



Original Article

# Eyes on the future: buffering increased costs of incubation by abandoning offspring

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Life history theory states that the resources invested in current reproduction must be traded off against resources needed for survival and future reproduction. Long-lived organisms have a higher residual reproductive value and are therefore expected to be sensitive to reproductive investments that may reduce survival and future reproduction. Individuals within a population may vary in phenotypic quality, experience, access to resources etc. This may affect their optimal reproductive investment level. In this study we manipulated reproductive costs by shortening and extending the incubation period in common eiders *Somateria mollissima* without altering clutch size. Females whose incubation time was prolonged experimentally, suffered higher mass loss and increased clutch loss/nest desertion. These females were also more prone to abandon their brood after hatching. Both clutch loss and brood abandonment decreased with clutch size in all treatment categories, indicating higher phenotypic quality and/or better access to resources for females producing more eggs. However, although females with prolonged incubation were lighter at hatching, their return rate and breeding performance in the following year were unaffected. These results show that individual quality as expressed through clutch size and body mass is affecting current reproductive investment level as well as future survival and breeding performance. The results also show that individual birds are sensitive to changes in their own condition, and when reproductive effort is approaching a level where survival or future survival may be compromised, they respond by terminating their current reproductive attempt.

**Key words:** body mass, common eider, cost of reproduction, parental effort, reproductive value, trade-off.

## INTRODUCTION

The cost of reproduction is a fundamental concept in the evolution of life-history strategies. That reproduction may compromise survival is well documented (Roff 1992, Stearns 1992, Barnes and Partridge 2003), but the mechanisms that link reproduction to survival are not so well understood (Hamel et al. 2009, Cox et al. 2010, Williams and Fowler 2015, Williams 2012, 2018). One such link suggested is the principle of resource allocation (Williams 1966). Time and energy are limited, and the resources invested in current reproduction must be traded off against resources needed for survival and future reproduction (Williams 1966, Tinbergen and Daan 1990, Roff 1992; Stearns 1992).

Costs of reproduction have been the subject of many empirical and theoretical studies on various organisms. Although some

experimental studies have shown that parents are able to increase their reproductive effort above their normal levels, and that this leads to a reduction in adult survival and/or future fecundity, the results are still ambiguous (Lindén and Møller 1989, Jacobsen et al. 1995, Hanssen et al. 2005, Hanssen 2006, Hadley et al. 2007, Erikstad et al. 2009, Cox et al. 2010, Santos and Nakagawa 2012, but see Leach et al. 2019). One topic that has been much debated is the cost of reproduction in long-lived versus short-lived species (Lindén and Møller 1989, Erikstad et al. 1998, 2009, Wernham and Bryant 1998, Golet et al. 2004). Long-lived species can be expected to be more reluctant to increase their reproductive effort than short-lived species, because even a small reduction in adult survival will greatly reduce the number of subsequent breeding attempts and thus their lifetime reproductive success (Curio 1988, Wooller et al. 1992, Charlesworth 1994). In contrast to this theoretical prediction, the available empirical evidence suggests that long-lived birds are more willing to accept survival costs than

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short-lived species (see review by Golet et al. 1998). However, many of the studies reviewed by Golet et al. (1998) based their conclusions on return rate rather than robust capture-recapture analyses which may erroneously register skipped breeding as mortality (see Leach et al. 2020). Alternatively, one explanation to the former pattern, as suggested by Wernham and Bryant (1998), is that many studies on short-lived birds are brood enlargements, and if such species normally work at maximum reproductive effort, increasing clutch size may not alter their effort. However, long-lived species may, under average conditions, have a lower-than-maximum effort and therefore be more likely to respond to experimentally increased broods by increasing their effort. This increased effort may translate into long-term costs such as reduced future reproduction (Leach et al. 2019, but see Santos and Nakagawa 2012).

Essential for the understanding of the resource allocation principle and the cost of reproduction is therefore detailed knowledge of the mechanisms that underlie the parental effort and allocation of time and energy to the different phases of reproduction. Such an allocation of resources is suggested to be driven by a complex interaction between the parents' own body condition, the fitness value of the brood and the parents' own survival chances and future reproductive prospects (Erikstad et al. 1998, 2009). According to this hypothesis, the individual parents' quality may to a large extent determine their ability to invest in reproduction, and high-quality individuals may do better in all regards (van Noordwijk and de Jong 1986, Hamel et al. 2009, Caro et al. 2016, Merckling et al. 2017, Montoya et al. 2016).

