

Differential investment and costs during avian incubation determined by individual quality: an experimental study of the common eider (*Somateria mollissima*)

Sveinn Are Hanssen^{1,2*}, Kjell Einar Erikstad^{1,2}, Vigdis Johnsen^{1,2} and Jan Ove Bustnes²

¹Biology Department, Faculty of Science, University of Tromsø, N-9037 Tromsø, Norway

²Norwegian Institute for Nature Research, Polar Environmental Centre, N-9296 Tromsø, Norway

Individuals of different quality may have different investment strategies, shaping responses to experimental manipulations, thereby rendering the detection of such patterns difficult. However, previous clutch-size manipulation studies have infrequently incorporated individual differences in quality. To examine costs of incubation and reproductive investment in relation to changes in clutch size, we enlarged and reduced natural clutch sizes of four and five eggs by one egg early in the incubation period in female common eiders (*Somateria mollissima*), a sea duck with an anorectic incubation period. Females that had produced four eggs (lower quality) responded to clutch reductions by deserting the nest more frequently but did not increase incubation effort in response to clutch enlargement, at the cost of reduced hatch success of eggs. Among birds with an original clutch size of five (higher quality), reducing and enlarging clutch size reduced and increased relative body mass loss respectively without affecting hatch success. In common eiders many females abandon their own ducklings to the care of other females. Enlarging five-egg clutches led to increased brood care rate despite the higher effort spent incubating these clutches, indicating that the higher fitness value of a large brood is increasing adult brood investment. This study shows that the ability to respond to clutch-size manipulations depends on original clutch size, reflecting differences in female quality. Females of low quality were reluctant to increase investment at the cost of lower hatch success, whereas females of higher quality apparently have a larger capacity both to increase incubation effort and brood care investment.

Keywords: clutch size manipulation; life history; parental investment; brood abandonment; cost of incubation; quality

1. INTRODUCTION

Clutch size has been the focus of extensive theoretical and empirical effort since David Lack (1947) indicated that the number of offspring produced reflects the maximum number that the parents can provide for. Incorporating the cost of reproduction has shown that in iteroparous organisms parents should produce fewer offspring than the 'Lack clutch size' (Williams 1966; Charnow & Krebs 1974). Life-history theory assumes that individuals allocate their resources optimally to the different phases of each reproductive event, i.e. for birds: egg production, incubation and brood care (Stearns 1992). In altricial birds the costs of rearing young have been considered to be important for clutch-size regulation (Perrins & Moss 1975; Lessells 1986; Pettifor *et al.* 1988; Tinbergen & Daan 1990; Tinbergen & Both 1999). In precocial species where costs of brood care often do not increase with brood size (Lazarus & Inglis 1978, 1986) it has been assumed that energy limitations during egg laying limit clutch size (Lack 1968; Winkler & Walters 1983; Ankney & Afton 1988). However, incubation costs such as increased

energy expenditure or mass loss (Biebach 1981, 1984; Haftorn & Reinertsen 1985; Coleman & Whittall 1988; Erikstad & Tveraa 1995), prolonged incubation (Moreno & Carlson 1989), higher predation risk (Inglis 1977) or reduced hatch success (Coleman & Whittall 1988; Briskie & Sealy 1989; Moreno *et al.* 1991; Siikamäki 1995) may increase in larger clutches and this may also limit clutch size (Arnold *et al.* 1987; Heaney & Monaghan 1995). The increased costs of incubating a larger clutch may be compensated for by the higher fitness value of the larger clutch as predicted by parental investment theory (Coleman & Gross 1991). In addition, parental investment theory predicts adaptive abandonment of a clutch or brood if the brood's survival prospect is too low or if the number of offspring is reduced to a number where the costs of deserting is lower than the cost of continued investment (Coleman & Gross 1991). Abandonment is also predicted if adult survival prospect and hence future reproductive value is decreased (Monaghan *et al.* 1989; Erikstad *et al.* 1998a).

Parental quality is expected to affect the outcome of clutch-size manipulation experiments (see Monaghan & Nager 1997). Negative effects are most likely to be found in poorer quality individuals (Heaney & Monaghan 1995; McNamara & Houston 1996; Pettifor *et al.* 2001). In a review of studies of optimal clutch size in birds the authors

* Author and address for correspondence: Norwegian Institute for Nature Research, Polar Environmental Centre, N-9296 Tromsø, Norway (sveinn@ibg.uit.no).

recommend that effects of manipulations are examined separately in birds of different quality (e.g. different original clutch sizes; Monaghan & Nager 1997). Our study species, the common eider (*Somateria mollissima*), is a capital breeder that relies upon accumulated body reserves during egg laying and incubation (Drent & Daan 1980; Erikstad *et al.* 1993). Anorexia during the incubation period (22–26 days) leads to a body mass loss during egg laying and incubation of more than 40% (Korschgen 1977; Parker & Holm 1990). The common eider is long-lived, yearly survival has been reported to be 85% (Baillie & Milne 1982; Yoccoz *et al.* 2002), and we expect that eiders adjust their investment level during reproduction so as not to jeopardize their own survival prospects (Charlesworth 1980; Lindén & Møller 1989). Eiders with low clutch size have been found to have lower nest success (success defined as hatching at least one egg; Erikstad & Tveraa 1995), increased abandonment of ducklings (Erikstad *et al.* 1993) and also lower return rate and survival (Yoccoz *et al.* 2002). Clutch size may hence reflect phenotypic quality also in this species.

