and survival, differences in capture rates being taken into account.

## 2 Material and methods

### 2.1 The study site and design

The observational and experimental studies were conducted during the period 1985 to the present in a common eider colony on Grindøya near Tromsø, in north Norway (69°49'N, 18°15'E). Grindøya is a small island (0.65 km<sup>2</sup>) where c. 400 to 500 pairs of eider breed.

Eider start laying eggs around mid-May, and the colony was visited daily to determine start of incubation and clutch size (a clutch size being complete when no egg is laid in a 2-day period; rate of nest parasitism was very low in this colony, less than 1%; Erikstad *et al.*, unpublished data). Females were caught on their nest during the incubation period and individually marked with metal rings if they had not been marked before. The age of the individual females was not known.

The experimental manipulation of clutch size (Hanssen *et al.*, forthcoming) was done by adding/removing one egg for original clutches of 4/5 eggs, creating therefore clutch size of 3 to 6 eggs, which is the normal range of clutch size in eider (Erikstad *et al.*, 1993). The control group was made of birds with unmanipulated clutches as well as nests where an egg was swapped between clutches of equal clutch size and date of laying. The manipulation was done in 1995 and 1996.

## 2.2 Statistical analyses

Clutch size in common eiders vary mostly from 3 to 6, 4 and 5 eggs being the most commonly observed clutch size (Erikstad *et al.*, 1993). In order to obtain adequate sample sizes for analysis, we split the distribution of clutch sizes in two classes: small clutch size (S;  $\leq 4$  eggs) and large clutch size (L;  $\geq 5$  eggs). We then considered multi-strata models (e.g. Nichols *et al.*, 1992) as implemented in MARK (White & Burnham, 1999) to analyse the survival rates of individual females laying small and large clutches respectively, as well as the transition rates (expressed conditional on survival in the MARK parameterization) from small to large clutch and large to small clutch strata. Only data for the period 1986–99 were used, as clutch sizes were not recorded in 1985.

The analysis of observational data (862 females) was done by investigating all models generated under the assumption of either temporal variation or constancy for each of the six sets of parameters (survival and capture rates for S and L strata, and the two transition rates S to L and L to S). The model selection was based on the AIC<sub>C</sub> (Burnham & Anderson, 1998). Individual birds that were manipulated during the study period (in addition to the manipulation of clutch size, incubation period was experimentally manipulated in 1993 and 1994; Erikstad *et al.*, forthcoming; eighty-one birds were used in both experiments (1993–94 and 1995–96)) were censored, i.e. assumed not to be released when manipulated. Goodness-of-Fit (GOF) is a complex issue for multi-strata capture-recapture models. Here, we considered first the GOF tests provided by RELEASE (Burnham *et al.*, 1987), that is, ignoring the two strata defined by clutch size. Both tests 2 and 3 indicated a lack of fit (test 3.SR:  $\chi^2 = 27.46$  on 12 d.f., test 3.Sm:  $\chi^2 = 7.22$  on 11 d.f., test 2:  $\chi^2 = 70.04$  on 40 d.f.; overall test: 104.72 on 63 d.f.). However, this lack of fit was not very pronounced (i.e. overdispersion factor less than 2; see Lindsey, 1999, for a discussion), and was at least partly due to the large heterogeneity in capture rates found among females (see below). The lack of fit of the two-strata model, if any, should therefore be relatively minor.

The analysis of the experimental data involved the building of a design matrix describing the assignment of individual birds to the different treatments (M = minus one egg; C = control; P = plus one egg; the C group was not split to reduce the number of model parameters and because previous analyses have indicated egg swapping had a negligible effect, Erikstad *et al.*, unpublished). Because assignment of treatment was randomized each year within the whole colony, individual birds could belong to different experimental groups in 1995 and 1996 (see Table 1 for sample sizes in the different groups). We therefore considered design matrices incorporating short-term (one year) effects on survival, recapture and transition rates. Such a design matrix, together with the definition of parameters and possible constraints on these parameters, are given in Table 2 for survival rates (similar constraints were used for recapture and transition rates).

TABLE 1. Sample sizes for the different combinations of experimental treatments used in 1995 and 1996. M = minus one egg, C = control (unmanipulated and swapped), P = plus one egg. 1 = 1995, 2 = 1996

M1M2	M1C2	M1P2	C1M2	C1C2	C1P2	P1M2	P1C2	P1P2
5	35	6	30	155	34	3	34	2

TABLE 2. Definitions of survival parameters, and of some of the constraints applicable to this set of parameters. No temporal variation in effects:  $\beta_1 = \beta_2, \beta_3 = \beta_4$ , symmetry of adding versus removing eggs:  $\beta_1 = \beta_3, \beta_2 = \beta_4$ .