Most waterfowl species rely heavily on body reserves for egg production and incubation (reviewed in Ankney et al. 1991, Arnold and Rohwer 1991). In common eider ducks (*Somateria mollissima*, hereafter "eider") as well as in some Arctic geese, this strategy is at its extreme, because females normally do not feed at all between egg laying and hatching (Ankney and MacInnes 1978, Parker and Holm 1990, but see Hobson et al. 2015). Female eiders may lose up to 46% of their body reserves during this period (Korschgen 1977, Parker and Holm 1990). Furthermore, eiders have a communal brood rearing system, where many females abandon/lose their young soon after hatching, and the young are adopted by other females (Munro and Bedard 1977, Bustnes and Erikstad 1991a, Erikstad et al. 1993, Bustnes et al. 2002, Jaatinen et al. 2011).

Previous studies have shown that incubation costs in eiders are higher in birds incubating more eggs (Erikstad and Tveraa 1995, Hanssen et al. 2003a, 2005). A larger clutch size (whether experimentally enlarged or not) is associated with a higher mass loss but the birds do not seem to compensate for the higher incubation costs by abandoning their brood. It was even shown that this continued investment in brood tending despite high incubation costs led to reduced future reproduction (Hanssen et al. 2005). This points to a limitation in these studies: the larger the clutch size, the higher the fitness value of the clutch, and this may have led to an increased female willingness to invest in current reproduction. Accordingly, it is desirable to use an experimental setup where energy demands are manipulated without altering the fitness value of the brood, and where also the individuals' possibility of compensating for the increased physiological cost by increasing food intake is limited/controlled (Tuomi et al. 1983, Bonnet et al. 2002, Hamel et al. 2009).

We, therefore, designed an experiment in female eiders to examine the possible trade-offs between the use of body reserves for incubation, brood care, survival, and future fecundity, without altering clutch size. We manipulated the duration of the incubation

period by swapping whole clutches of similar size between nests with known laying dates. A trade-off between reserve use for incubation and other aspects of reproduction is likely in eiders because females feed very little or not at all during the entire incubation period (Korschgen 1977, Parker and Holm 1990, Gabrielsen et al. 1991). Females are thus faced with trade-offs between resources used for current reproduction (incubation and brood rearing) and future reproduction (survival and future fecundity). Females with experimentally prolonged incubation may direct resources to their residual reproductive success by deserting their clutches or abandoning their brood. Such decisions are expected to depend on two parameters that are also indicating individual quality: body mass (affecting subsequent survival) and clutch size (the potential value of the clutch).

## MATERIALS AND METHODS

### Field methods and sampling

The study was carried out in a common eider breeding colony near Tromsø in northern Norway (69°38'N, 18°51'E) in 1993–1995. The colony was on a 650 ha island (Grindøya) and contained about 400 breeding pairs. The colony has been studied extensively since 1985. The eider produces 3–6 eggs, which are incubated by the female for 22–26 days (mean = 24 days; Erikstad et al. 1993).

During the 1993–1995 breeding seasons, we visited the island daily to determine the laying date (date of a clutch's first egg laid) and clutch size in marked nests. If a nest was found with more than one egg, the laying date was estimated by assuming that one egg was laid per day (Hanssen et al. 2002). A clutch was assumed to be complete when no egg was laid for 2 days. Any nest in which > 1 egg was laid per day was excluded because of the possibility of nest parasitism. Although occurring in the eider (Bjørn and Erikstad 1994, Waldeck et al. 2011), the frequency of nest parasitism in the study area is very low (<1%, unpublished data). Incubation was assumed to start when the last egg was laid. Hatching date was defined as the day when the brood left the nest.

On day 5 of the incubation period, each female was captured, ringed, and weighed ( $\pm 5$  g; "early body mass"). The female was again weighed when the eggs had been incubated for 20 days ("late body mass"). At the same occasion, they were color-marked with tags on the back of their neck. The tags were made of tape and attached with superglue and were observed to last for up to 23 days (Bustnes and Erikstad 1991a). Based on early ( $m_1$ ) and late body mass ( $m_2$ ), we calculated (relative) mass loss as  $(m_1 - m_2)/m_1$ .

During incubation, nests were checked from a distance (without flushing the female) at least every second day. We classified clutches as lost if all eggs had disappeared. Clutches that were abandoned/depredated before or during manipulation (i.e., before day 5 after the start of incubation, see below), were omitted from analyses. Because unattended clutches are rapidly predated by crows (*Corvus corone*) or gulls (*Larus* spp.), we could not determine whether predation occurred before or after desertion (Swennen et al. 1993). The date of egg loss was recorded ( $\pm 1$  day). Nesting success was defined as the proportion of nests that hatched.

