Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size

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Summary

1. Optimality theory predicts that both timing of arrival and arrival state on the breeding area will determine reproductive timing and investment in migratory organisms. We tested this idea using a condition-dependent individual optimization model (*Ardea* **68**, 1980, 225 and *The American Naturalist* **143**, 1994, 698) in common eider ducks through descriptive data, path analyses and experimental manipulation.

2. Our results support the causal pathways drawn from the optimization model indicating that individuals adjust their reproductive decisions as a function of their arrival date and body condition at arrival.

3. Independent of body condition, early-arriving females had a longer pre-laying period, but still initiated their nests earlier, and produced larger clutches than late-arriving birds. Independent of arrival date, females in good condition laid earlier than those in poor condition. Manipulation of pre-laying female body condition confirmed that the relationship between condition and laying date was causal.

4. Female common eiders appear to optimize reproductive decisions in response to both their external (i.e. environmental conditions affecting the egg-value) and internal (i.e. body condition) states. These adjustments seem to minimize the fitness costs of reproduction, in which higher clutch size is not associated with an apparent lower survival or future breeding probability.

5. Our study emphasizes the importance of (i) simultaneously considering the timing of migration, the state of individuals and the seasonal change in egg-value to understand clearly birds' breeding decisions and (ii) appreciating the potential proximate and ultimate factors explaining why some individuals delay breeding and/or produce small clutches.

Key-words: common eider, cost of reproduction, d-sep tests, egg value, individual optimization, path analysis, pre-laying body condition, *Somateria mollissima,* state-dependent reproduction

Introduction

Two of the most important decisions for seasonally breeding organisms are when to initiate reproduction and how many offspring to produce. For example, in bird species living in seasonal environments, hatching success and offspring post-hatching survival are generally higher for individuals that reproduce early compared to late (e.g. Perrins 1970), typically because the environment is less favourable later in the season (Verhulst & Nilsson 2008). Such environmental changes during a given breeding season lead

to changes in egg-value, with eggs laid early in the season being of greater value (i.e. having a higher recruitment probability) than eggs laid late in the season (Lepage, Gauthier & Menu 2000). Parental characteristics, such as body condition, are also expected to affect reproductive output. Indeed, as producing an offspring is energetically demanding, the number and quality of eggs or offspring produced and the parental provisioning or parental care can be affected by parental body condition (e.g. Karell *et al.* 2008; Öst, Smith & Kilpi 2008). Theoretically then, there should be a conflict between the advantages of breeding early to maximize the value of the eggs vs. the advantages of delaying breeding to improve parental body condition and

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increase energetic allocation to reproduction (i.e. to lay a larger clutch or increase the ability to raise a larger brood). In a state-dependent life history framework, individuals breeding in seasonal environments are expected to adjust their breeding decisions (timing and investment) to their external (i.e. the environment) and internal (i.e. their condition) states (sensu McNamara & Houston 1996; McNamara 1998). In the case of migratory organisms, reproductive timing and investment should thus be determined by the seasonal variation in egg-value, the timing of migration (and then the date of arrival at the breeding grounds) and the body condition at arrival.

This idea was first proposed by Drent & Daan (1980) and then formulized by Rowe, Ludwig & Schluter (1994) into a dynamic model that predicts the optimal laying date and clutch size as a function of arrival date and body condition at arrival. To obtain an accurate understanding of what determines reproductive decisions in seasonal breeding birds requires concurrent consideration of arrival date, body condition at arrival, laying date and clutch size (see Bêty, Gauthier & Giroux 2003 for an example with snow geese). As all of these variables may affect one another reciprocally, and appear in the model as both a response variable and a predictor, analysing all the relationships between these variables simultaneously is not an easy task. However, structural equation modelling techniques (Shipley 2000) provide an ideal statistical framework for such analyses (see Thomas *et al.* 2007 for an application on blue tits); these multiple-equation regression models represent structural relationships among a number of variables, some of which may affect one another mutually.

We begin by testing Drent & Daan (1980) and Rowe, Ludwig & Schluter (1994) optimization model (simply called hereafter: the optimization model) in Arctic-breeding common eiders (*Somateria mollissima*) using long-term individual monitoring data and structural equation modelling. The relationships between arrival date on the breeding grounds, condition at arrival, delay between arrival and laying, laying date and clutch size expected from this model are schematized in Fig. 1 and on the path diagram in Fig. 2. The model assumes that there (i) are direct negative effects of arrival date and condition at arrival on the delay before laying, (ii) is a direct positive effect of arrival date on laying date, (iii) is a direct negative effect of laying date on clutch size, (iv) is no direct effect of body condition on laying date and clutch size, (v) is no direct effect of arrival date on clutch size, and (vi) is no covariance between date of and condition at arrival. Finally, there should be an obvious direct effect of the delay before laying on laying date (Table 1). The optimization model is based on some basic assumptions. First, individuals are predicted to improve their condition after arrival on the breeding grounds; based on the model, this improvement is expected to lead to a greater clutch size and thus greater fitness benefits (Rowe, Ludwig & Schluter 1994; Fig. 1). A previous study conducted at our focal eider colony showed that females feed after their arrival on the breeding grounds and partially use nutrients acquired during the pre-laying and laying periods to
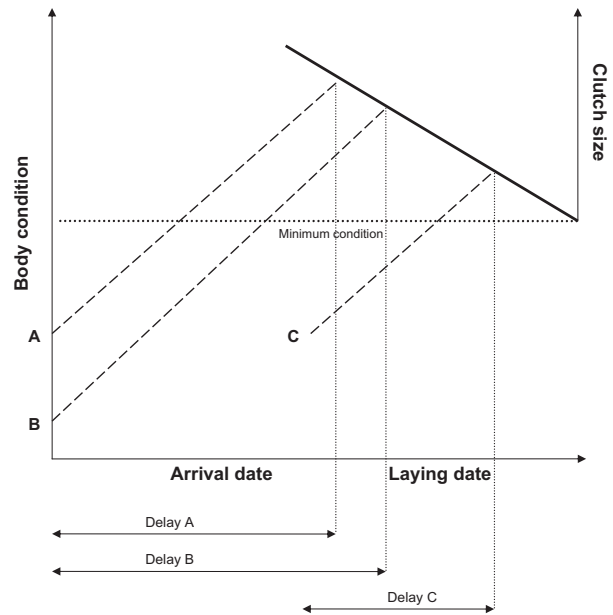

