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Original Article

Interactions between lay date, clutch size, and postlaying energetic needs in a capital breeder

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The condition-dependent model of optimal clutch size assumes body reserves required to initiate egg production include those for subsequent breeding phases. The threshold is expected to be similar among individuals, and hence postlaying condition should be independent of clutch size and lay date. Alternatively, the cost of incubation hypothesis predicts that females laying larger clutches should secure extra resources for incubation, and the expected fitness hypothesis suggests females adjust their condition according to the anticipated fitness benefits of the clutch. In these 2 cases, postlaying condition is predicted to be positively related to clutch size. We tested these predictions in common eider (*Somateria mollissima*), a precocial bird that produce eggs mostly from stored lipids and partly from endogenous proteins and rely extensively on reserves to incubate. We collected females at incubation onset and measured body condition indicators. Clutch size (number of eggs laid or number found in the nest at incubation onset) was not related to postlaying fat stores but females that laid fewer eggs maintained extra protein reserves. Timing of breeding was not related to postlaying body mass or protein reserves, whereas lay date's relationship with fat stores varied annually. Our results are generally consistent with the condition-dependent model and indicate variation in postlaying condition is mostly driven by factors other than clutch size and lay date. These data are inconsistent with the cost of incubation and the expected fitness hypotheses and suggest body store differences at incubation onset are mostly caused by environmental conditions encountered by laying females. *Key words:* breeding strategy, common eider, condition dependent, resource allocation, *Somateria mollissima.* *[Behav Ecol 22:162–168 (2011)]*

Reproduction involves major life-history trade-offs and parents should invest energy in order to maximize their fitness (Stearns 1992). In birds, strategic parental decisions regarding the number of eggs laid may act during 3 distinct phases: egg production, incubation, and brood rearing (Monaghan and Nager 1997; Nager 2006). In precocial species, it is generally recognized that clutch size limitation can operate at the egg-laying stage (Lack 1967; Bêty et al. 2003). However, the energetic investment in egg formation could potentially interact with subsequent investments in incubation and brood rearing (Moreno and Sanz 1994; Erikstad and Tveraa 1995; Kilpi and Lindstrom 1997; Reid et al. 2000; Bustnes et al. 2002). Although such interactions in energetic allocation could be especially critical in capital breeders (i.e., birds using stored resources to finance reproduction), they are rarely investigated within a single framework.

Rowe et al. (1994) proposed a model where individual optimal combinations of clutch size and lay date depended on prelaying body condition, rate of condition gain, and breeding ground arrival date. The model predicts a seasonal decline in clutch size and is essentially based on the outcome of a conflict between the advantage of early breeding (greater egg value due to increased juvenile survival and recruitment) and the advantage of delayed breeding (increase in body condition through energy acquisition and hence higher potential clutch size). According to this condition-dependent model, a female arriving late at the breeding site or with poor body condition should strategically produce a smaller clutch in order to maximize her reproductive success during the breeding season (Rowe et al. 1994; Bêty et al. 2003). The model assumes that a minimum condition threshold must be reached to produce eggs and that this threshold should include the energy requirement needed to incubate eggs and rear young (Rowe et al. 1994). The basic model presumes that the condition threshold does not vary over time (i.e., independent of lay date) and is not affected by clutch size (i.e., no interaction between energetic investment in egg formation and energy requirement needed for subsequent breeding phases). Once the minimum threshold is exceeded, females that reach the optimal combination of lay date and clutch size in good condition should not save extra body reserves for subsequent breeding stages, instead they should lay more eggs than females which reach the optimal combination in poor condition (Figure 1). Consequently, postlaying condition should be independent of clutch size or lay date (Figure 1).

Optimal breeding decisions could, however, involve a flexible threshold condition associated with current reproductive effort and interactions between the allocation of body reserves in egg formation, incubation, and parental care. Females producing larger clutches might experience a higher cost of incubation than females laying smaller broods (Thomson et al. 1998; Hanssen et al. 2005; de Heij et al. 2006). The cost of incubation hypothesis predicts that females laying larger clutches should secure extra resources to compensate for higher costs of incubation and start incubating in better body condition (Erikstad et al. 1993; Erikstad and Tveraa 1995). Alternatively, the expected fitness hypothesis proposes females adjust their postlaying condition according to the anticipated fitness benefits of the clutch, which is typically