We classified females as "abandoners" or "tenders" according to their post-hatch behaviour (Kehoe 1989, Bustnes and Erikstad 1991a, Bustnes et al. 2002). "Abandoners" were females known to have left the colony with young and then observed during the first week after hatching without young. As we did not observe the females continuously after hatching we could not distinguish between females abandoning young and females that lost their whole brood to predators. "Tenders" were females observed caring for young,

alone or with other females, during the first week after hatching. Tenders always have some of their own young and frequently some adopted from abandoners (Bustnes and Erikstad 1991a). Females who abandon their brood generally do so within two days after hatching (Bustnes and Erikstad 1995, Bustnes et al. 2002).

## Experimental manipulation

In 1993 and 1994, whole clutches of the same size (3–6 eggs) that had been incubated for 5 and 10 days, respectively, were exchanged pairwise in order to prolong and shorten the duration of incubation of individual females by 5 days. The treatment groups are thus referred to as “shortened” ( $n = 59$ ) (i.e., the female received a clutch that had been incubated longer than her own, thereby shortening her expected incubation time) and “prolonged” ( $n = 68$ ) (i.e., the female received a clutch that had been incubated shorter than her own, thereby prolonging her expected incubation time). To ensure sufficient samples, some of the clutches exchanged differed in size and/or by 4 or 6 days in age ( $n = 23$ ). The unmanipulated clutch group ( $n = 34$ ) consisted of clutches that were not exchanged between nests. Any effect of exchanging eggs between nests have been tested in this population before, by swapping eggs between nests without altering clutch size, without any measurable effect on mass loss, incubation time, nest predation, or brood tending (Hanssen et al. 2003a).

We define incubation time as the number of days a female was incubating, as opposed to the number of days a clutch was incubated. Thus, at the day of second capture, all clutches had been incubated for 20 days, although the females’ incubation time varied from 15 days in the shortened treatment group, via 20 days in the control group, to 25 days in the prolonged treatment group.

## Statistical analyses

The sample analyzed consisted of 91 and 70 nests in 1993 and 1994, respectively. Eiders included in the experiment in 1993 were not included in the sample from 1994.

Continuous responses were analyzed using ANOVA and ANCOVA (PROC GLM, SAS Institute 1990, Littell et al. 1991) and ordinal responses using logistic models (PROC GENMOD, Stokes et al. 1995) with the binomial response distribution and the logit link function. Year and treatment were included in the models as categorical effects, whereas laying date, clutch size, and early body mass were included as continuous covariates. To analyze the effect of brood behavior (tending/abandoning the brood) on return rate, we also included this as a binary variable in the models. We examined the effect of treatment on laying date, clutch size, and early body mass in the following season. We expressed variables as deviations from the annual mean and controlled for repeatability of the variables by performing an ANCOVA with the respective variable in the year of treatment as a covariate.

Models are sorted using their Akaike’s Information Criterion (AIC), expressed more conveniently as the deviation ( $\Delta\text{AIC}$ ) of each model’s AIC from the best model’s AIC. AIC weights ( $w_i = \exp(-\frac{1}{2}\Delta\text{AIC}_i) / \sum(\exp(-\frac{1}{2}\Delta\text{AIC}_i))$ ) indicate the relative information-theoretic weightings obtained by competing models.

All statistical tests are two-tailed. Estimates are provided as mean  $\pm$  standard error (SE).

## Survival and recapture analyses

Apparent survival ( $\phi$ ; hereafter, survival) and re-sighting rates ( $p$ ) were analyzed in a capture–mark–recapture framework, using

program MARK (for documentation, cf. White and Burnham 1999). Initial data inspection was carried out using program RELEASE (cf. Burnham et al. 1987). Although TEST 3.SM was accepted ( $\chi^2_{10} = 25.40$ ,  $P = 0.15$ ), the assumptions underlying test 3.SR (encounter rate does not differ between newly marked and other individuals;  $\chi^2_{20} = 39.43$ ,  $P = 0.0059$ ) and TEST 2 (independence of prior capture histories;  $\chi^2_{19} = 61.75$ ,  $P = 0.000002$ ) were rejected. Correcting for trap dependence (Pradel 1993) considerably improved the global model ( $\chi^2_2 = 39.57$ ,  $P < 10^{-6}$ ), but was not sufficient to remove the lack of fit (two years of trap dependence were accounted for, denoted “h2” in model notation). The remaining overdispersion ( $\chi^2_{36} = 87.00$ ,  $P = 0.0058$ ) was taken into account using a correction factor of  $\hat{c} = 1.55$  in calculating quasi-AIC<sub>C</sub> (QAIC<sub>C</sub>).