Fig. 1. Graphical representation of the condition-dependent optimization model (modified from Bêty, Gauthier & Giroux 2003 and Rowe, Ludwig & Schluter 1994). The thick line represents optimal combinations of clutch size and laying date assuming a trade-off between the cost (decreasing offspring value) and the benefit (increasing condition and hence clutch size) of a delay in laying date. Letters A, B and C represent individuals with different initial condition (A and C have the same condition, and B has a lower condition) or arrival date on the breeding grounds (A and B arrive at the same date and C arrives later). Dashed lines illustrate the increase in condition; bottom arrows indicate the delay between arrival and laying. Individuals must first reach a minimum condition threshold (dotted line) before they can produce a clutch and incubate eggs. Our body condition experiment (see Methods for details) can be represented by individuals A (control individuals) and B (individuals with experimentally decreased body condition). The expected responses of our treatment are thus a later lay date and a smaller clutch size.

cover the costs of egg formation (Sénéchal 2009; Sénéchal, Bêty & Gilchrist in press). This agrees with the idea that pre-laying female eiders need to acquire resources on the breeding areas, and thus gives some support to this first assumption. Secondly, egg value (i.e. the probability that an egg survives until recruitment) is expected to decline with increasing laying date. It has been shown that duckling post-hatching survival is typically higher in earlier than later broods in this eider colony (Love *et al.* 2010). Here, we also tested whether laying date was negatively associated with the probability that an egg survives from laying to hatching. Combined together, these results would support the hypothesis that egg-value decreases as the season progresses.

Structural equation models examine potential causal relationships using observational data, but cannot actually prove causality. As such, we combined descriptive analyses with an experimental decrease in female eider body condition prior to laying to confirm that the relationship between body condition and delay before laying, and hence lay date and clutch size, was causal. Experimental approaches testing for causal relationships between body condition and breeding parameters
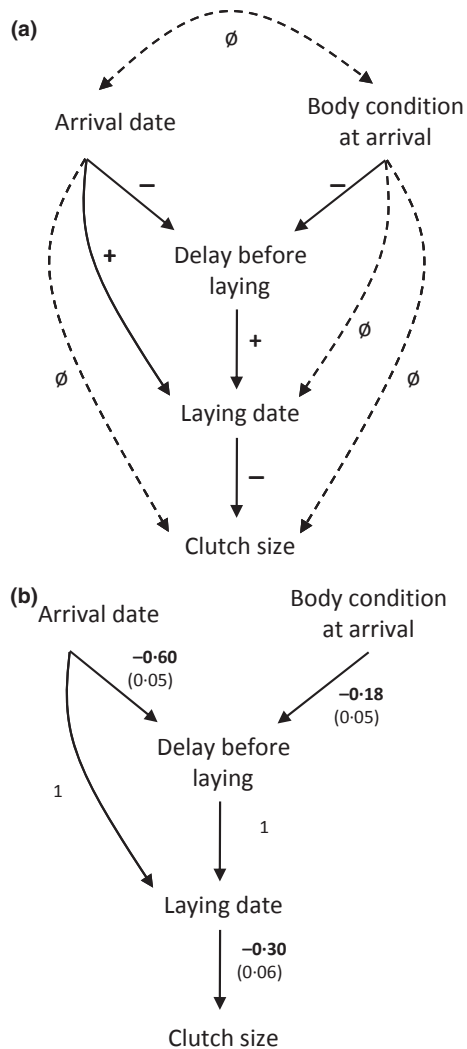
Fig. 2. (a) Path diagram showing the hypothesized causal structure linking arrival date and body condition at arrival to breeding parameters (delay between arrival and laying, laying date and clutch size) in a common eider colony, East Bay, Southampton Island, Nunavut, Canada. Solid lines indicate the predicted structure based on optimal model shown in Fig. 1. Dashed lines indicate other alternative paths. Signs above each arrow indicate the sign of the predicted effect (positive, negative or no effect); bidirectional arrow represents the covariance between date of and condition at arrival. (b) Standardized path coefficients in hypothesized structural model ($n = 318$).

(clutch size and laying date) are rare (but see Nooker, Dunn & Whittingham 2005), and most studies have tried to manipulate female condition with food supplementation (see Boutin 1990; Schoech & Hahn 2008 for reviews). However, a major drawback of food supplementation is that providing food *ad libitum* can affect several parameters at once, including pre-laying condition and the rate of condition gain (through changes in feeding rates). Such changes in the rate of condition gain could affect the predicted relationships between condition, laying date and clutch size (see Rowe, Ludwig & Schluter 1994 for details) and even lead to counter-intuitive relationships. Indeed, in some circumstances (see Rowe, Ludwig & Schluter 1994, p. 710 and Fig. 4), for the same arrival date and body condition at arrival as un-manipulated birds, individuals food-supplemented prior to laying could actually lay later (but with a larger clutch). This can lead to an apparent negative relationship between body condition and laying date. As such, manipulating body condition prior to laying rather than feeding rate during reproduction is required to understand adequately the proximate role of body condition in reproductive decisions. Our experimental approach should thus provide strong insight into our understanding of the proximal role of body condition during reproduction; we predicted that for a given arrival date, females with experimentally reduced pre-laying condition should lay later, and hence produce smaller clutches, than controls.

Finally, we investigated the long-term fitness consequences of reproductive decisions in female eiders. Indeed, based on the optimization model, individuals are expected to adjust their reproductive decisions to their state (i.e. it is expected that large clutches characterize females in good condition and/or arriving early and small clutches characterize females in poor condition and/or arriving late). Consequently, large clutches should not represent a greater investment in reproduction (sensu Evans 1990) than small clutches, and an increase in clutch size should not be associated with any apparent decrease in survival or future breeding probability. This does not mean that reproduction does not incur any fitness cost, but rather that such costs should not be apparent in a state-dependent reproductive framework (Reznick 1992). Similarly, in the context of our experiment, individuals with reduced pre-laying condition are expected to adjust their laying date and clutch size so that they do not jeopardize their

Table 1. Test of conditional independence implied by the path diagram (Fig. 2a). $(X; Y) \mid \{Z\}$ means that variables X and Y are independent conditional of variable Z (i.e. if Z is held constant, variation in X does not imply variation in Y). The associated mixed model used to test the independence claims are $Y \sim Z + X + 1 \mid Year$, where *Year* represents a random effect

Basis set	Partial slope $\pm$ SE (variable tested)	*t*-value	Null probability
(Body condition; Arrival date) | {ø}*	1.81 ± 1.96	0.93	0.35
(Clutch size; Arrival date) | {Laying date}	-0.013 ± 0.012	-1.14	0.26
(Laying date; Body condition) | {Arrival date; Delay}	$0.12 \times 10^{-3} \pm 0.14 \times 10^{-3}$	0.88	0.38
(Clutch size; Body condition) | {Laying date}	$0.36 \times 10^{-3} \pm 0.33 \times 10^{-3}$	1.09	0.28
(Clutch size; Delay) | {Arrival date; Body condition; Laying date}	0.095 ± 0.14	0.70	0.49

*Variables Body condition and Arrival date are expected to be independent if we hold constant none of the other variables.

future survival and/or reproductive prospects. Therefore, manipulated females should achieve the same subsequent survival and future breeding probabilities as controls.