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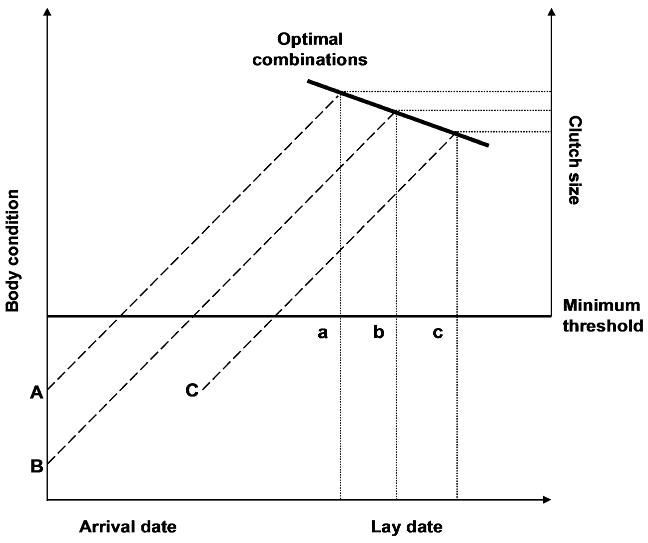

Figure 1
Graphical representation of the condition-dependent model of clutch size and lay date (modified from Rowe et al. 1994). Letters represent individuals with different initial body condition or arrival dates on breeding grounds (upper case) and illustrate the predicted postlaying condition (lower case). Dashed lines represent the increase in body condition before egg laying; the thick line illustrates the optimal combinations of clutch size and lay dates assuming a trade-off between the costs (decreasing offspring value) and the benefit (increasing condition and hence clutch size) of a delay in lay date; dotted lines connect optimal lay dates and clutch sizes for individuals reaching the optimal at different times. Before producing a clutch, individuals must first reach the minimum threshold condition, which should include the energy needed to incubate and rear the eggs.

higher for large clutches. In this case, females laying more eggs should start incubating in better condition in order to increase the likelihood of 1) successfully completing incubation (higher condition leads to increased nest attendance and lower nest predation risk; Wiebe and Martin 2000; Criscuolo et al. 2002; Gorman and Nager 2003) and 2) successfully rearing their young (higher condition reduces the likelihood of brood abandonment; Kilpi et al. 2001; Bustnes et al. 2002; Ost et al. 2003; Robinson et al. 2005; Green et al. 2007). Thus, the cost of incubation hypothesis and the expected fitness hypothesis both predict a positive relationship between postlaying condition and clutch size.

We investigated the relationships between energetic allocation of body reserves in egg production and the body reserves available for subsequent breeding phases for common eider ducks (*Somateria mollissima*, here after eider) nesting in the Canadian Arctic. Eiders are precocial birds that produce eggs mostly from stored lipids and partly from endogenous proteins (Sénéchal et al. 2011) and rely extensively on body reserves to incubate (Bottitta et al. 2003). Females in better body condition during incubation show higher nest attendance and are less vulnerable to nest predation (Hanssen et al. 2002; Andersson and Waldeck 2006). Parental care is generally shared among individuals in a multifemale brood-rearing coalition. However, mothers with greater body reserves at hatching are more likely to care for their ducklings and are less likely to give them to other females (Ost et al. 2003, 2008), which increases the survival prospects of juveniles and in turn the reproductive success of the mother (Ost and Back 2003). Therefore, eiders appear to be a good model species to examine potential interactions between the investment in egg production, incubation, and parental care. Based on a 3-year study, we tested whether individual variation in endogenous reserves at incubation onset were 1) driven by individual investment in egg formation and 2) affected by the timing of breeding. We specifically tested predictions derived from the condition-dependent model as well as the cost of incubation and the expected fitness hypotheses.