The sample used in survival models included all eiders marked at Grindøya between 1985 and 2005 ( $n = 1212$ ). Sightings until 2006 were considered, which is twelve years after the experiment, allowing us to disentangle mortality and non-breeding in the year after the experiment. All non-experimental birds were coded as a separate attribute group whose vital rates varied in parallel (additively) to experimental birds. The effect of their inclusion was solely to increase the precision of estimates, because the inter-annual variation in re-sighting effort might otherwise have been confounded with experimental effects. Only estimates of experimental birds are discussed below. A fully time-dependent model  $\{\phi(t) p(t + h2)\}$  was preferred over models with constant survival ( $\Delta\text{QAIC}_C = 11.88$ ) or re-sighting ( $\Delta\text{QAIC}_C = 105.04$ ), and was thus used as the starting point of analyses. The effects of explanatory variables were considered only for the first year after treatment.

## RESULTS

### Before manipulation

Clutch sizes at the time of manipulation did not differ between the treatment groups (Table 1). Mean clutch size was not different between the two years ( $F_{1,155} = 1.7$ ,  $P = 0.20$ ).

The egg laying date was earlier in 1993 ( $25.57 \pm 0.55$ ) than in 1994 ( $27.13 \pm 0.53$ ,  $F_{1,155} = 4.7$ ,  $P = 0.032$ ) and  $4.4 \pm 0.8$  days earlier in the prolonged than in the shortened group (Table 1). The difference in laying date between the treatment groups was a consequence of the experimental design. Prolonging and shortening the duration of incubation by pairwise switching of clutches requires early-laid clutches to be switched with later clutches.

Female body mass at day 5 in the incubation period was somewhat higher in 1993 ( $1895 \text{ g} \pm 14 \text{ g}$ ) than in 1994 ( $1843 \text{ g} \pm 15 \text{ g}$ ,  $F_{1,155} = 6.4$ ,  $P = 0.012$ ). In addition, females in the unmanipulated group were slightly lighter than in the treatment groups (Table 1;  $P = 0.047$ ).

There were no significant year  $\times$  experiment interactions with any of the parameters measured before manipulation (all  $F_{2,155} < 1.1$ , all  $P > 0.35$ ). Overall, this suggests that laying date was the only parameter that was strongly biased between treatment groups.

### After manipulation

Incubation time, late body mass and mass loss varied between treatment groups as a direct consequence of experimental design (Table 1). The time females spent incubating increased from the shortened via the unmanipulated to the prolonged group, differing by  $4.3 \pm 0.2$  days between treatments. This difference is virtually identical to the difference in laying dates, suggesting that treatment did not affect the time of incubation received by clutches.

**Table 1**

**Clutch size, laying date, hatching date, incubation time, body mass and relative mass loss of female common eiders before and/or after experimental manipulation of their incubation time (mean  $\pm$  SE). Late and early measures were taken at after 5 and 20 days of incubation, respectively. Treatment represents females assigned to groups where the incubation period was shortened and prolonged with 5 days. Control nests are unmanipulated clutches. Pooled data for two different seasons (see text for further explanation). Sample sizes (number of nests) are given in parentheses. Asterisks indicate significance levels ( $P^{***} < 0.001$ ,  $0.05 \leq P^{\dagger} < 0.1$ )**

	Treatment			<i>F</i>
	Shortened	Unmanipulated	Prolonged	
Before manipulation				
Clutch size	4.54 $\pm$ 0.10 (59)	4.62 $\pm$ 0.14 (34)	4.50 $\pm$ 0.09(68)	0.3
Laying date (day in May)	28.56 $\pm$ 0.64 (59)	26.41 $\pm$ 0.64 (34)	24.16 $\pm$ 0.56 (68)	14.7***
Early body mass (g)	1878 $\pm$ 20 (59)	1825 $\pm$ 20 (34)	1892 $\pm$ 14 (68)	3.0 <sup>†</sup>
After manipulation				
Hatching date (day in June)	21.84 $\pm$ 0.65 (52)	24.08 $\pm$ 0.80 (26)	25.47 $\pm$ 0.65 (47)	8.1***
Incubation time (d)	18.81 $\pm$ 0.20 (52)	23.35 $\pm$ 0.22 (26)	27.49 $\pm$ 0.24 (47)	431.2***
Late body mass (g)	1615 $\pm$ 18 (55)	1465 $\pm$ 21 (28)	1437 $\pm$ 13 (53)	35.1***
Body mass loss (%)	14.24 $\pm$ 0.40 (55)	20.37 $\pm$ 0.48 (28)	24.66 $\pm$ 0.56 (53)	131.0***

In correspondence with the variation in females' incubation time, the late body mass of incubating females decreased, and the mass loss increased from the shortened via the unmanipulated to the prolonged group (Table 1). None of the three parameters mentioned differed between years (all  $F_{2,119} < 2.4$ ,  $P > 0.12$ ) or showed significant year  $\times$  experiment interactions (all  $F_{2,119} < 0.9$ ,  $P > 0.43$ ).