Materials and methods

STUDY POPULATION

The study was conducted on Mitivik Island (64°02′N, 81°47′W), which supports the largest known nesting colony of common eiders in the Canadian Arctic (up to 8500 pairs annually). Details of the colony and the biology and capture of eiders are given in Appendix S1 (Supporting Information). Mass at capture (mean ± SD: 2174 ± 165 g), delay between capture and laying (mean ± SD: 9 ± 7 days), laying date (date of first egg laid; mean ± SD: June 30th ± 7), clutch size (maximum number of eggs found in a nest after the start of incubation; mean ± SD: 2·8 ± 1·0 eggs) and hatching success (probability to hatch ≥1 egg; mean ± SD: 0·58 ± 0·5) were determined for 318 nasal-tagged females. Among these females, the number of hatched ducklings was known for 49 individuals (mean ± SD: 2·1 ± 1·1 ducklings).

Females were caught very early in the season when they were flying above the colony as soon as the first eiders arrive at the colony; we therefore assumed that capture date was a good proxy of arrival date at the colony (see also Discussion). A previous study in the same eider population indicated that body mass (not corrected for structural size) of pre-laying females explains 60% of individual variation in pre-laying abdominal fat mass and performs as well as body mass adjusted for structural size as a measure of condition (Descamps *et al.* 2010). Indeed, structural size (tarsus length) explains only 1% of body mass variation in our colony (Descamps *et al.* 2010). We thus used body mass at capture as a proxy of female condition at arrival.

STUDY DESIGN

To test the condition-dependent optimization model in our common eider population, we proceeded in four steps. First, we tested the assumption that egg value decreases as laying date increases within a given reproductive season. Specifically, we tested for the effect of laying date on hatching success (i.e. the probability to hatch ≥1 offspring), and then for the effect of laying date on the number of hatched ducklings among successful nests (i.e. nests that hatched ≥1 duckling) while controlling for clutch size. This should tell us whether or not clutches laid late in the season were less successful and productive than clutches laid early in the season (for a given clutch size). This result, combined with the observed negative association between laying date and post-hatching survival (Love *et al.* 2010), should confirm that egg value generally decreases with increasing laying date. Our second step was to test Drent & Daan (1980) and Rowe, Ludwig & Schluter (1994) optimization model through descriptive data and structural equation models as described in Fig. 2a. Then, in the third step, we used data from an experimental manipulation of pre-laying body condition (see below) to test for a causal relationship between condition at arrival, laying date and clutch size. Finally, in the fourth step, we tested the fitness costs of reproductive decisions through modelling of capture–mark–recapture data.

EXPERIMENT

In 2002, 2003 and 2004, we kept 112 females in outdoor cages (wooden structure surrounded by wire mesh, 1·2 × 2·5 × 1·2 m) for 24 h with water but no food. Manipulated birds were randomly chosen among all captured individuals. Thirty-five manipulated females were re-sighted as breeders (34 of known laying date and 31 of known clutch size). Some of the manipulated females may have bred following the manipulation, but remained undetected in the colony because of a high bird density and re-sighting rate <1. For the 35 detected females, we used the body mass at release as a proxy of their body condition at arrival, and release date (capture date + 1 day) as a proxy of their arrival date. For these 35 females, mass loss averaged 126 g ± 54 SD (80% lost between 70 and 180 g). The number of unmanipulated/control females of known laying and/or clutch size for years 2002, 2003 and 2004 was 162 (160 of known laying date and 149 of known clutch size). Body mass at capture and body size (tarsus length) of manipulated and control females were similar (2138 g ± 132 SD vs. 2144 g ± 168 SD, and 48·7 mm ± 2·1 SD vs. 49·1 ± 2·1 SD, respectively; *P*-values from one-way ANOVAS > 0·3).

Our experiment lacks a true control group, that is, a group of females kept in captivity for 24 h with both water and food to prevent any decrease in body condition. A previous experiment (G. Gilchrist, unpublished data) indicated that eiders temporarily held in captivity do not feed even if food is provided *ad libitum*. Therefore, it was simply impossible to have this type of control group for such an experiment. However, it is important to note that 'unmanipulated' females were also kept in captivity after capture for *c*. 1 h (time needed to remove, measure and mark a group of individuals captured in the nets). This absence of this control group will be discussed in light of our results.

STATISTICAL ANALYSES

Decrease in egg-value with increasing laying date (test of model assumption)

To test for a decrease in hatching success and number of hatched ducklings with increasing laying date (step 1), we performed linear mixed models with a binomial (and logit link function) or normal error distribution, respectively. We used the *lmer* and *lme* functions of software R (R Development Core Team, 2010) and included a random *Year* effect in each model. Inspection of residuals from the model with the number of hatchlings as a dependent variable indicated no violation of the assumption of normality (Shapiro–Wilk test, *P* = 0·083). Dispersion parameter from the model with hatching success as a dependent variable was close to 1 ($\hat{c}$ =1·28), indicating that our model did not suffer from significant over-dispersion.

Path analysis

To test the optimization model and thus the structural relationships between reproductive parameters, we performed a path analysis (i.e. a special case of structural equation model with no latent variable, Shipley 2000). The principle of the method is to specify how the variables are linked together in terms of direct and indirect causal effects. Figure 2a shows the expected causal relationships based on Drent & Daan (1980) and Rowe, Ludwig & Schluter (1994) model (Fig. 1). We first tested whether the direct causal relationships defined in this model were significant or not. To do so, and obtain path coefficients, we performed linear mixed models to regress each variable on its direct causes using the *lme* function of R software (R Development Core Team, 2010). A random *Year* effect was included in each model. Then, to test the validity of our causal model as a whole, we performed simultaneous tests of all independence claims, known as a

directional-separation test (d-sep tests of path models, Shipley 2009). The validity of the model is based on a statistic C that follows a chi-square distribution with $2k$ degrees of freedom, k being the number of independence claims (see details in Appendix S2).