To explore if investment level and costs during incubation are different among high- and low-quality individuals, we enlarged and reduced clutches of four (lower quality individuals) and five (higher quality individuals) common eider eggs by one egg early in the incubation period in three breeding seasons. Possible effects of a change in clutch size upon mass loss, nest success, hatch success, brood care and return rate were examined. If increased clutch size is associated with an obligate increase in energetic requirements of maintaining incubation temperature in larger clutches, then we expect a lower mass loss in reduced clutches and higher in enlarged clutches compared with controls regardless of original clutch size. If females are not able to increase investment in enlarged clutches then we expect this to affect hatch success negatively and possibly increase the incubation period. If costs of incubating an enlarged clutch are too large then females may desert their eggs or the brood after hatching; however, the larger expected fitness from an enlarged clutch may increase reproductive investment. Additionally, if females facultatively regulate incubation investment according to own status, then we expect that higher-quality females, i.e. with a higher capacity, should increase investment in enlarged clutches whereas females of lower quality may choose not to increase investment accordingly. In order to test possible differences in strategies between females of different quality it is valuable to statistically test the interaction term between quality (here clutch size) and manipulation of reproductive demand.

2. MATERIAL AND METHODS

(a) Study area and study species

The study was conducted in an eider colony (ca. 400 breeding pairs) on Grindøya, an island of 0.65 km², near Tromsø, northern Norway (69°49' N, 18°15' E). During the 1995–99 breeding seasons the colony was visited daily from the start of egg laying in mid-May to determine the laying date and clutch size. The eider lays one egg per day (Watson *et al.* 1993) and the clutch was assumed to be complete when no new eggs were laid over a 2-day period. The common eider produces from three to six eggs, but clutches of four and five eggs are most common

(13% three eggs, 42% four eggs, 40% five eggs and 5% six eggs; S. A. Hanssen, unpublished data).

(b) Experimental design

The experimental manipulations were performed in the 1995, 1996 and 1998 seasons. Five days after the laying of the last egg, females were randomly assigned to four groups; two clutch-size manipulation groups and two control groups. Clutches of four and five eggs (the most common clutch sizes) were enlarged or reduced by one egg. The two control groups were unmanipulated nests (control 1) and nests where one egg was swapped between nests of equal clutch size to control for any effects directly related to the manipulation method (control 2). Because natural three- and six-egg clutches with the same date of laying were infrequent we could not perform any clutch-size manipulations of these nests. The range of experimental clutch sizes (three to six eggs) is hence equal to the naturally occurring clutch sizes in the study area. The laying date and clutch size were equal in the two control groups. Also, no differences were found when comparing the two manipulation groups and the pooled control group, thus indicating successful randomization of all manipulation groups. The double control setup was used in 1995 and 1996; in 1998 we only included one control group (control 1). Relative body mass loss (percentage of body mass lost from day 5 to day 20 in the incubation period), length of the incubation period, hatch success, nest success, brood tending and return rate in the control 1 group, were in both years (1995 and 1996) similar to the control 2 group (all p values ≥ 0.37). Accordingly, egg swapping, as such, did not have any effect on the parameters measured and the two control groups are pooled in all further analyses.

Partial clutch loss was significantly related to clutch size ($\chi^2 = 5.10$, d.f. = 1, $p = 0.02$, four-egg clutches 19% partly predated, five-egg clutches 23% partly predated), but not to manipulation ($\chi^2 = 0.31$, d.f. = 1, $p = 0.58$) or nest success ($\chi^2 = 0.57$, d.f. = 1, $p = 0.45$). This means that loss of single eggs is not a consequence of manipulation nor does it increase the probability of total nest loss (decreasing nest success rate). Nevertheless, to prevent interference with the manipulation of clutch size, all partly predated nests were removed from the analyses.

(c) General procedures

When clutch size was manipulated the females were captured and weighed (± 2.5 g). The females were recaptured and weighed 15 days later (day 20). Relative mass loss is the percentage of initial body mass lost between day 5 and day 20. Incubation period is the time from laying of the last egg until hatching. To control for structural size when analysing effects of body mass we initially used wing length as a covariate in all these analyses according to García-Berthou (2001) and Freckleton (2002). Wing length did not, however, affect any of the dependent variables significantly, neither did including it alter the way body mass affected the dependent variables, so we present results without using wing length. Nest success is defined as the percentage of nests that hatched at least one egg. Hatch success is the percentage of hatched eggs in the nest.

At day 20 we also tagged the females with brood-specific colour-coded tape tags (Bustnes *et al.* 2002) to distinguish between the females while observing brood-tending behaviour after hatching. The tags were attached to the back of their head with superglue. After hatching, female eiders disperse over a large area in the fjords surrounding Grindøya (72 km of coastline).