MATERIALS AND METHODS

Study design

This study was conducted from 2002 to 2004 on Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada (lat 64°02′N, long 81°47′W), where up to 8000 eider pairs breed annually. Nests were found during the early laying period, and females were trapped on their nest at the end of laying (i.e., sitting on a full clutch for 24–48 h: $n = 14$, 16, and 17 in 2002, 2003, and 2004, respectively). Each year, we attempted to trap females regularly throughout the laying period (late-June to late-July). Females were euthanized using halothane and dissected within 24 h following Jamieson et al. (2006). We took morphometric measurements (tarsus, total head, and wing chord lengths; ±0.01 mm) and weighed total body mass (food items and eggs were subtracted from gizzards and oviducts, respectively) using a spring scale (±10 g). We also weighed wet masses of the abdominal fat pad (without intestinal fat), right breast muscle (pectoralis and supracoracoid), and total right leg mass (including all muscles that originate at or insert in the femur or tibiotarsus bones) using electronic scale (±0.1 g). These proxies are strongly correlated with total endogenous reserves in wintering female eiders and mostly reflect either protein (breast and leg) or fat reserves (abdominal fat and total body mass; Jamieson et al. 2006). Clutch size, defined as the total number of eggs laid by a female, was determined by the number of postovulatory follicles. This likely represents the actual number of eggs produced during a sole breeding attempt for most females as renesting is rare in the study colony (the estimated proportion of breeding females laying 2 clutches in a given summer is below 2%, $n = 188$ individuals; Bêty J and Gilchrist G, unpublished data). The number of eggs found in the nest at the onset of incubation was also recorded (i.e., the number of eggs within the nest when a female was trapped). Partial egg loss is predominantly caused by herring gulls (*Larus argentatus*) predation (Allard and Gilchrist 2002). The beginning of incubation was validated by the absence of remaining developing follicles. Lay date was back-calculated according to the number of postovulatory follicles, assuming a 28-h interval between laid eggs (Watson et al. 1993).

Statistical analysis

We used measurements of the right wing chord length, right tarsus length, and total head length to run a principal component analysis and adjusted, when necessary, endogenous reserve masses to body size (Sedinger et al. 1997). The first principal component (PC1) explained 46% of the variation and eigenvectors were all positive, ranging from 0.18 to 0.69. PC1 scores were used as an integrated index of individual structural size. General linear regression models were used to examine the relationship between the PC1 and the different proxies of endogenous reserves. As individual variation in body mass, abdominal fat, and leg was partly explained by PC1 ($P \leq 0.07$), we adjusted those 3 dependent variables with body size using residuals from the regression models (i.e., size-corrected values; Schulte-Hostedde et al. 2005).

We used least-squares general linear models to examine the influence of lay date, clutch size, and year on postlaying

Table 1

Interannual variation in lay date, clutch size (based on postovulatory follicle counts), and postlaying body reserves of arctic-nesting common eiders collected from Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada

	2002 ($n = 14$)	2003 ($n = 16$)	2004 ($n = 17$)
Breeding information			
Lay date^{a}	178.0 (171–190)^{A}	181.5 (170–201)^{AB}	185.0 (170–195)^{B}
Clutch size^{b}	4.1 ± 0.2^{A}	3.9 ± 0.2^{A}	3.9 ± 0.2^{A}
Body reserves (g)^{b}			
Total body weight	1691.1 ± 20.9^{A}	1777.0 ± 27.0^{B}	1761.1 ± 19.0^{AB}
Right breast muscles	144.4 ± 3.7^{A}	169.3 ± 3.7^{B}	171.0 ± 2.9^{B}
Abdominal fat	21.6 ± 1.1^{A}	26.6 ± 2.0^{A}	22.3 ± 1.8^{A}
Right leg	83.4 ± 1.5^{A}	89.8 ± 1.6^{B}	88.5 ± 1.2^{B}

Years accompanied by different letters differed significantly ($\alpha = 0.025$, Bonferroni correction).

[a] Median (5th–95th percentile), expressed in Julian date, January 1 = 1.

[b] Mean ± standard error.

abdominal fat, leg, breast muscles, and body masses. To account for annual variation, lay dates were expressed as relative lay date (i.e., deviation from the yearly median). All possible interactions between explanatory variables (clutch size, lay date, and year) were tested and sequentially removed according to their P values (type III sum of squares). Annual differences in endogenous reserves and clutch sizes were estimated with one-way analysis of variance, and annual lay dates were compared with a nonparametric median one-way analysis. Post hoc comparisons of least mean squares were performed with Tukey–Kramer pairwise tests, and we used the Dunn method of pairwise nonparametric comparisons to compare median lay dates. Residuals from our models indicated no strong violation of the assumptions of normality (all $P > 0.05$; Shapiro–Wilk test) and homogeneity of variance (all $P > 0.05$, except for body mass: $P = 0.01$, due to 2 heavy females captured in 2003; Levene's test). The covariates lay date and clutch size were correlated, but the relationship was not strong enough to generate collinearity in statistical models (following Quinn and Keough 2002). All statistical analyses were performed with the software SAS V 9.1 (SAS Institute 2002–2003), and significance levels were set at 0.05 unless other levels are specified.