Manipulation of pre-laying body condition

To test for an effect of our body condition manipulation on the delay before laying and then clutch size, we performed linear mixed models with a normal error distribution, using the *lme* function of R software (R Development Core Team, 2010) with a random *Year* effect. Inspection of residual distribution indicated no departure from normality when considering the model with delay before laying as dependent variable (Shapiro–Wilk test: $P = 0.088$), and a moderate departure from normality when considering the model with clutch size as the dependent variable (Shapiro–Wilk test: $P = 0.021$). Results were the same for this later model when considering a *Poisson* error distribution (and indicated no over-dispersion, $\hat{c} < 1$), so that we are confident that this lack of normality did not affect our conclusions.

Fitness consequences of reproductive decisions

To test for potential fitness costs of reproduction in relation to clutch size, we carried out survival analyses using capture-mark-recapture methods (Lebreton *et al.* 1992), implemented in software MARK (White & Burnham 1999). Clutch size is considered a good proxy of eider reproductive effort as a larger clutch is more expensive to produce and to incubate (Erikstad & Tveraa 1995; Thomson, Monaghan & Furness 1998; Williams 2005), and eiders producing large clutches are more likely to complete the incubation (Bourgeon *et al.* 2006) and less likely to abandon their brood after hatching (Erikstad, Bustnes & Moum 1993).

Goodness-of-fit tests of the Cormack-Jolly-Seber (CJS) model (i.e. the full time dependent model $\phi_t p_t$, where ϕ represents survival probabilities, p represents re-sighting probabilities and subscript t represents the year effect) was performed with the software U-CARE (Choquet *et al.* 2003). These tests indicated a good fit between female eider data and the CJS model (*P*-values > 0.27). Therefore, the 'iii' assumption (i.e. independence of fates and identity of rates among individuals), required for CMR analyses was met.

As non-breeders rarely come to the colony before the hatching period (mid/end of July) and because re-sighting mostly occurred early in the season, a vast majority of females re-sighted at the colony were likely breeding females or failed breeders. As a consequence, re-sighting probability at the colony should represent a good proxy of breeding probability.

To test for a negative association between clutch size in year t and survival between years t and $t + 1$ or breeding probability in year $t + 1$, we tested for a clutch-size effect using clutch size as an individual covariate. Clutch size was available only in the year of first capture, so we tested for an effect of clutch size on survival only for the year following banding. We started our model selection from a general model including a year (t) effect and two 'age-classes' (i.e. year following capture and 1 year after capture onwards; model $\phi_t^{a_1} \phi_t^{a_{2+}} p_t^{a_1} p_t^{a_{2+}}$). We considered the same sample of females used in previous steps, but restricted our sample to years 2002–2005. Indeed, from 2006 onwards, severe avian cholera outbreaks occurred in our colony and costs of reproduction were likely greater, leading to a negative association between survival and clutch size (see Descamps *et al.* 2009 for details). This variation in costs of reproduction with

the presence of avian cholera in the context of the condition-dependent optimization model will be discussed. Our data set used for survival analyses thus corresponded to 189 females with known clutch size, banded from 2002 to 2005 and monitored from 2002 to 2006.

To test for an effect of our body condition manipulation on future survival and breeding probability, we considered two groups of individuals (manipulated and control) and tested for a group effect. Our sample consisted of 109 manipulated and 398 control females with known capture-recapture history. We started our model selection from a general model including a year effect and two groups (i.e. groups of manipulated [m] and control [c] females; model $\phi_t^m \phi_t^c p_t^m p_t^c$). We considered the time period 2002–2006 which represents the period before the severe cholera outbreaks (Descamps *et al.* 2009).

In both cases, model selection was based on the Akaike Information Criterion corrected for small sample sizes (AICc), as recommended when several non-nested models are fitted (Burnham & Anderson 2002). We used ΔAICc (difference in AICc between a given model and the model with lowest AICc) as a criterion to choose the best models among all tested models. A ΔAICc < 2 between two competing models means that they cannot be distinguished in their ability to model the data (Burnham & Anderson 2002). When ΔAICc between two nested models was < 2, the simplest one was selected.

Results

RELATIONSHIP BETWEEN LAYING DATE AND EGG VALUE

The probability of hatching at least one egg in a clutch decreased with increasing laying date (slope of -0.07 ± 0.02 SE on a logit scale; $z = -3.58$, $P = 0.0003$; Fig. 3), after controlling for clutch size (slope of the clutch-size effect: 0.34 ± 0.13 SE on a logit scale; $z = 2.66$, $P = 0.008$). The interaction between laying date and clutch size was not significant ($P = 0.84$) and was therefore not included in the previous model. Among successful nests with
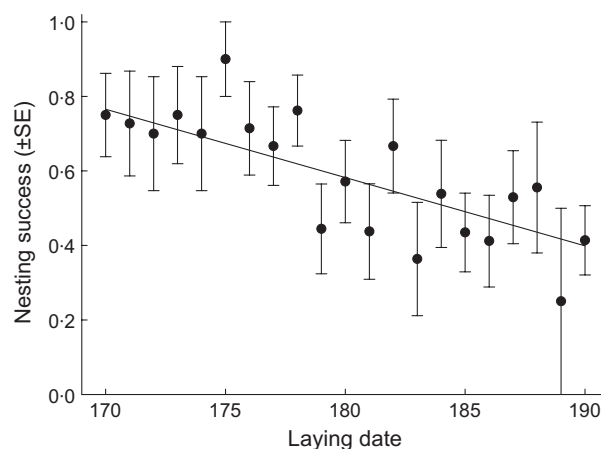

Fig. 3. Hatching success (probability to hatch ≥1 egg) as a function of laying date (expressed in days since January 1) in a common eider colony, East Bay, Southampton Island, Nunavut, Canada ($n = 318$; for the sake of clarity, data have been pooled for laying dates ≥190 and ≤170).

a known number of hatchlings, the number of hatched off-spring in a given clutch did not vary with laying date (slope of 0.004 ± 0.022 SE; $t = 0.18$, $P = 0.86$), after controlling for clutch size (slope of 0.63 ± 0.13 SE; $t = 4.70$, $P < 0.001$). Again, the interaction between laying date and clutch size was not significant ($P = 0.93$) and was not included in the previous model.

TEST OF THE CONDITION-DEPENDENT OPTIMIZATION MODEL: A PATH ANALYSIS APPROACH

Three structural equations linking date of arrival, condition at arrival, delay before laying, laying date and clutch size can be derived from Fig. 2, but only two are of interest. Indeed, the delay before laying was calculated as (laying date-arrival date) so that the structural equation linking laying date to arrival date and delay before laying is simply Laying date = Arrival date + Delay before laying (i.e. the path coefficient is equal to 1).