Table 1. Relative mass loss (percentage of mass lost from days 5 to 20), incubation period, nest success (frequency of clutches hatching at least one egg), hatch success (frequency of eggs hatching) and frequency of brood tenders in relation to manipulation group for female common eiders laying four eggs and five eggs. (Values are expressed as mean \pm s.e. Sample sizes in parentheses.)

	manipulation			
	reduced	control ^a	enlarged	
four-egg clutches				
relative mass loss (%)	20.8 ± 0.5 (17)	19.9 ± 0.4 (27)	20.0 ± 0.5 (15)	1.12 ^b , <i>p</i> = 0.29
incubation period (days)	23.3 ± 0.14 (21)	23.2 ± 0.16 (39)	23.4 ± 0.18 (22)	0.01 ^b , <i>p</i> = 0.90
nest success (%)	58 (36)	79 (53)	79 (29)	4.03 ^c , <i>p</i> = 0.05
hatch success (%)	100 ± 0 (15)	92 ± 2.9 (23)	83 ± 6.4 (15)	8.19 ^d , <i>p</i> = 0.02
brood tending (%)	75 (16)	52 (23)	64 (14)	0.44 ^c , <i>p</i> = 0.51
return rate (%)	48 (21)	50 (42)	25 (24)	2.56 ^c , <i>p</i> = 0.11
five-egg clutches				
relative mass loss (%)	20.0 ± 0.4 (17)	20.6 ± 0.4 (28)	21.4 ± 0.5 (23)	4.63 ^b , <i>p</i> = 0.04
incubation period (days)	23.1 ± 0.14 (28)	23.4 ± 0.15 (37)	23.0 ± 0.18 (24)	0.04 ^b , <i>p</i> = 0.84
nest success (%)	90 (31)	78 (50)	78 (32)	1.54 ^c , <i>p</i> = 0.22
hatch success (%)	89 ± 4.6 (16)	91 ± 2.8 (26)	89 ± 3.9 (16)	0.13 ^d , <i>p</i> = 0.94
brood tending (%)	57 (21)	61 (23)	88 (16)	3.60 ^c , <i>p</i> = 0.06
return rate (%)	39 (28)	51 (39)	44 (25)	0.14 ^c , <i>p</i> = 0.71

^a Pooled data for the two control groups.

^b The test statistic is a F -value from a general linear model.

^c The test statistic is χ^2 from the logistic model.

^d The test statistic is χ^2 from a Kruskal–Wallis test.

About half of the eider females abandon their own ducklings to the care of other females. Tending females may also join other tending females, forming so-called ‘crèches’ (Munro & Bedard 1977; Bustnes & Erikstad 1991). We classified the females as to whether they were ‘tenders’ or ‘abandoners’ (Kehoe 1989; Bustnes & Erikstad 1991). Abandonment usually occurs within the first 2 days after hatching (Bustnes & Erikstad 1995). Abandoners are females known to have left the colony with young and then observed during the first week after hatching not caring for young. Tenders are females observed caring for young alone or with other females during the first week after hatching. In the present study we do not distinguish between birds exclusively caring for their own young and birds tending multiple broods together with other females (crèching). We checked for differences between the females observed and not observed after hatching in relation to clutch size, late body mass and hatching date and found no significant differences (two-way ANOVA, $p \geq 0.47$ in all cases).

When the birds were captured their ring number was recorded and unbanded birds were ringed. On the basis of individual rings the females that returned to breed the next year were identified.

(d) Data analysis

t -tests were used when comparing the two control groups. We expected linear relationships between the extent of manipulation (i.e. -1 , 0 and $+1$ egg) and dependent variables; effects of manipulation were hence analysed with a linear fit (Pettifor 1993; Pettifor *et al.* 2001). However, the brood tending and nest success results (table 1) may indicate that a linear fit of manipulation may not be appropriate; we therefore also calculated models where manipulation was entered as a categorical variable. We compared the fit of these alternative models (linear versus categorical) with the Akaike Information Criterion (AIC; Burnham & Anderson 1998) and found that in all models the

linear fit was actually the best; hence we chose to retain the linear fit of manipulation. For clarity of results manipulation effects are presented as means \pm standard error in the tables. Nest success, post-hatch behaviour (tending or abandoning) and return rate were analysed with logistic models. The hatch success values were not normally distributed and were hence analysed using the Wilcoxon two-sample test or Kruskal–Wallis test in non-parametric ANOVAs. All values are presented as means \pm s.e. and all tests are two-tailed. p values that were less than 0.05 were considered statistically significant.

3. RESULTS

(a) Body mass loss and length of the incubation period

The manipulation \times clutch-size interaction was significant ($F_{1,126} = 4.82$, $p = 0.03$, controlling for clutch size $F_{1,126} = 3.26$, $p = 0.07$, manipulation $F_{1,126} = 4.64$, $p = 0.03$ and year $F_{2,126} = 5.62$, $p = 0.005$) showing that manipulation affected mass loss differently for the two original clutch sizes. In original four-egg clutches manipulation did not affect relative mass loss, but among females with an original clutch size of five eggs there was a positive relationship between manipulation and relative mass loss (table 1, figure 1). Relative body mass loss tended to be higher in five-egg clutches (four eggs 0.202 ± 0.003 , five eggs 0.207 ± 0.003). The length of the incubation period was not affected by the manipulation (manipulation $F_{1,170} = 0.03$, $p = 0.87$, clutch size $F_{1,170} = 0.06$, $p = 0.81$, manipulation \times clutch-size interaction $F_{1,170} = 0.06$, $p = 0.81$, year $F_{2,170} = 0.96$, $p = 0.39$; table 1).