RESULTS

The median lay date of collected birds varied annually ($\chi^2 = 7.28$, degrees of freedom [df] = 2, $P = 0.03$), whereas average clutch size was similar between years ($F = 0.38$, df = 2, $P = 0.69$; Table 1). Average postlaying abdominal fat did not vary significantly between years, but females showed lower breast muscles, leg, and total body masses in 2002 (Tables 1 and 2).

Partial nest depredation during laying was found for 28 females (60%; the number of postovulatory follicles was higher than numbers of eggs found in nests). Evidence of nest parasitism (more eggs present in the nest than the number of postovulatory follicles) was detected for only 2 females (4%). Late breeders tended to lay smaller clutches but, interestingly, the seasonal decline was stronger when using the number of eggs found in the nests at incubation onset ($r = -0.49$, $P < 0.001$) than the number of postovulatory follicles ($r = -0.26$, $P = 0.07$). As we are confident in our postovulatory follicle counts, the difference likely resulted from a higher partial predation rate in late breeders. Estimates of postlaying body reserves did not differ between females with intact or partially depredated clutches (all $P > 0.50$). Therefore, we combined all females in subsequent analyses.

Postlaying body condition was slightly lower in females that laid larger clutches (negative slopes for all proxies of endogenous reserves), but the relationships were significant only for total body mass and breast muscles (Table 2 and Figure 2; effect of clutch size on: abdominal fat, $F_{1,47} = 0.14$, $P = 0.71$; leg, $F_{1,45} = 1.30$, $P = 0.26$). None of these relationships were significant when using the number of eggs found in the nest at the start of incubation (all $P > 0.50$).

Timing of breeding was systematically related to only one body reserve estimate, with late breeders having significantly heavier postlaying leg mass than earlier breeders (Figure 3). Lay date also had a significant effect on postlaying abdominal fat, but the strength and the direction of the relationship (positive or negative) varied between years (Figure 3). In 2002, late breeders had higher postlaying fat reserves than early breeders (slope ± 95% confidence interval [CI] = 0.51 ±

Table 2

Relationship between lay date or clutch size (based on postovulatory follicle counts) and postlaying endogenous reserves of common eider females collected in 2002, 2003, and 2004 from Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada

	Variable	Partial r^2	Coefficient estimates	SE	df	F	P
Body mass^{a}	Year	0.15			2	3.4	0.04
	Clutch size	0.08	−31.8	15.1	1	4.4	0.04
Abdominal fat^{a}	Year	0.10			2	2.6	0.09
	Lay date	0.00	−0.5	0.2	1	0.2	0.67
	Lay date × year	0.15			2	4.0	0.03
Breast muscles	Year	0.45			2	17.5	<0.0001
	Clutch size	0.05	−4.6	2.3	1	4.0	0.05
Leg^{a}	Year	0.19			2	7.1	0.002
	Lay date	0.22	0.4	0.1	1	16.0	<0.001

Covariates and interactions (denoted by ×) were reported only when significant ($P < 0.05$); SE, standard error.

[a] Corrected for structural size, see MATERIALS AND METHODS.