The two other structural equations obtained from linear mixed models are:

$$\text{Delay before laying} = 157.17(12.16) - 0.77(0.07) \\ \times \text{Arrival date} - 0.007(0.002) \\ \times \text{Body condition at arrival} + 1|\text{Year}$$

$$\text{Clutch size} = 10.93(1.61) - 0.045(0.009) \\ \times \text{Laying date} + 1|\text{Year}.$$

Numbers in brackets represent the standard errors of the path coefficients. All path coefficients are significantly different from 0 at the 0.001 level. 1|*Year* represents the random year effect. Body condition at arrival and arrival date (and the random year effect) explained 39% of the variation in delay before laying, and laying date (and the random year effect) explained 13% of variation in clutch size (calculated as
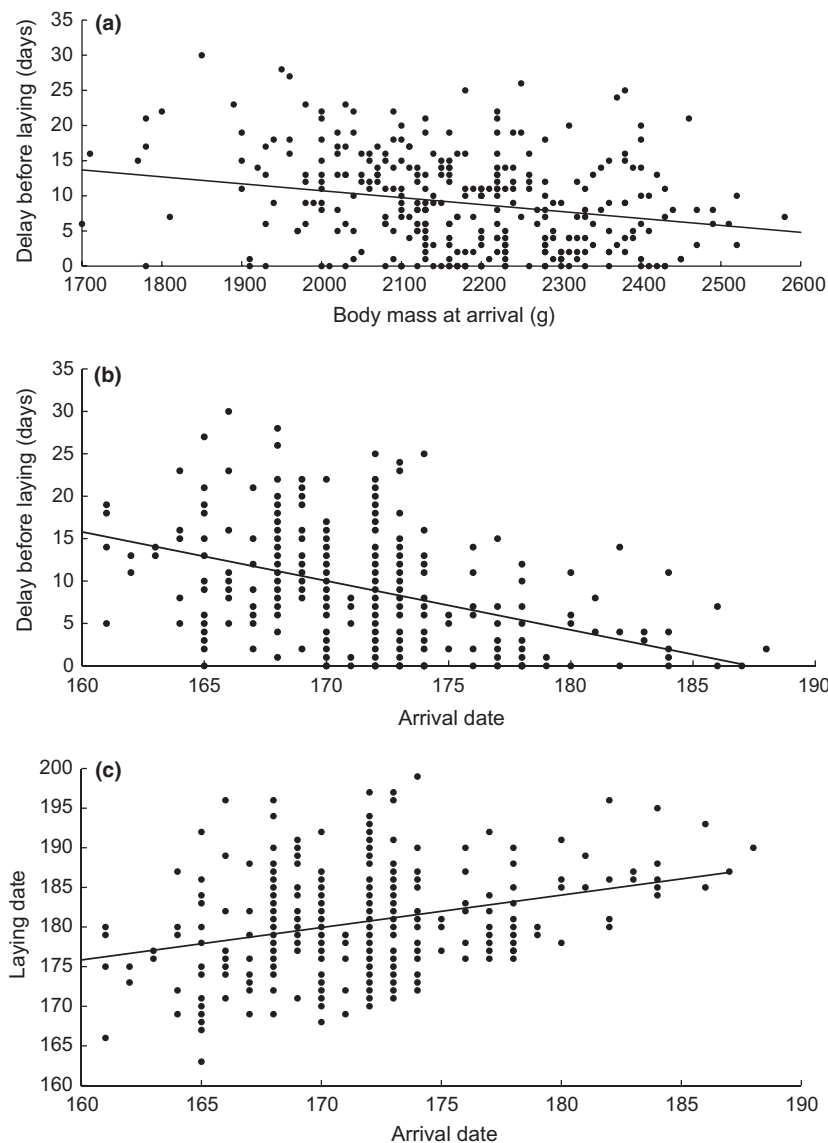

Fig. 4. Relationships between body mass at capture, arrival date and delay between capture and laying date in the East Bay common eider colony, Southampton Island, Nunavut, Canada ($n = 318$). Arrival dates are expressed in days since January 1.
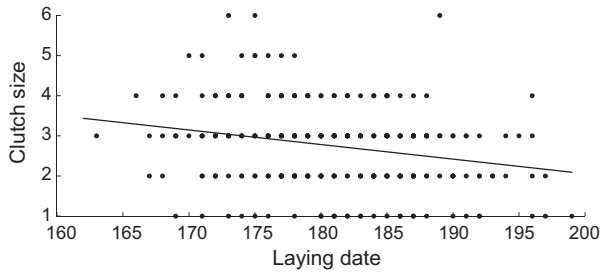
Fig. 5. Effect of laying date (expressed in days since January 1) on clutch size in the East Bay common eider colony, Southampton Island, Nunavut, Canada ($n = 318$).

Fig. 6. Average number of days ($\pm$SE) between arrival and laying date for female common eider breeding at East Bay, Southampton Island, Nunavut, Canada. Solid line and black circles correspond to control (unmanipulated) females ($n = 160$) and dashed line and white symbols to manipulated ones (females with experimentally reduced pre-laying body mass, $n = 35$; see Methods for details).

$1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{Y})^2}$, where $\bar{Y}$ represents the average value for the trait considered, $\hat{y}_i$ the predicted value for individual i and y_i the observed value for individual i). Figure 2b shows the standardized path coefficients, and Figs 4 and 5 the relationships between reproductive parameters.

The causal model we defined provided a strong fit to the data as indicated by the high P-values of the goodness-of-fit test (Table 1, $C = 10 \cdot 70$, d.f. $= 10$, $P = 0 \cdot 38$). Consequently, data agree with the causal pathways indicated in Fig. 2. Body condition at arrival had a direct negative effect on the delay before laying (Fig. 4a), but no direct effect on laying date and clutch size. The overall indirect effect of body condition on clutch size was positive, but relatively weak (equal to $-0 \cdot 18 \times 1 \times -0 \cdot 30 = 0 \cdot 054$; Fig. 2b). This means that if body condition at arrival increases by 1 standard deviation from its mean, clutch size is expected to increase by only $0 \cdot 054$ standard deviations from its own mean. Arrival date affected clutch size through its effect on the delay before laying and laying date (Figs 4 and 5). The overall effect of arrival date on laying date (i.e. the sum of its effect) was positive and equal to $0 \cdot 40$ ($1 - 0 \cdot 60 \times 1$, see Fig. 2b), indicating that, as predicted by the optimization model, an increase in arrival date led to an increase in laying date (Fig. 4c), despite a negative effect on the delay before laying (Fig. 4b).