Experimental groups	$\phi_{95-96}$	$\phi_{96-97}$
M1M2 <sup>a</sup>	$\phi_{95} + \beta_1$	$\phi_{96} + \beta_2$
M1C2	$\phi_{95} + \beta_1$	$\phi_{96}$
M1P2	$\phi_{95} + \beta_1$	$\phi_{96} - \beta_4$
C1M2	$\phi_{95}$	$\phi_{96} + \beta_2$
C1C2	$\phi_{95}$	$\phi_{96}$
C1P2	$\phi_{95}$	$\phi_{96} - \beta_4$
P1M2	$\phi_{95} - \beta_3$	$\phi_{96} + \beta_2$
P1C2	$\phi_{95} - \beta_3$	$\phi_{96}$
P1P2	$\phi_{95} - \beta_3$	$\phi_{96} - \beta_4$

<sup>a</sup>Experimental groups are defined in Table 1.

### 3 Results

#### 3.1 Analysis of observational data

The best models in terms of  $\text{AIC}_C$  are given in Table 3. They indicate a substantial temporal variation in most parameters and, in particular, in the recapture rates for both small clutch (S) and large clutch (L) groups. In order to understand the main patterns in this data set, we decided to base our interpretation on the model  $\phi_S \phi_L p_{S,t} p_{L,t} \psi_{S \rightarrow L} \psi_{L \rightarrow S}$  (see Table 3). This model has fewer parameters (and would likely be selected if we allowed for some lack of fit), and is therefore a better summary than the more complex models. The parameter estimates for this model are given in Fig. 1.

The parameter estimates clearly indicated (1) an overall high survival for both S and L, with a somewhat higher survival for the L class; (2) much lower capture rates for females with small clutch size; and (3) a high transition rate from L to S, but a low transition rate from S to L.

TABLE 3. Model selection for the analysis of the observational data. The  $\Delta\text{AIC}_C$  values for the best five models are given (by definition it is 0 for the best model), as well as for the simplest (all parameters constant) and the most complex model (all parameters varying in time).  $\phi$  indicates survival rates,  $p$  recapture rates and  $\psi$  transition rates

Model	$\Delta\text{AIC}_C$	Number of (estimable) parameters
$\phi_S \phi_L p_{S,t} p_{L,t} \psi_{S \rightarrow L} \psi_{L \rightarrow S,t}$	0	53
$\phi_S \phi_L p_{S,t} p_{L,t} \psi_{S \rightarrow L,t} \psi_{L \rightarrow S,t}$	0.04	45
$\phi_{S,t} \phi_L p_{S,t} p_{L,t} \psi_{S \rightarrow L} \psi_{L \rightarrow S}$	1.38	36
$\phi_{S,t} \phi_L p_{S,t} p_{L,t} \psi_{S \rightarrow L,t} \psi_{L \rightarrow S,t}$	4.06	38
$\phi_S \phi_L p_{S,t} p_{L,t} \psi_{S \rightarrow L} \psi_{L \rightarrow S}$	5.72	28
$\phi_S \phi_L p_S p_L \psi_{S \rightarrow L} \psi_{L \rightarrow S}$	47.23	5
$\phi_{S,t} \phi_{L,t} p_{S,t} p_{L,t} \psi_{S \rightarrow L,t} \psi_{L \rightarrow S,t}$	21.96	65

A: Observational data

$$\psi = 0.69 [0.61 ; 0.76]$$

$$\phi = 0.85 [0.77 ; 0.90] \quad \text{L} \quad \text{S} \quad \phi = 0.81 [0.79 ; 0.84]$$

$$p \in 0.40 - 1.0 \quad \quad \quad p \in 0.15 - 0.35$$

$$\psi = 0.20 [0.15 ; 0.25]$$

B: Experimental data

$$\psi = 0.73 [0.66 ; 0.79]$$

$$\phi = 0.78 [0.68 ; 0.86] \quad \text{L} \quad \text{S} \quad \phi = 0.74 [0.68 ; 0.79]$$

$$p = 1.00 \quad \quad \quad p = 0.44$$

$$\psi = 0.19 [0.15 ; 0.23]$$

FIG. 1. Estimated survival ( $\phi$ ), recapture ( $p$ ) and transition rates ( $\psi$ ) for the observational data (A-top) and the experimental data (B-bottom). 95% confidence intervals are given for parameters assumed to be constant in time (survival and transition rates), whereas range of variation is given for the temporally varying recapture rates. S = small clutch size, L = large clutch size. Note that the data sets are complementary, as birds manipulated are censored in the observational study data set.

3.2 Analysis of clutch size manipulation experimental data

We first fitted models with temporal variation in survival, recapture and transition rates, as well as various combinations of the experimental treatment effects. These models gave systematically a better fit than the models assuming constant rates, but they also exhibited problems of parameter identifiability. Such models were therefore difficult to interpret biologically as some parameter combinations were not estimable. We give below the results for models assuming constant parameter values (which are similar to an estimate of an average effect) and incorporating various combinations of effects of the experimental treatments, ranked according to  $AIC_C$  (Table 4). There was some difference in the ranking of the models (depending on the inclusion or not of temporal variation), but the two best models were the models assuming no effect of the experimental treatment (see Fig. 1(b) for parameter estimates), and the model with a difference in transition rates according to treatment levels (see Table 4). The estimates obtained from the latter model were not consistent with the cost of reproduction hypothesis: the transition