### Nest success

The probability of successful hatching increased with early female body mass and from the prolonged via unmanipulated to the shortened treatment group (Figure 1, Table 2, Appendix S1: Table S1). In addition, there was a tendency that nest success increased with clutch size ( $P = 0.069$ ). Nest success did not differ between years.

The timing of nest loss clearly differed between treatments (Figure 2). Whereas nest losses in the shortened and unmanipulated groups occurred randomly throughout the incubation period, nest losses in the prolonged treatment happened much later compared to the shortened (+9.3  $\pm$  1.9 days) and the control group (+6.6  $\pm$  1.9 days;  $F_{2,33} = 14.78$ ,  $R^2 = 0.47$ ,  $P = 0.00003$ ). All but one nest loss in the prolonged treatment was at or after the expected length of the incubation period (mean incubation time in the unmanipulated group, cf. Table 1).

### Brood care

We were not able to sight all females with successful nests after hatching to classify their brood behavior. However, there were no statistical differences in hatching date, clutch size, and late body mass among females that were successful and sighted on one hand ( $n = 83$ ), and successful and non-sighted on the other hand ( $n = 41$ ); two-way ANOVA, all  $P > 0.12$ ).

Based on the subsample of females sighted, the likelihood that females tended their young was highest in the shortened treatment group (Table 2, Figure 3, Appendix S1: Table S2). Clutch size had a marginal positive effect on the likelihood of tending. Tending did not differ between years.

### Survival

Survival to the year after the experiment was not affected by treatment or by any of the other covariates considered (Table 3).

Re-sighting, too, was unrelated to treatment (Table 2). However, clutch size and early female body mass were both positively correlated to re-sighting rates, although the latter effect only marginally so (Appendix S1: Table S3). This means that, of all experimental birds that survived to the next year, heavier females and females laying larger clutches were more likely to be breeding the year after the experiment.

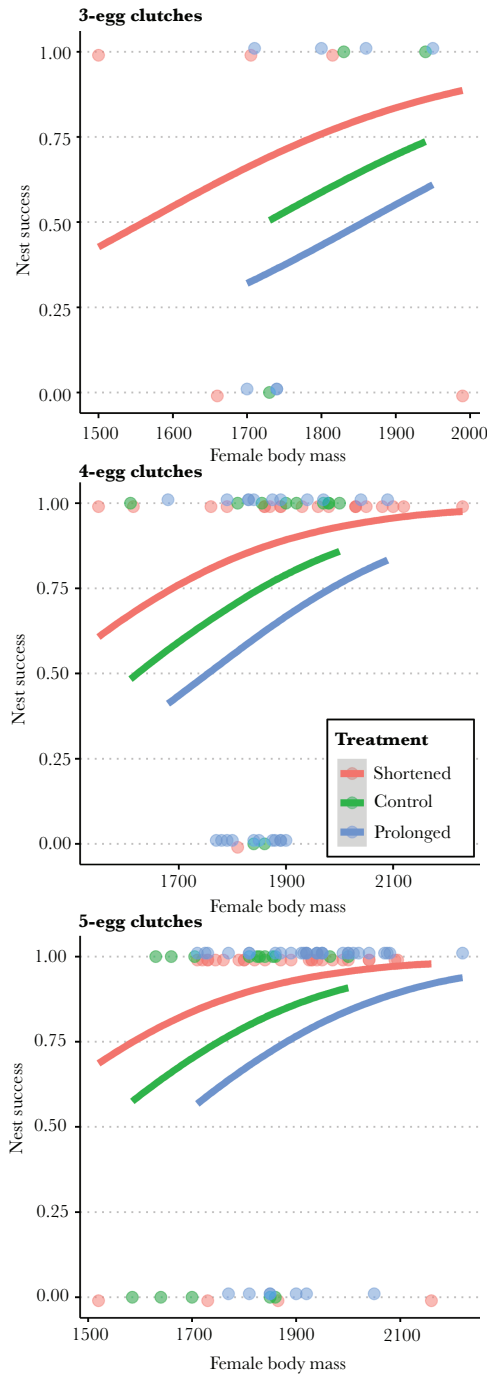
### Future fecundity

Laying date and early body mass were highly repeatable from one year to the next, whereas clutch size was not (Appendix S1: Table S4). These variables were not affected by treatment the year before (all  $P > 0.3$ ) and did not differ between years (all  $P > 0.2$ ).