EXPERIMENTAL DECREASE IN PRE-LAYING BODY CONDITION

After controlling for release date (slope of $-0 \cdot 86 \pm 0 \cdot 08$ SE; $t = -10 \cdot 58$, $P < 0 \cdot 001$), female eiders with experimentally reduced pre-laying body condition tended to lay 2 days later than unmanipulated individuals (manipulation effect: $2 \cdot 2$ days $\pm 1 \cdot 13$ SE; $t = 1 \cdot 92$, $P = 0 \cdot 057$; Fig. 6). This effect of approximately 2 days is higher than that expected from our descriptive data (i.e. a decrease in body mass of about 130 g should lead to a delay of about 1 day). When we included the mass at release in the model (effect of the mass at release: $P = 0 \cdot 050$), the effect of treatment was no longer significant and the estimated effect of the manipulation decreased to $0 \cdot 67$ day $\pm 1 \cdot 15$ SE ($t = 0 \cdot 58$, $P = 0 \cdot 56$). Thus, the effect of our treatment on the delay between release date and laying date mainly resulted from its effect on female pre-laying body mass.
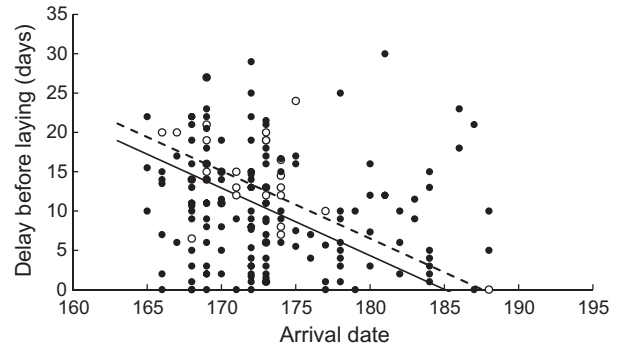
Females with experimentally reduced body condition laid the same number of eggs as control females (manipulation effect: $0 \cdot 11$ egg $\pm 0 \cdot 22$ SE; $t = 0 \cdot 51$, $P = 0 \cdot 61$), after controlling for release date (slope of $-0 \cdot 02 \pm 0 \cdot 02$ SE; $t = -1 \cdot 52$, $P = 0 \cdot 13$).

REPRODUCTIVE DECISIONS AND THE FITNESS COSTS OF REPRODUCTION

Clutch size, and subsequent survival and breeding probability

Based on AICc values, we found that clutch size did not affect survival or re-sighting rates of female eider ducks (Table 2;

Table 2. Clutch-size effect on survival and re-sighting probabilities for female common eiders breeding at the East Bay colony, Southampton Island, Nunavut, Canada ($n = 189$ females). A females' clutch size was known for the year of initial capture and unknown thereafter. Super-script 'a' refers to time-after banding ('age') effect: a_1 represents the year following first capture, and a_{2+} the subsequent years. Subscript 't' refers to the year effect. We only considered an effect of clutch size the year following the initial capture (i.e. when clutch size was known)

Model	np*	Deviance	AICc†	ΔAICc‡
$\phi^{a_1} \phi^{a_{2+}}_t p^{a_1}_t p^{a_{2+}}$	8	641·153	657·582	0·000
$\phi^{a_1/\text{clutchsize}} \phi^{a_{2+}}_t p^{a_1}_t p^{a_{2+}}$	9	641·115	659·654	2·072
$\phi^{a_1} \phi^{a_{2+}}_t p^{a_1/\text{clutchsize}}_t p^{a_{2+}}$	9	641·146	659·685	2·103
$\phi^{a_1} \phi^{a_{2+}}_t p^{a_1}_t p^{a_{2+}}$	7	646·077	660·410	2·828
$\phi_t p_t§$	8	644·828	661·258	3·676
$\phi^{a_1} \phi^{a_{2+}} p^{a_1} p^{a_{2+}}$	4	655·449	663·567	5·985
$\phi^{a_1}_t \phi^{a_{2+}}_t p^{a_1}_t p^{a_{2+}}$	11	640·845	663·640	6·058
$\phi^{a_1}_t \phi^{a_{2+}} p^{a_1}_t p^{a_{2+}}$	9	645·575	664·114	6·532
$\phi^{a_1}_t \phi^{a_{2+}}_t p^{a_1}_t p_t$	12	639·302	664·244	6·662
$\phi^{a_1}_t \phi^{a_{2+}}_t p^{a_1} p_t$	10	646·501	667·161	9·579
$\phi^{a_1}_t \phi^{a_{2+}}_t p^{a_1} p^{a_{2+}}$	9	648·665	667·204	9·622

*Number of identifiable parameters.
†Akaike Information Criterion corrected for small sample size.
‡Difference between the AICc of the model considered and the lowest AICc value.
§Cormack-Jolly-Seber (CJS) model.

average survival for females that laid 1, 2, 3 and ≥4 eggs were 0.91 ± 0.09 SE, 0.90 ± 0.08 SE, 0.85 ± 0.07 SE and 0.89 ± 0.10 SE, respectively; average re-sighting rate for females that laid 1, 2, 3 and ≥4 eggs were 0.75 ± 0.11 SE, 0.58 ± 0.08 SE, 0.64 ± 0.07 SE and 0.67 ± 0.11 SE, respectively). The absence of an effect on re-sighting probabilities suggests that clutch size in a given year did not affect the breeding probability in the subsequent year.

Body condition manipulation, and subsequent survival and breeding probability

Survival of female eiders was constant in the period considered and adding a 'manipulation effect' into the model did not lead to a lower AICc. Survival of both groups of females was very similar and averaged 0.91 ± 0.05 SE and 0.89 ± 0.01 SE for the manipulated and control females respectively (estimates from model $\phi^m \phi^c p_t$; see Table 3 for details). Moreover, re-sighting rates of females were time-dependent (they varied from 0·48 to 0·67; estimates from model $\phi^m \phi^c p_t$) and were not a function of the treatment (Table 3).

