GLOBAL CHANGE ECOLOGY - ORIGINAL PAPER

Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird

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Abstract Individuals breeding in seasonal environments are under strong selection to time reproduction to match offspring demand and the quality of the post-natal environment. Timing requires both the ability to accurately interpret the appropriate environmental cues, and the flexibility to respond to inter-annual variation in these cues. Determining which cues are linked to reproductive timing, what these cues are predicting and understanding the fitness consequences of variation in timing, is therefore of paramount interest to evolutionary and applied ecologists, especially in the face of global climate change. We investigated inter-annual relationships between climatic variation and the timing of reproduction in Canada's largest breeding population of Arctic common eiders (*Somateria mollissima*) in East Bay, Nunavut. Warmer spring temperatures predicted both earlier mean annual laying dates and the earlier ice-free conditions required by ducklings for post-natal growth. Warmer springs had higher variation in this temperature cue, and the population laying distribution became increasingly positively-skewed in warmer summers, potentially indicating that more low-quality females had the opportunity to commence laying in warmer years. Females that timed laying to match duckling hatching just prior to fully ice-free conditions obtained the highest duckling survival probability. Inter-annual data on repeated breeding attempts revealed that the individuals examined show a similar degree of laying flexibility in response to climatic variation; however, there was significant individual variation in the absolute timing of laying within an average year. This work sheds light on how reproductive timing is related to and influenced by variation in local climate and provides vital information on how climate-related variation in reproductive timing influence a fitness measure in an Arctic species. Results are especially relevant to future work in polar environments given that global climatic changes are predicted to be most intense at high latitudes.

Keywords Timing of breeding · Temperature cue · Climatic variability · Offspring survival · Common eider (*Somateria mollissima*)

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Introduction

Understanding how individuals optimize reproductive strategies to maximize fitness in the face of variation in their surrounding environment remains a central issue in evolutionary ecology (Stearns 1992; Réale et al. 2003; Both et al. 2006; Garant et al. 2007; Charmantier et al.

2008). In seasonal environments, individuals improve their chances of maximizing their reproductive success if they can time reproduction to achieve the best match between offspring demand and the quality of the rearing environment (Perrins 1970; Pettifor et al. 1988; Lepage et al. 2000; Dunn 2004). Identifying the underlying cues that individuals use to time reproduction and the fitness consequences for variability in these cues is more relevant than ever given the predicted degree of global warming (Intergovernmental Panel on Climate Change 2007; Dickey et al. 2008; Visser 2008).

Unfortunately, we know rather little about how polar-breeding species time reproduction and hence we know little about how potential climate-induced changes in these decisions will affect fitness traits (Gaston et al. 2005a; Jónsson et al. 2009; Post et al. 2009; Reed et al. 2009). In greater snow geese (*Chen caerulescens atlantica*) breeding in the eastern Canadian Arctic, high mean spring temperatures were associated with early egg-laying and hatching dates (Dickey et al. 2008), and heavy snow cover has been associated with later laying dates (Gauthier et al. 2003; Bêty et al. 2003) and reduced breeding propensity (Reed et al. 2004). Gaston et al. (2005a, 2009) found that Brunnich's guillemot (*Uria lomvia*) breeding in a low Arctic colony initiated egg-laying earlier with warmer spring temperatures, likely acting via changes in the energetic costs of foraging through changes in ice conditions. Finally, egg-laying in thick-billed murres (*Uria lomvia*), black-legged kittiwakes (*Rissa tridactyla*) and glaucous gulls (*Larus hyperboreus*) was delayed in cooler springs in a high Arctic breeding colony when the subsequent ice edge was farther offshore compared with warmer springs (Gaston et al. 2005b). The mechanistic links between climatic variability and reproductive timing are likely complex (since effects are mediated through integrated behavioral, physiological and life-history responses (Sutherland 1996; Visser 2008; Reed et al. 2009) and climatic variability can act as a direct cue as well via more complex pathways (i.e., influences on food availability or energetics). Nonetheless, polar systems are ideal models for understanding the evolution of environment-driven reproductive decisions across multiple habitats given (1) the large degree of climatic variability, (2) the strong effect that the timing of breeding has on fitness, and (3) the small window of breeding opportunity (Bêty et al. 2003; Gaston et al. 2005a, 2009; Dickey et al. 2008).