## DISCUSSION

The main results from the present study can be summarised as follows: female common eiders whose incubation time was prolonged experimentally suffered higher mass loss and increased clutch loss/nest desertion. These females were also more likely to abandon their brood after hatching. Both clutch loss and brood abandonment decreased with clutch size in all treatment categories. However, although females with prolonged incubation were lighter at hatching, both their return rate, survival, and breeding performance in the following year were unaffected. Body mass measured early in the incubation period and clutch size were the only variables related to return rate in the following year.

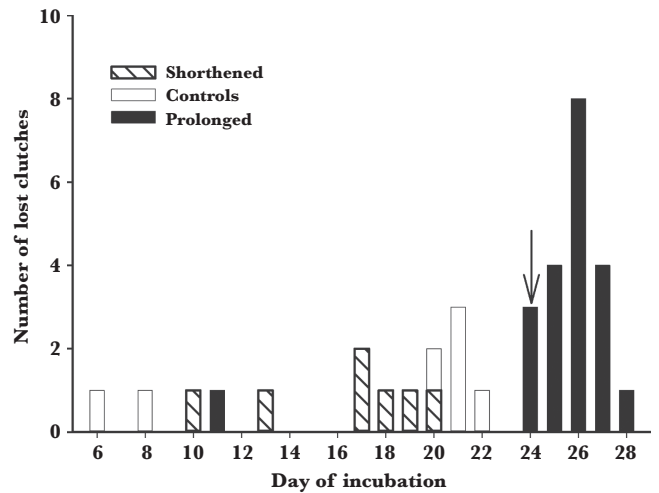
These results lend support to the hypothesis that phenotypic quality and/or access to resources as expressed through clutch size and body mass are affecting both current reproductive investment level and future survival and breeding performance in the same direction (e.g., van Noordwijk and de Jung 1986). For each individual female, one can assume a physiological trade-off between investment in clutches and investment in chicks, even though both are positively correlated across females (Fig. 4). Our manipulation increased or decreased the investment in clutches, but the females responded by adjusting their investment in chicks (Fig. 4). These results show that, despite experimental manipulation, females adjust their overall reproductive effort to a level where survival and future reproduction are not compromised.



**Figure 1** Nest success (the probability of hatching) in common eiders in relation to clutch size and early female body mass for three treatment groups. Experimentally shortened (red), unmanipulated (green), and prolonged incubation time (blue). (Estimates are from the top-ranked logistic model in Table 2).

**Individual quality and investment level**

Individual quality and its consequences for reproductive costs have for decades drawn attention to ecologists (e.g., van Noordwijk and de Jong 1986, Caro et al. 2016, Montoya et al. 2016, Merklings et al. 2017, Williams 2018). Birds that started incubation with a higher body mass and birds with larger clutch size had a higher probability



**Figure 2** Number of clutch losses in common eiders during the incubation period among the treatment groups (experimentally shortened, unmanipulated, and prolonged incubation time) in relation to day (days after start of incubation). The arrow indicates the mean length of the incubation period for unmanipulated clutches.

of completing incubation and tending for ducklings. These females also had a higher return rate to the next breeding season. From a life history perspective, several partly overlapping explanations may be given to these results. First, these birds may show higher investment levels because they are at the end of their life (i.e., terminal investment) (Hanssen 2006), however, their higher return rate does not support this. Second, a previous study where one group of birds were experimentally depredated showed that successful breeding tended to lead to a higher probability of breeding in the colony the following year (Hanssen and Erikstad 2013); however, this does not explain the higher body mass and larger clutch size. Third, a larger clutch size has a higher reproductive value, and this may incite females to invest more in current reproduction, however, this should have a neutral or more likely a negative effect on survival. A final and most likely explanation is that females of better quality are able to gain more body reserves before breeding and, therefore, to allocate more resources to all life-history traits. This means that they can invest more in egg production, incubation, and brood rearing without compromising survival (e.g., van Noordwijk and de Jong 1986, Garant et al. 2007), and they even have higher re-sighting rate compared to females with lower body mass and smaller clutch size.