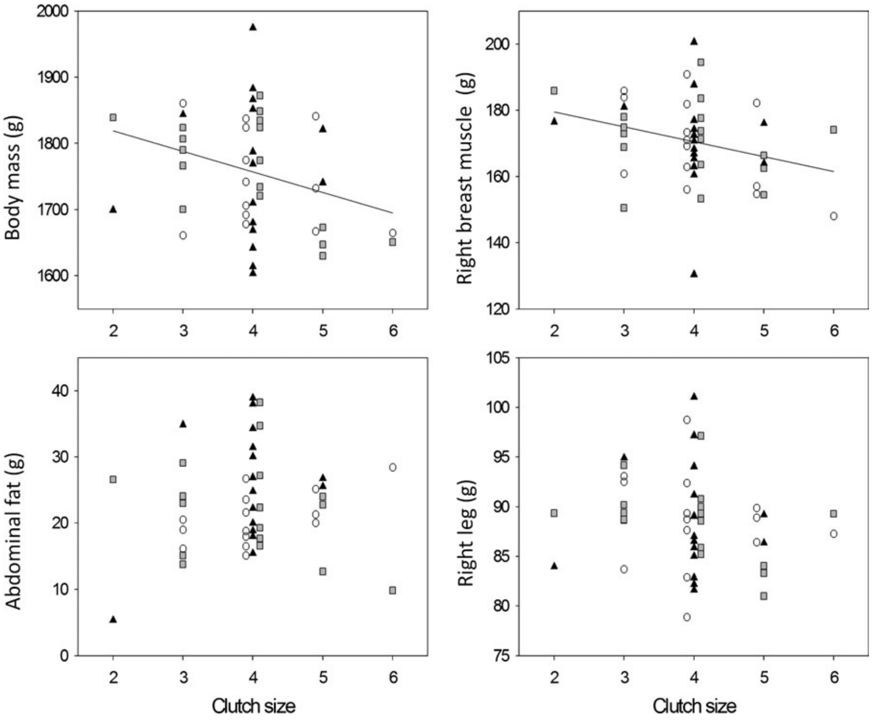

Figure 2
Relationships between clutch size (based on postovulatory follicle counts) and endogenous reserves of postlaying female common eiders from Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada. Values were corrected for the effect of other variables, when significant (Table 2). Circles, triangles, and squares represent, respectively, data from 2002, 2003, and 2004. Some points are offset in order to display full sample size.

0.16), whereas the opposite relationship was observed in 2004 (slope ± 95% CI = −0.51 ± 0.24). Interestingly, no effect was detected in 2003 (slope ± 95% CI = 0.19 ± 0.26), which corresponded to a season with average breeding phenology (Table 1). Total body mass and breast muscles did not vary with timing of breeding (Table 2 and Figure 3; effect of lay date on: body mass, $F_{1,47} = 0.08$, $P = 0.77$; breast muscles, $F_{1,47} = 1.63$, $P = 0.21$).

DISCUSSION

Our results allow us to generate 4 main conclusions regarding timing of breeding, egg production, and postlaying energetic condition. First, we reject the cost of incubation hypothesis, which predicted that females laying larger clutches should have secured extra resources to compensate for higher costs of incubation. Indeed, we found nonsignificant or weak negative relationships between postlaying body reserve estimates

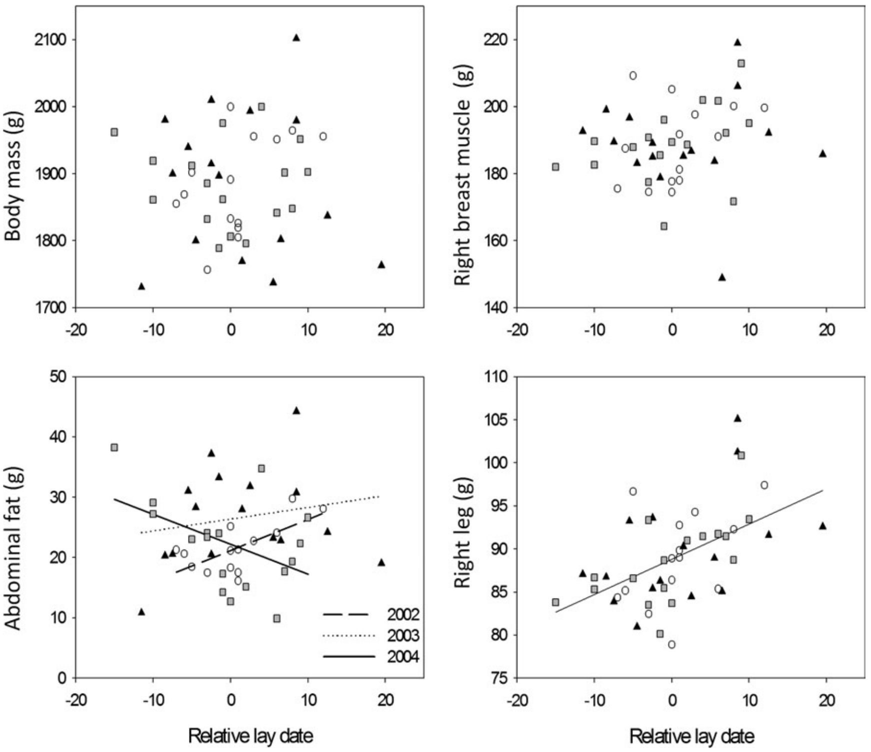

Figure 3
Relationships between lay date (relative to the yearly median) and endogenous reserves of postlaying female common eiders from Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada. Values were corrected for the effect of other variables, when significant (Table 2). Circles, triangles, and squares represent, respectively, data from 2002, 2003, and 2004. Some points are offset in order to display full sample size.