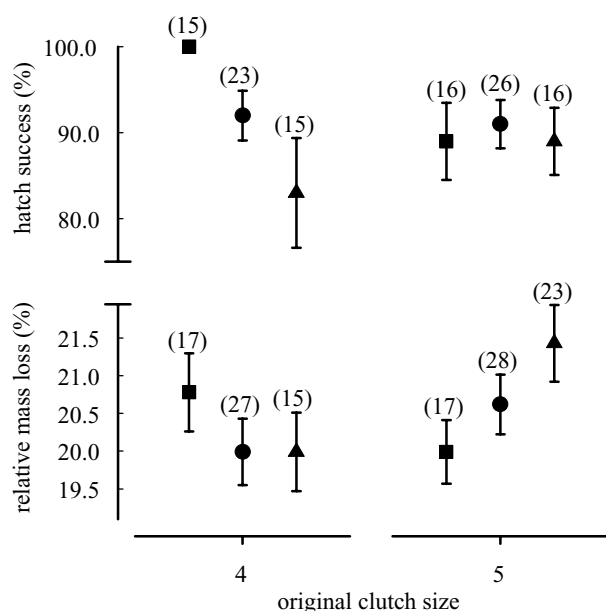


Figure 1. Relative mass loss (percentage of initial body mass lost) and hatch success (percentage of eggs in the nest hatched) in relation to original clutch size and manipulation (-1 , 0 and $+1$ egg) in common eider females during the incubation period. Sample sizes (number of females) are given above each bar. Pooled data for the three years (1995, 1996 and 1998). Squares, reduced; circles, control; triangles, enlarged. See text and table 1 for statistical analyses.

(b) Nest success and hatch success

The interaction term of manipulation \times clutch size was significant, which indicates differential responses to manipulation in the two clutch-size groups (table 2). Manipulation (-1 , 0 and $+1$ egg) was significantly positively related to nest success rate (table 1). Manipulation did not affect nest success significantly among five-egg clutches (table 1). Nest success was not related to original clutch size (table 2). However, females with lower body mass had a lower probability of nest success (table 2).

Hatch success was not related to original clutch size (Wilcoxon sum rank test $Z = -1.11$, $p = 0.27$). Furthermore, manipulation did not affect hatch success significantly among original five-egg clutches (table 1 and figure 1). However, among original four-egg clutches all reduced clutches hatched all eggs, whereas mean hatch success was $92 \pm 2.9\%$ among controls and only $83 \pm 6.4\%$ among enlarged four-egg nests (table 1, figure 1), thus showing that females producing five eggs apparently are able to hatch enlarged clutches with equal success, whereas reducing and enlarging four-egg nests respectively increased and reduced hatch success.

(c) Brood care

The interaction term manipulation \times clutch size was significant, indicating differential responses for the two clutch sizes (table 3). Manipulation (-1 , 0 or $+1$ egg) was positively related to the probability for brood tending among five-egg clutches (tables 1 and 3). Manipulation did not affect brood care in four-egg clutches (tables 1 and 3). Heavier birds had a lower probability of abandoning their brood (table 3).

(d) Return rate

The return rates of female eiders in relation to manipulation and original clutch size are shown in table 1. A logistic regression analysis showed no effect of manipulation or the interaction between manipulation and clutch size on return rate, but return rate was different between years (1995, 57% $n = 49$; 1996, 47% $n = 49$; 1998, 13% $n = 16$; $\chi^2 = 10.75$, d.f. = 2, $p = 0.005$), including females that were not observed during the brood rearing period gave a similar result (1995, 55% $n = 53$; 1996, 44% $n = 88$; 1998, 27% $n = 31$; $\chi^2 = 8.65$, d.f. = 2, $p = 0.01$).

4. DISCUSSION

(a) Clutch size and quality

Clutch size has been shown to relate to traits indicating quality of parents in both observational (De Steven 1980; Nisbet *et al.* 1984; Coulson & Porter 1985; Cooch *et al.* 1991; Lepage *et al.* 1998; Yoccoz *et al.* 2002) and experimental (Pettifor *et al.* 1988, 2001) studies. We therefore expected positive correlations between condition-quality-dependent traits and original clutch size. Early body mass did not differ between females with different clutch sizes, and, assuming the same rate of mass loss before first capture, body mass was higher before egg laying in females laying five eggs compared with those producing four eggs (one egg is *ca.* 100 g; Erikstad *et al.* 1998b, see also Korschgen 1977). Relative mass loss tended to be higher in females laying five eggs, which has also been observed in an earlier study from the same population (Erikstad & Tveraa 1995) and thus indicates larger obligate costs of incubation or increased facultative incubation investment for larger clutches. The return rate was not related to the original clutch size in this study; however, a long-term study from the same population shows that females producing larger clutches have higher survival (Yoccoz *et al.* 2002), indicating that these females are of higher quality.