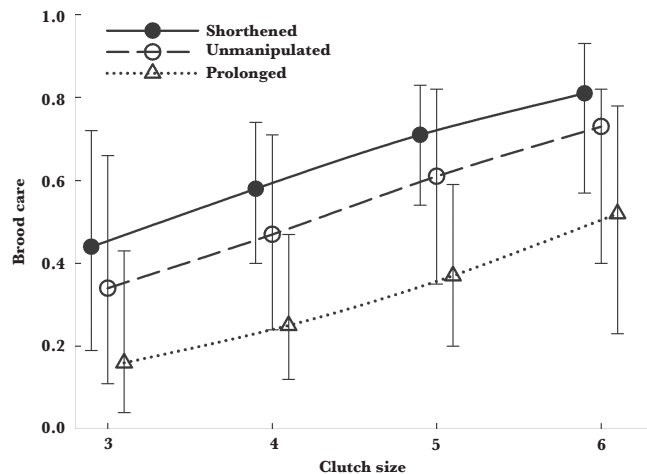
**Experimental mass loss**

The study design in the present study allowed us to manipulate body mass (available body reserves) without altering the reproductive value of the clutch (clutch size). It can, however, be argued that prolonging the incubation period leads to later hatch dates, and that the value of offspring is reduced when hatched later in the season (e.g., Drent and Daan 1980, Curio 1983). Thus, the question is whether a ~4 day difference in laying/hatching dates could explain the reduced interest in brood care in the prolonged group. In this study colony the potential effect of laying date on brood care has been evaluated on several occasions without uncovering any effect of laying date on the probability of tending/abandoning the brood after hatching (Hanssen et al. 2003a, 2003b, Hanssen

**Table 2**

**Variables in the best models describing (A) nest success, (B) brood care, and (C) re-sighting rates of female common eiders after experimental manipulation of their incubation time. Models presented are (A + B) binomial GLMs or (C) capture–mark–recapture models investigating the effect of treatment (shortened, unmanipulated and prolonged incubation time) and covariates on the likelihood that (A) females complete the incubation period and hatch their eggs, (B) females care for their young after hatching, or (C) females are re-sighted the year after, given they are alive (binary responses). Test statistics are (A + B) Wald  $X^2$  or (C) likelihood ratio tests.  $\Delta\text{AIC}_C$  values indicate the difference between Akaike's Information Criterion (corrected for small sample size) of the model described and the null model. For results of model selection, see Appendix S1: Table S1, S2 and S3, respectively**

Variables	<i>N</i>	Mean	Estimate	$c^2$	$R^2$	$\Delta\text{AIC}_C$
(A) Nest success					0.11	-12.81
Treatment						
shortened	59	88%	1.42 ± 0.52	8.3**		
unmanipulated	34	77%	0.79 ± 0.60	1.2		
prolonged	67	69%				
Early female body mass (kg)			4.80 ± 1.71	7.8**		
Clutch size			0.49 ± 0.27	3.3 <sup>+</sup>		
(B) Brood care					0.12	-3.94
Treatment						
shortened	41	66%	0.62 ± 0.31	3.9*		
unmanipulated	18	50%	0.18 ± 0.38	0.2		
prolonged	24	33%				
Clutch size			0.57 ± 0.33	2.9 <sup>+</sup>		
(C) Re-sighting rates						-2.84
Treatment						
shortened	59	52%	0.43 ± 0.34			
unmanipulated	34	35%	-0.26 ± 0.43	2.7		
prolonged	68	61%	0.79 ± 0.34			
Early female body mass (kg)			0.43 ± 0.20	3.3 <sup>+</sup>		
Clutch size			0.46 ± 0.19	3.9*		

**Figure 3**

Brood care (the probability of tending young) in common eiders in relation to clutch size for three treatment groups (experimentally shortened, unmanipulated, and prolonged incubation time). Error bars indicate 95% confidence limits. (Estimates are from the top-ranked logistic model in Table 2).

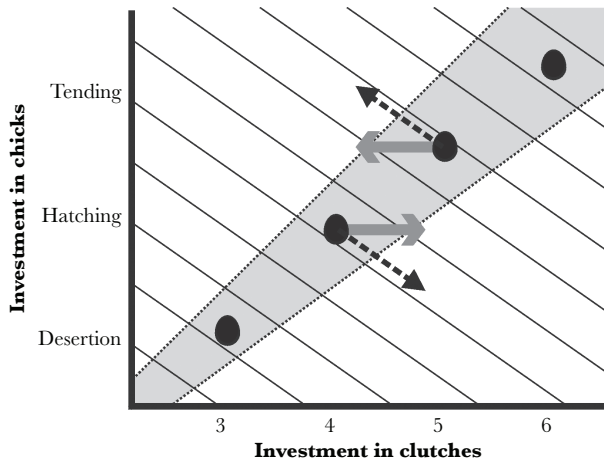
2006). We here found that, as experimental mass loss increased, the likelihood of continued investment in the current clutch or brood decreased, females tended to lose/desert their clutch before hatching or abandon their brood after hatching. Given a constant daily predation rate/clutch abandonment rate, we would of course expect a higher total nest abandonment rate in the prolonged incubation group, simply as a consequence of the 5 day longer exposure to the daily predation risk. However, what we found was that the daily predation/abandonment rate was not constant during