and clutch size. Second, we did not find that females which laid earlier or larger clutches started incubating in better condition (which would allow them to increase the likelihood of successfully incubating and rearing the young). We thus reject the expected fitness hypothesis. Third, after controlling for clutch size, it appears that individual timing of breeding can affect postlaying body nutritional reserves, but the relationships (positive or negative) may differ depending on the environmental conditions (early or late breeding season). Finally, our data are generally consistent with predictions of the condition-dependent model and indicate that the large individual variation in endogenous reserves at the onset of incubation is mostly driven by factors other than clutch size and lay date in arctic-nesting common eiders. We suggest that such variation is likely caused by the unpredictable foraging and environmental conditions experienced by laying females. We will discuss these conclusions in turn, as well as potential alternative mechanisms that could explain our results.

Clutch size and cost of incubation

The condition-dependent model predicts that females reaching the optimal combination of lay date and clutch size in better body condition should lay more eggs rather than saving body stores for incubation and brood rearing (Rowe et al. 1994; Figure 1). Our results are generally consistent with this prediction (i.e., postlaying fat reserves were independent of clutch size), but nonetheless suggest that females which invested less in clutch production had higher postlaying protein reserves. Proteins are known to be one of the main limiting nutrient during egg formation for several bird species (Meijer and Drent 1999; Klaassen 2003). We found at our study site that most egg proteins are derived from exogenous nutrients acquired during egg formation, whereas body reserves contribute to a lesser extent (maximum possible endogenous protein contribution of 40%; Sénéchal et al. 2011). Based on an average egg mass of 104 g (Parker and Holm 1990) and a dry protein content of 20% (Williams 1999), the mean body mass decrease of 31.8 g per egg observed in postlaying females could be partly explained by the endogenous investment in egg formation (Table 2). Females that laid small clutches may have started egg production with similar protein reserves compared with females laying large clutches, which allowed them to finish laying in better condition. Alternatively, females that laid large clutches may have started egg production in better condition but were not able to acquire enough exogenous nutrients to cover the full costs of laying their extra eggs. Even if the real start of incubation (i.e., embryonic development) does not appear to be related to clutch size in eiders (Hanssen et al. 2002), most precocial birds tend to increase the time spent at the nest with the progression of the laying period (Poussart et al. 2000; Andersson and Waldeck 2006). Therefore, female eiders laying large clutches may have spent more time at their nest during the laying period, which could have lowered their foraging rate and increased endogenous energetic investment during egg formation. Higher energetic investment may negatively affect immune function of nesting eider females (see Hanssen et al. 2005). Although such effects could have few, if any, fitness consequences under favorable environmental conditions, potential cascading effects on future fitness prospects can occur when conditions are unfavorable (e.g., increase mortality in the presence of a highly virulent pathogen; see Descamps et al. 2009). Clearly, further investigations are needed to identify the exact mechanisms leading to, and the fitness consequences of, lower postlaying body stores in eiders laying large clutches.

Our results do not support previous studies that suggest female eiders which produce large clutches are in better body condition at the start of incubation compared with females producing small clutches (Erikstad et al. 1993; Erikstad and Tveraa 1995). Erikstad and Tveraa (1995) also found no effect of clutch size on body condition measured during the early incubation period (typically at day 5). They nonetheless argued, based on increasing incubation costs with clutch size, that females producing large clutches were in better body condition at the start of incubation than females producing small clutches. Our study design allowed us to better test such hypothesis because 1) we measured body condition at the very beginning of incubation (on the first day in most cases), 2) we simultaneously tested for seasonal and annual variation, and 3) we used various proxies of body condition. Although energy expenditure is higher in eiders incubating large clutch size (20.5% mass loss for females incubating 6 eggs vs. 18% for females incubating 3 eggs from day 5 to day 20 in the incubation period: Hanssen et al. 2005), the extra energetic investment appears relatively modest. This may explain why female eiders producing large clutches do not strategically save endogenous reserves during laying to cover the extra incubation costs.