(b) Nest success and brood tending

Nest success (percentage of nests hatching at least one egg) and brood tending (percentage of females tending broods) increased among females with higher body mass. Also, nest success rate was reduced when removing one egg from low-quality (four-egg) females. Several studies have shown that birds desert their eggs or chicks when their own body mass is low (Drent 1975; Ankney & MacInnes 1978; Jones 1987; Bustnes & Erikstad 1991; Chaurand & Weimerskirch 1994a,b; Olsson 1997; Kilpi *et al.* 2001; Bustnes *et al.* 2002) or when clutch size is low (Armstrong & Robertson 1988; Forbes *et al.* 1994; Erikstad & Tveraa 1995). Furthermore, brood abandonment rate increased in experimentally reduced clutches of goldeneye ducks, *Bucephala islandica* (Eadie & Lyon 1998) and in reduced broods in fishes, *Aequidens coeruleopunctatus* (Sargent 1997; Jennions & Polakow 2001; Vélez *et al.* 2002). These results could be interpreted as adaptive abandonment of the nest or brood when either adult body condition (Sæter *et al.* 1993; Weimerskirch *et al.* 1995) or the reproductive value of the current brood (Coleman & Gross 1991) is reduced to a level where continued investment will jeopardize future reproduction. Alternatively, it is possible that body mass is related to individual quality and that light birds more frequently desert because they

Table 2. Nest success in common eider in relation to early body mass, clutch size and manipulation (removing or adding one egg and controls).

(Nest success (at least one egg hatched or no eggs hatched) was used as the dependent variable in a logistic regression model. The deviance of the null model was 176.14 with 165 d.f., whilst after fitting the final model the deviance was reduced to 158.73 with residual d.f. = 161. Year, laying date and wing length were initially included in the model but were removed as they did not contribute significantly ($p > 0.05$).)

variable	Δ deviance	Δ d.f.	p	estimates of coefficients (mean \pm s.e.)
+ body mass	10.56	1	0.002	0.007 \pm 0.002
+ clutch size	5.98	1	0.02	
+ manipulation	4.98	1	0.03	5.66 \pm 2.61
+ manipulation \times clutch size	4.57	1	0.0008	-1.21 \pm 0.58

Table 3. Brood care behaviour in the common eider (abandoners or tenders) in relation to late body mass, clutch size, manipulation and the interaction term manipulation \times clutch size.

(Brood care behaviour (tending or abandoning) was used as the dependent variable in a logistic regression model. The deviance of the null model was 142.65 with 110 d.f., whilst after fitting the final model the deviance was reduced to 126.94 with residual d.f. = 106. Year, laying date, number of eggs hatched and wing length were initially entered but did not contribute significantly to the model and were hence removed. Non-significant interactions were removed from the final model.)

variable	Δ deviance	Δ d.f.	p	estimates of coefficients (mean \pm s.e.)
+ late body mass	9.82	1	0.002	0.006 \pm 0.002
+ clutch size	3.60	1	0.06	
+ manipulation	4.31	1	0.04	-5.29 \pm 2.61
+ manipulation \times clutch size	4.87	1	0.03	1.24 \pm 0.58

are inexperienced or of inferior health. The reduced nest success rate for reduced four-egg clutches may also be a response to the actual clutch size, i.e. a general increase in the propensity for nest desertion if clutch size is reduced to below four eggs. Additionally, the reduced nest success rate for reduced four-egg clutches may be related to the marginally higher incubation costs (mass loss) in this group. In starling (*Sturnus vulgaris*) it has been shown that cooling rates during recesses are probably higher for smaller clutch sizes, possibly indicating an increased cost of incubation (Reid *et al.* 2000). Broods from enlarged five-egg clutches were more often cared for by their mother. A large fraction of ducklings abandoned by their mother are adopted by other females, forming crèches (Bustnes & Erikstad 1991). Costs of brood tending are related to increased antipredator behaviour and leading young to food (Boyd 1953; Black & Owen 1989; Sedinger & Raveling 1990; Bustnes & Erikstad 1991); tending costs probably do not increase in larger broods since ducklings feed themselves, i.e. unshared investment (Lazarus & Inglis 1978, 1986), whereas the gain from tending is higher survival of ducklings cared for by their own mother (Bustnes & Erikstad 1991; Eadie & Lyon 1998). The results from the present study may support the hypothesis presented by Eadie & Lyon (1998, but see Pöysä *et al.* 1997), that crèching behaviour is driven by parental decisions where a larger fraction of parents care for young when brood size is large because of the higher cumulative fitness prospects of a large brood.