**Table 3**

**Adult survival rates of female common eiders during the first winter after experimental manipulation of their incubation time. Columns show the number of parameters (*K*); the quasi-Akaike's Information Criterion, corrected for small sample size, relative to the best model ( $\Delta\text{QAIC}_C$ ); the  $\text{QAIC}_C$  weight (*w*); and the likelihood ratio test  $X^2$  of the deviances of pairs of nested models (all  $P > 0.1$ ). The parameterization of re-sighting rate in all models of this Table was model 1 from Supplementary Table 3. The top model had a  $\text{QAIC}_C$  of 5136.00**

Model	<i>K</i>	$\Delta\text{QAIC}_C$	<i>w</i>	$c^2$
1 Null model	72	0.00	0.592	0.00
2 Treatment	74	3.40	0.108	0.81
3 Treatment + early female mass	75	4.93	0.050	1.38
4 Treatment + clutch size	75	5.00	0.049	1.32
5 Treatment + nest success	76	7.14	0.017	1.29
6 Treatment + tending young	76	7.60	0.013	0.82

incubation, it tended to increase towards the end of incubation in all groups. The result that almost no birds in the prolonged group lost their nest until the end of incubation suggests that these birds were in better condition or of better quality than the birds in the unmanipulated group. This is probably a consequence of the bias in laying date that derives from the experimental design, because the birds in the prolonged group consists of birds with earlier laying dates than the shortened group and are therefore presumably of higher quality or more experienced birds. It should be noted that most of these females in the prolonged group lost their clutch after having incubated beyond the time where a "normal" clutch would have hatched, and that the desertion/abandonment may be a response to this. Nevertheless, birds in the prolonged group more often abandoned their ducklings to other females after hatching.



**Figure 4**

Although investment in clutches (before hatching) and investment in chicks (after hatching) are expected to exhibit intra-individual trade-offs (thin black lines) and thus be negatively correlated, the observed phenotypic pattern at the population level is a positive correlation (black eggs). This is due to fixed allocation rules (grey area). Without manipulation, investment in clutches is determined by the clutch size that any female chooses to lay (x-axis). Manipulation decreased or increases the clutch investment, however (grey arrows). The response of individuals (broken black arrows) follows the intra-individual black contour lines, leading to an increased or decreased probability of hatching and/or tending.

The cost of this abandonment seems to be lower survival of abandoned young, probably as a consequence of being forced by their foster mother into more disadvantageous positions in the brood (Bustnes and Erikstad 1991b, Ost and Bäck 2003). The costs to the adopting females are probably negligible as the young feed themselves, i.e., increasing brood size does not lead to increased costs of care (Lazarus and Inglis 1978, 1986). This brood abandonment strategy ensures that after abandonment the broods still have a chance of survival (albeit reduced) and the current reproductive effort is not wasted (Bustnes and Erikstad 1991b, Öst and Bäck 2003). Given that the birds in the prolonged group may presumably be of slightly higher quality it is not impossible that this may have weakened the experimental effect and even higher desertion/abandonment rates may have been expected if laying dates in all groups had been equal.

### Cost of reproduction

The population dynamics of long-lived species have been shown to be sensitive to changes in adult survival (Stearns 1992, Caswell 2000, Sæther and Bakke 2000), and these species are therefore predicted to be restrictive with activities that reduce adult survival (e.g., Lindén and Møller 1989, Charlesworth 1994). We found that birds that suffered a very high experimental mass loss, even though they may be of higher individual quality, more often abandoned their eggs and chicks but had a similar return rate to the next season, when compared to unmanipulated and birds with an experimentally reduced mass loss. Thus, as has been shown in other long-lived birds (Erikstad et al. 2009), female eiders have a highly flexible parental investment, which they adjust according to their individual quality and state. They seem able to compensate for the increased mass loss by abandoning their brood, thereby avoiding reaching a condition where their own survival and future reproduction would be at risk (Fig. 4).

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

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Data availability: Analyses reported in this article can be reproduced using the data provided by Hanssen et al (2022).

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