Kilpi et al. (2001) found that body condition at hatching was not related to clutch size or timing of breeding. They also suggested that optimal female brood abandonment decisions would be more likely driven by energetic considerations rather than the value of the brood (given eiders long lifetime, numerous breeding opportunities, and small clutch size variation). Indeed, females with greater body stores at hatching are less likely to give their ducklings to other females (Ost et al. 2003, 2008). Our findings clearly showed that birds laying more eggs do not save extra endogenous reserves during egg production to increase the likelihood of successful incubation and brood rearing. Assuming the large individual variation we observed in postlaying body stores generates variation in female posthatching energetic status, foraging and environmental conditions experienced by a laying female could thus affect its body stores at hatching and hence the likelihood of brood abandonment.

Timing of breeding and interannual variations

Our results showed that late breeders and early breeders typically start incubation with similar breast muscle and total body masses (as predicted by the condition-dependent model), but late breeders systematically had heavier leg mass, and either greater or smaller fat reserves, depending on year. We suggest that seasonal variation in leg mass may reflect differences in the main prey consumed by eiders at our study site. Females arriving early at the breeding site feed extensively on amphipods found in shallow water at river mouths and along shorelines during their prelaying period (Sénéchal et al. 2011) as extensive ice cover restricts access to benthic invertebrates such as clams and limpets at this time. As the season progresses and ice cracks appear, females can increase their consumption of preferred prey and dive in deeper water to acquire exogenous resources critically needed for egg formation (Sénéchal et al. 2011). As eiders use foot propulsion to forage on the sea floor (Heath et al. 2006), late breeders could benefit from stronger leg muscles. As postlaying total body mass was similar between early and late breeders, the difference in leg mass may simply reflect an energy reallocation in breeding females (i.e., an adjustment of organ sizes to ecological conditions), as detected in other species (e.g., European starlings: Vézina and Williams 2003).

Moreover, annual differences in seasonal trends of postlaying fat reserves may reveal the role of environmental factors encountered by females during egg formation. However, as total body mass was similar between early and late breeders in all years (indicating similar level of total body reserves;

Figure 3), we must be cautious with our interpretation. In 2002, early breeders showed lower abdominal fat reserves at the beginning of incubation compared with late breeders, whereas the opposite trend was observed in 2004. Early breeders may have started egg production in relatively lower body condition in 2002 or may have invested more fat reserves in egg production than in 2004. The 2002 summer was characterized by an early ice breakup, and a greater investment of fat reserves in egg production could have been advantageous for early breeding females as egg value (juvenile survival prospect) is typically higher early in the season (Love et al. 2010). Moreover, endogenous reserves of females were generally smaller in 2002 (Table 1), which may indicate that birds faced more difficult wintering and/or migration conditions that year (Lehikoinen et al. 2006). Late-breeding females may have benefited from important open water areas near the colony and higher food resource availability before and during laying could have allowed them to save some endogenous fat (contrary to early nesters). In contrast, the 2004 breeding season was particularly late, with thicker ice and snow cover near the breeding site during the egg formation period. Late-breeding females apparently could not take advantage of higher food availability near the colony and may have used extra endogenous fat reserves to produce their eggs early enough during the breeding season. Such seasonal pattern has been shown in geese and eiders using stable isotopes (Gauthier et al. 2003; Sénéchal et al. 2011).

Postlaying body condition: strategic adjustment or good fortune?

There is growing evidence that environmental factors can play an important role in breeding trade-offs such as nest site selection (Robertson 1995), nest desertion (Bourgeon et al. 2006), yolk hormone concentration (Love et al. 2009), and immune function (Descamps et al. 2009). A small proportion of the variation in the postlaying body condition of females appears to be explained by timing of breeding and clutch size, suggesting that it may be more influenced by environmental factors such as food availability, egg predation rates (during laying), nest site quality, and weather conditions (during or before the breeding season). Female intrinsic quality or previous experience may be another source of variation in laying behavior and postlaying condition. For instance, Hanssen et al. (2002) found that female eiders that start incubation earlier in the laying sequence are in poorer condition at the onset of incubation. However, factors generating such behavioral differences remain unknown.

Following the optimal decision curve of the condition-dependent model, a female in better prelaying body condition is predicted to increase her fitness by laying extra eggs rather than keeping reserves for subsequent reproductive stages such as incubation and brood rearing (Figure 1). Our results generally support this rationale, although females that laid fewer eggs apparently had extra protein reserves available at the end of laying. Based on small sample size, Spaans et al. (2007) reached a similar conclusion in dark-bellied Brent Geese (*Branta bernicla bernicla*). Finally, we conclude that there is no strategic adjustment of postlaying body condition associated to higher costs of incubation or higher reproductive value of larger broods in common eiders.

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