(c) Incubation investment and costs

Enlarging clutches of four eggs to five eggs resulted in no change in nest success and no increase in relative body

mass loss; however, hatch success declined relative to controls and reduced clutches, indicating that females with enlarged four-egg clutches did not increase their incubation investment at the cost of reduced hatch success of eggs. Female eiders with an original clutch size of five eggs, however, were apparently able to incubate an extra egg successfully by facultatively increasing relative mass loss, thereby maintaining hatch success of eggs. It should be noted, however, that differences in hatch success in eggs from original four- and five-egg clutches could be due to inherent quality differences between eggs originating from different clutch sizes. This is not controlled for in this study as eggs were swapped between nests of equal clutch size; however, hatch success did not differ between control nests of the two clutch sizes, indicating that such an effect may be negligible. Females with reduced five-egg clutches experienced reduced incubation costs (i.e. a lower relative body mass loss) without this affecting the hatch success of the clutch. By contrast other bird studies have shown that reduced hatch success is associated with larger clutches (Coleman & Whittall 1988; Briskie & Sealy 1989; Moreno *et al.* 1991; Siikamäki 1995). Some studies have reported increased mass loss (Moreno & Carlson 1989) and higher daily energy expenditure (Moreno *et al.* 1991) in response to clutch-size enlargements, whereas other studies conclude that no such increased mass loss occurs (Rohwer 1985; Harvey *et al.* 1989, but see Hepp *et al.* 1990). The present study is, to our knowledge, the first to document both incubation 'strategies' in the same species, depending on individual quality. The results indicate that incubation costs limit clutch size for females laying four eggs, as these females were not able to, or willing to, increase incubation investment when clutch size was

enlarged, possibly ensuring that return rate and future reproductive value is not reduced. By contrast, females laying five-egg clutches apparently are able to successfully hatch and rear for more young; hence other factors (i.e. lower quality of late laid eggs or longer nest period) seem to limit clutch size in the latter group of females. Manipulation did not affect the length of the incubation period in this study, indicating that increased incubation effort in enlarged five-egg clutches does not lead to a shorter incubation period. However, the length of the incubation period may be determined by the timing of incubation start that in the common eider is flexible and related to body mass (Hanssen *et al.* 2002), and hence not affected by the manipulation of clutch size, which occurred at least 5 days after incubation start.

The present study demonstrates the different potential for reproductive investment in individuals with different original clutch size—individuals apparently differing in quality. These quality differences seem to translate into two different ‘strategies’ for incubation investment, which may be termed restrictive and flexible for low- and high-quality individuals, respectively.

The authors thank H. Engebretsen, Ø. Holstad, H. Sandvik and T. Sigurdson for assistance in the field, and T. Tveraa, K. Lessells and an anonymous referee for valuable comments on the manuscript. The study was financed through grants from the Norwegian Research Council and the Directorate for Nature Management.

REFERENCES

- Ankney, C. D. & Afton, A. D. 1988 Bioenergetics of breeding Northern Shovelers: diet, nutrient reserves, clutch size, and incubation. *Condor* **90**, 459–472.
- Ankney, C. D. & MacInnes, C. D. 1978 Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* **95**, 459–471.
- Armstrong, T. & Robertson, R. J. 1988 Parental investment based on clutch value: nest desertion in response to partial clutch loss in dabbling ducks. *Anim. Behav.* **36**, 941–943.
- Arnold, T. W., Rohwer, F. C. & Armstrong, T. 1987 Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am. Nat.* **130**, 643–653.
- Baillie, C. D. & Milne, H. 1982 The influence of female age on breeding in the eider *Somateria mollissima*. *Bird Study* **29**, 55–66.