TABLE 4. Two-strata capture-recapture models fitted to the experimental data (only the five best models are shown). Models including experimental group effects are parameterized as described in Table 2. All models assumed constant survival, recapture and transition rates. The  $AIC_C$  for the most complex model with group and time-specific parameters is given

Model	$AIC_C$	$\Delta AIC_C$	$n$ par
$\phi$ $p$ $\psi$	1704.29	0.00	6
$\phi$ $p$ $\psi$ (exp groups)	1704.82	0.53	9
$\phi$ $p$ (exp groups) $\psi$	1707.16	2.87	9
$\phi$ $p$ (exp groups) $\psi$ (exp groups)	1708.84	4.55	11
$\phi$ (exp groups) $p$ $\psi$	1709.61	5.32	9
$\phi$ (exp groups) $p$ $\psi$ (exp groups)	1712.13	7.84	13
...			
$\phi$ ( $t$ ) $p$ ( $t$ ) $\psi$ ( $t$ ) by exp groups	1903.22	198.9	169

rate from L to S was higher for both the P group (+1 egg;  $\psi_{L \rightarrow S} = 0.82$ ) and the M group (-1 egg;  $\psi_{L \rightarrow S} = 0.81$ ) compared with the control group ( $\psi_{L \rightarrow S} = 0.68$ ; we would expect a higher transition for P and a lower one for M). The transition rate from S to L was, however, lower for the P group ( $\psi_{S \rightarrow L} = 0.10$ ), and higher for the M group ( $\psi_{S \rightarrow L} = 0.21$ ), the control group being intermediate ( $\psi_{S \rightarrow L} = 0.19$ ), as expected. Effects estimated under the model incorporating temporal variation were very close to those estimated under the constant model: for the transition L  $\rightarrow$  S, the estimates of the effect size on the logit scale (the  $\beta$ s of Table 2, i.e. the difference with the control group) were for the -1 egg group 0.71 (s.e. = 0.50) for the constant model, 1.03 (s.e. = 0.56) for the temporal variability model, and 0.76 (s.e. = 0.50), respectively 1.04 (s.e. = 0.57) for the +1 egg group.

#### 4 Discussion

Common eiders are long-lived species (estimated yearly survival close to 85%), and are therefore expected to exhibit reproductive costs in terms of future reproduction, rather than survival (see, for example, Stearns & Kawecki 1994). The observational and the experimental data showed indeed that females with higher reproductive effort had a higher or similar survival, a result consistent with the hypothesis that females laying large clutches were in a better condition and therefore survived as well as females laying small clutches. As females were measured and weighed at day 5 of the incubation period, body condition (obtained, for example, by regressing body mass on wing length) could have been used as an individual covariate, e.g. by considering two classes of body condition crossed with the classes defined by clutch size (see Nichols *et al.*, 1994).

The observational data showed clearly that females laying large clutches in a given year laid small clutches the year after, very few females doing the reverse transition. As close to half (41%; see Erikstad *et al.*, 1993) of the females laid clutches with five or more eggs, it is obvious that there is a missing transition from small to large clutch size. We can hypothesize that females have a tendency to show a sequence of reproductive events such as 'L  $\rightarrow$  S  $\rightarrow$  No breeding  $\rightarrow$  L ...' (see Cam *et al.*, 1998 for a general discussion of the importance of intermittent breeding, and Coulson, 1984, for a discussion of non-breeding in common eiders). As non-breeding females are not captured or resighted in this study, we cannot - without making very restrictive assumptions - estimate transition rates to and from a non-breeding stratum. We cannot therefore assess the full range of potential costs of reproduction, as the transition to non-breeding (the most costly transition in terms of reproductive success) cannot be properly estimated. Transition to a non-breeding state will be analogous to temporary emigration from the study area (see Kendall *et al.*, 1997 for a discussion), and will translate in lower recapture rates for the stratum with the highest transition rate to the non-breeding state (assuming random temporary emigration). Capture rates were indeed much lower for the small clutch size stratum, but this result may be partly confounded by the fact that females laying small clutch size have a higher tendency to abandon the nest (see Erikstad & Tveraa, 1995), and therefore may be less likely to be caught while incubating. We believe that the study design should be modified following two lines: using the robust design (Pollock, 1982; Kendall *et al.*, 1997), and capturing non-breeding females through the use of marks lasting for longer than one year and that could be resighted without physically capturing the individual. Further work should focus

on the number of non-breeding females that need to be caught in order to estimate, with some reasonable precision, the transition rates between the different strata.

There was no clear evidence that the experimental manipulation of clutch size resulted in changes in survival, recapture or transition rates. The treatments used in this study were of a small magnitude ( $\pm 1$  egg), in order to keep the clutch size within the natural range of variation. The absence of changes in survival rates was expected, but we could have expected a change in reproductive rates the year after. However, as we could not estimate properly the transition to the non-breeding state, we cannot in fact assess for example if females in poor condition (i.e. those laying small clutches) did not breed with a higher rate after having their reproductive effort experimentally manipulated. Clearly, the temporal variability of capture rates, together with the differences in capture rates between strata defined on the basis of clutch size, do not lead to reliable estimates of such transitions, and new study designs are therefore needed in the future.

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