Discussion

OPTIMAL REPRODUCTIVE DECISIONS IN FEMALE EIDER DUCKS

One of the main assumptions of Drent & Daan (1980) and Rowe, Ludwig & Schluter's (1994) model of optimal reproductive decisions is that egg-value decreases with increasing laying date. We found that the probability that an egg survived from laying to hatching decreased with increasing laying date. Moreover, it has been shown in a previous study in the same eider colony (Love *et al.* 2010) that later-hatched offspring generally had lower survival

Table 3. Effect of manipulation of pre-laying body condition on survival and re-sighting probabilities for female common eiders breeding at the East Bay colony, Southampton Island, Nunavut, Canada ($n = 109$ manipulated and 398 control females). Superscripts '*m*' (manipulated) and '*c*' (control) refer to the group of females; subscript '*t*' refers to the year effect and symbol '+' indicates additive effects

Model	np*	Deviance	AICc†	ΔAICc‡
ϕp_t	5	52·468	1923·964	0·000
$\phi^m \phi^c p_t$	6	52·336	1925·857	1·893
$\phi_t p_t$	8	51·469	1929·052	5·088
$\phi^m_{t+} \phi^c_{t+} p_t$	9	50·566	1930·186	6·222
$\phi^m_{t} \phi^c_{t} p_t$	12	48·400	1934·157	10·193
$\phi^m_t \phi^c_t p^m_{t+} p^c_{t+}$	13	48·013	1935·825	11·861
$\phi^m_t \phi^c_t p$	9	58·421	1938·042	14·078
$\phi^m_t \phi^c_t p^m p^c$	10	58·366	1940·028	16·064
$\phi^m_t \phi^c_t p^m_t p^c_t$	16	47·164	1941·163	17·199

*Number of identifiable parameters.
†Akaike Information Criterion corrected for small sample size.
‡Difference between the AICc of the model considered and the lowest AICc value.

than earlier-hatched ones. Combined, these results support the assumption of decreasing egg-value with increasing laying date.

Considering the potential benefits of delaying breeding to improve body condition (and hence lay a larger clutch) and the costs of breeding later (lower egg-value), the optimal decision, that maximizes fitness, is hypothesized to be mediated by body condition at arrival and date of arrival on the breeding grounds (Drent & Daan 1980, Rowe, Ludwig & Schluter 1994). Such an optimization was supported by our study. It indicated that the condition of female eider ducks at arrival on the colony and their date of arrival determined, at least partly, their laying date and hence clutch size. The laying date of female eiders increased with later arrival date and decreased with increasing condition, but the delay between arrival time and laying date decreased with increasing arrival date. Our manipulation of female pre-laying body condition confirmed that the relationship between body condition and laying date was causal: for a given arrival date, an experimental decrease in body condition led to a delay in laying date. One potential alternative explanation for this result could be that our experiment affected birds' laying date due to the stress it induced (Dickens, Delehanty & Romero 2009). If the stress induced by captivity has some delayed effect (that remains following release), it could affect bird's breeding decisions independent of the decrease in body condition. We would thus expect that the effect of our manipulation would remain when we controlled for female body mass at release (because changes in laying date would be independent of the decrease in body mass). However, the effect of the experiment on the delay before laying disappeared when we controlled for the effect of female body mass at release (i.e. the P-value associated with our manipulation became > 0.5, and the effect size declined by 70%). This suggests that our experiment affected the laying date mainly through its effect on body condition, and not simply through a potential stress effect on reproductive physiology or behaviour after release. However, such an additional stress effect could explain why the manipulation effect (delay of 2 days) was higher than the one expected from our descriptive data (expected delay of 1 day for a decrease in body mass of about 130 g, which represents the average decrease in body mass for manipulated females). This decrease in body condition may be due to both starvation and direct stress effects (Astheimer, Buttemer & Wingfield 2000), but this does not affect our conclusion that the increase in laying date for manipulated females was, at least partly, a direct consequence of a decrease in their body condition, whatever the determinant of this decrease.

We expected that manipulated females (i.e. females with lower body condition) would have laid smaller clutches, but did not find any effect of our treatment on clutch size. However, as our manipulation increased the pre-laying period by only *c.* 2 days, it is not surprising that no effect on clutch size was apparent over such a short time period. Based on the descriptive data of the seasonal decline in clutch size (Fig. 5), the effect of laying date on clutch size could only be

detected when considering a longer period. Our path analysis indicated that the effect of body condition at arrival on clutch size (through its effect on the delay before laying and hence laying date) was very weak (a delay of 2 days in laying date is expected to decrease clutch size by only *c.* 0·1 egg; see structural equations in Results). Consequently, a causal relationship between pre-laying condition and clutch size certainly remains possible despite the absence of an effect from our experiment. Furthermore, it has been found in the same eider colony that females strongly depend on body stores to produce their eggs (yolk lipids are constituted mostly from endogenous lipids; Sénéchal 2009) and that their post-laying fat stores are independent of clutch size (Sénéchal, Bêty & Gilchrist in press; see also Erikstad & Tveraa 1995 for similar results in another eider colony). This indicates that females laying more eggs are in better condition (i.e. more fat reserves) at the time of laying, which agrees with the hypothesis of a causal pathway between body condition and clutch size.

Our study provides compelling support to Drent & Daan (1980) and Rowe, Ludwig & Schluter (1994) model of optimal reproductive decisions, and to the hypothesis that female eider ducks adjust their laying date and clutch size according to their body condition at arrival, their date of arrival and the seasonal change in egg-value. However, one argument against this individual optimization hypothesis could be that clutch size and/or laying date were/was not driven by body condition and date of arrival *per se,* but by intrinsic individual quality (seen here as a set of permanent individual characteristics positively correlated with fitness, Wilson & Nussey 2010), with lower quality individuals laying fewer eggs later in the season (Verhulst & Nilsson 2008). Such a hypothesis would explain the absence of an effect of our body condition manipulation on clutch size (i.e. because relationships between condition and clutch size would not be causal); however, if quality is indeed a fixed trait, it would not explain the delay in lay date caused by the experimental reduction in pre-laying condition. Moreover, this 'individual quality' hypothesis does not explain the relationship between delay before laying and body condition or arrival date. Finally, there seems to be no repeatability in clutch size in common eiders (Erikstad, Bustnes & Moum 1993), subsequently clutch size does not probably represent a permanent characteristic of individuals, and is probably not related to individual quality (*sensu* Wilson & Nussey 2010). Therefore, variation in individual quality alone cannot explain all our results, whereas the individual optimization hypothesis can. Of course, both explanations are not mutually exclusive. The optimization model is based on the concept of individual state, which can be viewed as a set of dynamic traits (i.e. that can change with time, like body mass) characterizing the individual, whereas the concept of quality refers more to permanent characteristics (e.g. genes). With these definitions, state and quality may be linked so that both can affect individual reproduction (e.g. individual quality may affect foraging efficiency and thus individual body condition).