- Biebach, H. 1981 Energetic costs of incubation on different clutch sizes in starlings (*Sturnus vulgaris*). *Ardea* **69**, 141–142.
- Biebach, H. 1984 Effect of clutch size and time of day on the energy expenditure of incubating starlings (*Sturnus vulgaris*). *Physiol. Zool.* **57**, 26–31.
- Black, J. M. & Owen, M. 1989 Agonistic behaviour in Barnacle Goose flocks: assessment, investment and reproductive success. *Anim. Behav.* **37**, 199–209.
- Boyd, H. 1953 On encounters between wild White-fronted Geese in winter flocks. *Behaviour* **5**, 85–129.
- Briskie, J. V. & Sealy, G. S. 1989 Determination of clutch size in the Least Flycatcher. *Auk* **106**, 269–278.
- Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference. A practical information theoretic approach*. New York: Springer.
- Bustnes, J. O. & Erikstad, K. E. 1991 Parental care in the common eider (*Somateria mollissima*): factors affecting abandonment and adoption of young. *Can. J. Zool.* **69**, 1538–1545.
- Bustnes, J. O. & Erikstad, K. E. 1995 Brood abandonment in common eiders: a reply to H. Pöysä. *Can. J. Zool.* **73**, 1577–1578.
- Bustnes, J. O., Erikstad, K. E. & Bjørn, T. 2002 Body condition and brood abandonment in common eiders breeding in the high arctic. *Waterbirds* **25**, 63–66.
- Charlesworth, B. 1980 *Evolution in age-structured populations*. Cambridge University Press.
- Charnow, E. L. & Krebs, J. R. 1974 On clutch size and fitness. *Ibis* **116**, 217–219.
- Chaurand, T. & Weimerskirch, H. 1994a The regulation of short and long trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *J. Anim. Ecol.* **63**, 275–282.
- Chaurand, T. & Weimerskirch, H. 1994b Incubation routine, body mass regulation and egg-neglect in the blue petrel *Halobaena caerulea*. *Ibis* **136**, 285–290.
- Coleman, R. M. & Gross, M. R. 1991 Parental investment theory: the role of past investment. *Trends Ecol. Evol.* **6**, 404–406.
- Coleman, R. M. & Whittall, D. 1988 Clutch size and the cost of incubation in the Bengalese finch (*Lonchura striata* var. *domestica*). *Behav. Ecol. Sociobiol.* **23**, 367–372.
- Cooch, E. G., Lank, D. B., Dzubin, A., Rockwell, R. F. & Cooke, F. 1991 Body size variation in lesser snow geese: environmental plasticity in gosling growth rates. *Ecology* **72**, 503–512.
- Coulson, J. C. & Porter, J. M. 1985 Reproductive success of the Kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates, and parental quality. *Ibis* **127**, 450–466.
- De Steven, D. 1980 Clutch size, breeding success, and parental survival in the Tree Swallow (*Irodoprocne bicolor*). *Evolution* **34**, 278–291.
- Drent, R. 1975 Incubation. In *Avian biology*, vol. 5 (ed. D. S. Farner, J. R. King & K. C. Parkes), pp. 333–420. New York: Academic.
- Drent, R. H. & Daan, S. 1980 The prudent parent: energetic adjustment in avian breeding. *Ardea* **68**, 225–253.
- Eadie, J. McA. & Lyon, B. E. 1998 Cooperation, conflict, and creching behaviour in Goldeneye Ducks. *Am. Nat.* **151**, 397–408.
- Erikstad, K. E. & Tveraa, T. 1995 Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*? *Oecologia* **103**, 270–274.
- Erikstad, K. E., Bustnes, J. O. & Moum, T. 1993 Clutch-size determination in precocial birds: a study of the common eider. *Auk* **110**, 623–628.
- Erikstad, K. E., Fauchald, P., Tveraa, T. & Steen, H. 1998a On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* **79**, 1781–1788.
- Erikstad, K. E., Tveraa, T. & Bustnes, J. O. 1998b Significance of intraclutch egg-size variation in common eider: the role of egg size and quality of ducklings. *J. Avian Biol.* **29**, 3–9.
- Forbes, M. R. L., Clark, R. G., Weatherhead, P. J. & Armstrong, T. 1994 Risk-taking by female ducks: intra and inter-specific tests of nest defence theory. *Behav. Ecol. Sociobiol.* **34**, 79–85.
- Freckleton, R. P. 2002 On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J. Anim. Ecol.* **71**, 542–545.
- García-Berthou, E. 2001 On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *J. Anim. Ecol.* **70**, 708–711.
- Haftorn, S. & Reinertsen, R. E. 1985 The effect of temperature and clutch size on the energetic cost of incubation in a free-living blue tit *Parus caeruleus*. *Auk* **102**, 470–478.
- Hanssen, S. A., Engebretsen, H. & Erikstad, K. E. 2002 Incubation start and egg size in relation to body reserves in the common eider. *Behav. Ecol. Sociobiol.* **52**, 282–288.

- Harvey, W. F., Hepp, G. R. & Kennamer, R. A. 1989 Body mass dynamics of wood ducks during incubation: individual variation. *Can. J. Zool.* **67**, 570–574.
- Heaney, V. & Monaghan, P. 1995 A within-clutch trade-off between egg production and rearing in birds. *Proc. R. Soc. Lond. B* **261**, 361–365.
- Hepp, G. R., Kennamer, R. A. & Harvey, W. F. 1990 Incubation as a reproductive cost in female wood ducks. *Auk* **107**, 756–764.
- Inglis, J. R. 1977 The breeding behaviour of the pink-footed goose: behavioural correlates of nesting success. *Anim. Behav.* **25**, 747–764.
- Jennions, M. D. & Polakow, D. A. 2001 The effect of partial brood loss on male desertion in a cichlid fish: an experimental test. *Behav. Ecol.* **12**, 84–92.
- Jones, G. 1987 Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experimental study using precision electronic balance. *J. Anim. Ecol.* **56**, 229–245.
- Kehoe, F. P. 1989 The adaptive significance of crèching behaviour in the white-winged scoter (*Melanitta fusca deglandi*). *Can. J. Zool.* **67**, 406–411.
- Kilpi, M., Öst, M., Lindstrom, K. & Rita, H. 2001 Female characteristics and parental care mode in the crèching system of eiders, *Somateria mollissima*. *Anim. Behav.* **62**, 527–534.
- Korschgen, C. E. 1977 Breeding stress of female eiders in Maine. *J. Wildl. Manage.* **41**, 360–373.
- Lack, D. 1947 The significance of clutch size. *Ibis* **89**, 302–352.
- Lack, D. 1968 *Ecological adaptations for breeding in birds*. London: Methuen.
- Lazarus, J. & Inglis, I. R. 1978 The breeding behaviour of the Pink-footed Goose: parental care and vigilant behaviour during the fledging period. *Behaviour* **65**, 62–88.
- Lazarus, J. & Inglis, I. R. 1986 Shared and unshared parental investment, parent-offspring conflict and brood size. *Anim. Behav.* **34**, 1791–1804.
- Lepage, D., Gauthier, G. & Desrochers, A. 1998 Larger clutch size increases fledging success and offspring quality in a precocial species. *J. Anim. Ecol.* **67**, 210–216.
- Lessells, C. M. 1986 Brood size in Canada geese: a manipulation experiment. *J. Anim. Ecol.* **55**, 669–689.
- Lindén, M. & Möller, A. P. 1989 Cost of reproduction covariation of life history traits in birds. *Trends Ecol. Evol.* **4**, 367–371.
- McNamara, J. N. & Houston, A. I. 1996 State-dependent life histories. *Nature* **380**, 215–221.
- Monaghan, P. & Nager, R. 1997 Why don't birds lay more eggs? *Trends Ecol. Evol.* **12**, 270–274.
- Monaghan, P., Uttley, J. D., Burns, M. D., Thaine, C. & Blackwood, J. 1989 The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradiaea*. *Ardea* **80**, 71–82.
- Moreno, J. & Carlson, A. 1989 Clutch size and the costs of incubation in the pied flycatcher *Ficedula hypoleuca*. *Ornis Scand.* **20**, 123–128.
- Moreno, J., Gustafsson, L., Carlson, A. & Pärt, T. 1991 The cost of incubation in relation to clutch-size in the collared flycatcher *Ficedula albicollis*. *Ibis* **133**, 186–193.
- Munro, J. & Bedard, J. 1977 Crèche formation in the common eider. *Auk* **94**, 759–771.
- Nisbet, I. C. T., Winchell, J. M. & Heise, E. A. 1984 Influence of age on the breeding biology of common terns. *Colonial Waterbirds* **7**, 116–126.
- Olsson, O. 1997 Clutch abandonment: a state dependent decision in king penguins. *J. Avian Biol.* **28**, 264–267.
- Parker, H. & Holm, H. 1990 Patterns of nutrient and energy expenditure in female common eiders nesting in the high Arctic. *Auk* **107**, 660–668.
- Perrins, C. M. & Moss, D. 1975 Reproductive rates in the great tit. *J. Anim. Ecol.* **44**, 695–706.
- Pettifor, R. A. 1993 Brood-manipulation experiments. II. A cost of reproduction in blue tits (*Parus caeruleus*)? *J. Anim. Ecol.* **62**, 145–159.
- Pettifor, R. A., Perrins, C. M. & McCleery, R. H. 1988 Individual optimization of clutch size in great tits. *Nature* **381**, 565.
- Pettifor, R. A., Perrins, C. M. & McCleery, R. H. 2001 The individual optimization of fitness: variation in reproductive output, including clutch size, mean nestling mass and offspring recruitment, in manipulated broods of great tits *Parus major*. *J. Anim. Ecol.* **70**, 62–79.
- Pöysä, H., Virtanen, J. & Milonoff, M. 1997 Common golden-eyes adjust maternal effort in relation to prior brood success and not current brood size. *Behav. Ecol. Sociobiol.* **40**, 101–106.
- Reid, J. M., Monaghan, P. & Ruxton, G. D. 2000 Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proc. R. Soc. Lond. B* **267**, 37–41. (DOI 10.1098/rspb.2000.0963.)
- Rohwer, F. C. 1985 The adaptive significance of clutch size in prairie ducks. *Auk* **102**, 354–361.
- Sæter, B. E., Andersen, R. & Pedersen, H. C. 1993 Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the Antarctic petrel *Thalassoica arctica*. *Behav. Ecol. Sociobiol.* **33**, 147–150.
- Sargent, R. C. 1997 Parental care. In *Behavioural ecology of teleost fishes* (ed. J.-G. J. Godin), pp. 292–315. Oxford University Press.
- Sedinger, J. S. & Raveling, D. G. 1990 Parental behaviour of Cackling Canada Geese during brood rearing; division of labour within pairs. *Condor* **92**, 174–181.
- Siikamäki, P. 1995 Are large clutches costly to incubate—the case of the Pied Flycatcher? *J. Avian Biol.* **26**, 76–80.
- Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.
- Tinbergen, J. M. & Both, C. 1999 Is clutch size individually optimized? *Behav. Ecol.* **10**, 504–509.
- Tinbergen, J. M. & Daan, S. 1990 Family planning in the great tit (*Parus major*): optimal clutch size as integration of parent and offspring fitness. *Behaviour* **114**, 161–190.
- Veléz, M. J., Jennions, M. D. & Telford, S. R. 2002 The effect of an experimental brood reduction on male desertion in the Panamanian blue acara cichlid *Aequidens coeruleopunctatus*. *Ethology* **108**, 331–340.
- Watson, M. D., Robertson, G. J. & Cooke, F. 1993 Egg laying time and laying interval in the common eider. *Condor* **95**, 869–878.
- Weimerskirch, H., Chastel, O. & Ackermann, L. 1995 Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav. Ecol. Sociobiol.* **36**, 11–16.
- Williams, G. C. 1966 Natural selection, the cost of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**, 687–690.
- Winkler, D. W. & Walters, J. R. 1983 The determination of clutch size in precocial birds. *Curr. Ornithol.* **1**, 33–68.
- Yoccoz, N. G., Erikstad, K. E., Bustnes, J. O., Hanssen, S. A. & Tveraa, T. 2002 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. *J. Appl. Stat.* **29**, 57–64.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.