INDIVIDUAL OPTIMIZATION AND THE COSTS OF REPRODUCTION

In systems where individuals perfectly optimize their current reproduction in relation to their state, costs of reproduction should not be apparent (Tinbergen & Daan 1990). Indeed, an increase in reproductive effort (or energetic allocation to reproduction, Evans 1990) should characterize individuals in good condition, and/or breeding in a favourable habitat; individuals should be able to afford such a high effort without paying extra fitness costs (note, however, that such adjustments between reproductive effort and individual or environmental conditions may exist, but not be perfect, Schubert *et al.* 2009). Therefore, an increase in energetic allocation to reproduction should not be associated with an increase in investment (i.e. an evolutionary concept quantified by the magnitude of its costs to the parent, Trivers 1972; Evans 1990; Descamps *et al.* 2007), and no decline in survival or future reproduction should be apparent. Costs of reproduction should only be apparent when individual adjustments are not 'optimal' (i.e. not adjusted to their internal and external state, McNamara & Houston 1996). For instance, reproduction may not be optimal when environmental conditions vary unpredictably (McNamara, Webb & Collins 1995; McNamara 1998; see also Török *et al.* 2004 for an example in collared flycatchers). A previous study in the same eider colony found that in the presence of an infectious disease, avian cholera, naturally increasing clutch size among individuals was associated with a decrease in survival (Descamps *et al.* 2009), which does not fit with the hypothesis of optimal reproductive decisions. When avian cholera appeared in the colony, female eiders were likely unable to adjust their reproduction to this unpredictable change in the environment. As a consequence, their reproductive decisions were not optimal and led to apparent fitness costs (see Descamps *et al.* 2009 for more details about the potential mechanisms linking avian cholera, reproductive effort and survival).

In the absence of cholera epidemics, we found no evidence of the fitness cost of reproduction. Indeed, we observed no decrease in survival or future breeding probability associated with an increase in clutch size (assuming that re-sighting probability is a good proxy of breeding probability; see Methods for details). Similarly, females with experimentally decreased pre-laying body condition had similar survival and subsequent breeding probabilities to those of control females. We should also note that the mass of females during incubation was similar for experimental females and for control females (1286 g $\pm$ 33 SE vs. 1257 g $\pm$ 29 SE, respectively; $n = 39$, $P = 0.98$), after controlling for the number of days females had already incubated. Therefore, manipulated females seemed to have adjusted their breeding decisions before the start of incubation in a way that allowed them to achieve similar body condition during the incubation period, and thus not to jeopardize their future survival or reproduction. These results support the hypothesis of an optimization of individual reproductive decisions (in absence of unpredictable disease epidemics) to maximize the current reproductive

output and minimize the fitness costs of reproduction, while taking into account their body condition, arrival date and egg-value, and thus their internal and external state (McNamara & Houston 1996; McNamara 1998).

FEMALE EIDERS ARE PRUDENT PARENTS

The concept of individual optimization could explain, at least partly, why many birds in a population seem to breed too late and/or to lay a smaller clutch than the most productive individuals (Lack 1948; Perrins 1970). Indeed, those females that arrived late and/or in poor condition may make the best of their challenging situation by delaying reproduction and/or laying a smaller clutch. Female eider ducks can thus be seen as 'prudent parents' (Drent & Daan 1980). This concept of 'prudence' generally refers to the fact that in many bird species, some individuals (i.e. the prudent ones) skip the current reproductive event because of a lack of body condition or resource availability. Such a decision is expected to increase their chance of surviving and having improved breeding success in the future (Drent & Daan 1980; Cam *et al.* 1998; Verhulst 1998). Female eider ducks are also known to skip reproductive events sometimes (Coulson 1984). Non-breeding can be considered the extreme way of being prudent, that is, the strategy associated with a null reproductive effort. In our case, female eiders decrease their reproductive effort, measured in terms of clutch size, when their condition was low and/or when they arrive late at the colony, which can also be interpreted as prudence. Moreover, the probability of investing in parental care after hatching is also a function of body condition in common eiders: females in poor condition at hatching are more likely to abandon the brood than females in good condition (Kilpi *et al.* 2001). Therefore, the 'prudence' of female eider ducks can also be expressed after hatching, with poor condition females promoting their own survival prospects by decreasing investment in parental care.

Conclusion

By combining descriptive data and structural equation models with experimental data, and a study of the long-term fitness consequences of reproductive decisions, we provided a comprehensive test of Drent & Daan (1980) and Rowe, Ludwig & Schluter (1994) optimization model. Our results indicate that laying a small clutch may represent the optimal decision for a given individual considering its arrival date and condition at arrival. We believe that our study provides convincing explanations for the seasonal decline in clutch size observed in this population. Our study emphasizes the importance of simultaneously considering individual body condition and arrival date to increase our understanding of breeding decision determinants, and illustrates the usefulness of path analyses for such an approach.

Arrival date and body condition explained a significant part of the variation in laying date and clutch size, but not all (39% and 13%, respectively). Several explanations can be proposed for this unexplained variation in eider reproductive

traits. First, laying dates were estimated through candling and/or behavioural observations, so that true laying dates might differ by a few days from observed laying dates. In addition, some clutch-size measurements might have occurred after partial predation so that true clutch size might have been underestimated for some females. Some uncertainty might have also been present in arrival dates, estimated by capture dates. Consequently, this lack of precision in some parameters could have decreased the strength of associations between condition, arrival date, laying date and clutch size. Secondly, the model we used is based on the assumption that all individuals have similar rates of mass gain, which is unlikely. Indeed, depending on age, experience, size and/or condition, female eider ducks might have different foraging efficiencies and thus different rates of condition gain. Rowe, Ludwig & Schluter (1994) showed that such individual heterogeneity should affect optimal laying date and clutch size, and this could explain some additional variation in eiders reproductive traits. More generally, there might be inter-individual variation in the relationships between arrival date, condition and clutch size linked to variation in individual intrinsic quality. Heterogeneity in foraging efficiency and mass gain would represent only one factor leading to such heterogeneity, but many others could exist (e.g. variation in metabolism and thus costs of self maintenance; variation in trade-offs between egg quantity and egg quality) and affect the observed patterns. Studies examining this residual variation in laying date and clutch size, and thus investigating the effect of factors other than pre-laying body condition and date of arrival, should lead to a more accurate and comprehensive understanding of the causes and consequences of an individual's reproductive decisions.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details on the study colony.

Appendix S2. Description of the directional-separation test.

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