Here, we investigate potential links between climatic cues, the timing of breeding and measures of fitness in a large colony of Arctic common eiders (*Somateria mollissima*) nesting at East Bay, Nunavut, Canada. This is an excellent system for investigating reproductive timing since there is large inter-annual variation in local climatic conditions (Fig. 1). Moreover, birds are expected to accurately time laying to maximize the amount of time that ducklings have access to ice-free conditions in the marine bay (despite the bay being fully frozen at the time of laying), since ducklings require 10 weeks to reach adult body size (Pethon 1967; Goudie et al. 2000). Our specific questions were: (1) is the timing of reproduction related to climatic cues, (2) what do cues predict, (3) what are the fitness consequences for a mismatch between environmental conditions and the timing of breeding, and (4) what is the scope of climate-related reproductive plasticity among females? We made the following predictions: (1) the timing of laying would be related to local temperature cues, or snow cover, since these cues may be the easiest to integrate and track, respectively (Visser et al. 2009); (2) these climatic cues would predict the open water conditions required by ducklings to reach adult size and successfully migrate to wintering grounds, and hence laying would be timed to match hatching to ice-free conditions; (3) the
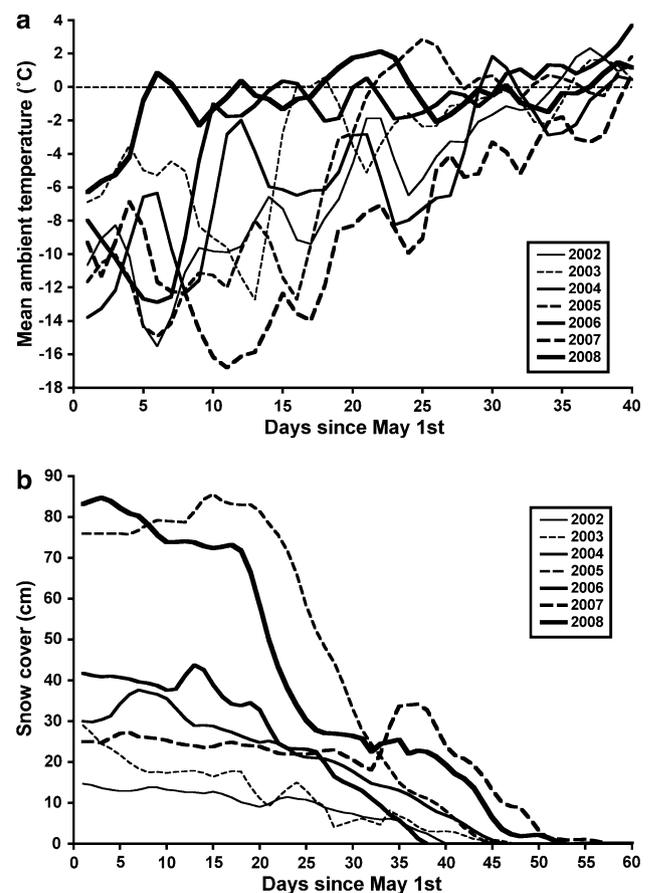
Fig. 1 Inter-annual variation in mean daily temperature and snow cover within the arrival and laying period for the East Bay population of common eiders (*Somateria mollissima*) for 2002–2008. Data were collected by Environment Canada at the Coral Harbour weather station, Nunavut (64°11′N, 83°21′W) to represent local climatic conditions at the eider colony on East Bay Island (64°02′N, 81°47′W) in the East Bay Migratory Bird Sanctuary, Nunavut, Canada

highest duckling survival would correspond to laying dates that matched duckling hatching to ice-free conditions; and (4) individuals would exhibit similar flexibility in response to inter-annual variation in climatic conditions, but differ in the accuracy of their decisions as has recently been seen in other species (e.g., Charmantier et al. 2008).

Methods

Study species and system

Common eiders are long-lived, iteroparous sea ducks with females exhibiting strong philopatry to breeding areas; first-time breeding females are also typically faithful to their natal colony (Wakeley and Mendall 1976; Swennen 1990; Tiedemann et al. 1999). Data were collected from the largest known nesting colony of common eiders in the Canadian Arctic (up to 9,000 pairs annually) between 2002 and 2008. The colony is located on Mitivik (East Bay) island (64°02′N, 81°47′W) in the East Bay Migratory Bird Sanctuary, Nunavut, Canada, a small (800 × 400 m), low-lying (<8 m elevation) island. Females at East Bay migrate from wintering grounds in May, arrive in early June and lay between mid-June and early July. Mean clutch size for our population is 2.85 ± 1.04 (SEM ± SD) eggs ($n = 345$ clutches, 2002–2008), clutch size declines seasonally (0.045 eggs/day; Descamps et al., submitted) and ducklings hatch following an incubation period of almost 24 days (Bottita et al. 2003). The island supports approximately 30 nesting pairs of herring gulls (*Larus argentatus*) (Allard et al. 2006), which mainly prey on eider eggs and some ducklings (Allard and Gilchrist, unpublished data). We collect accurate reproductive data (laying date of the first egg and hatching date) through the careful monitoring (via eight blinds within the colony) and nest visitation of individual females. Individuals are accurately tracked by the pre-breeding capture, banding (metal and alpha-numeric color bands) and unique marking (combination of temporary nasal-tags, i.e., lost before the next breeding season) of up to 350 females each year (McKinnon et al. 2006; Descamps et al. 2009). Banding is undertaken from early June to early July, and banding phenology is matched to coincide with arrival dates of eiders within each year (increase in the number of arriving and prospecting females determined from pre-breeding band-reading sessions).

Intra- and inter-annual variation in climatic cues

We focused on temperature and snow cover as possible cues/constraints to breeding females and examined whether these cues predicted laying and the timing of open water (ice-free) conditions. Data on mean daily spring temperature and snow cover (amount of snow on ground in cm) were collated from the weather station at Coral Harbour (64°11′N, 83°21′W; 68 km from East Bay) using Environment Canada's online climate archive database for 2002–2008. We calculated the mean temperature (± 5 days) within each year for: (1) June 1 (early June), (2) June 15 (mid-June), and (3) the mean start of rapid follicular growth—RFG (mean annual laying date of the first egg minus the 9 days required for common eiders to recruit and grow yolk follicles; Robertson 1995). We also calculated mean snow cover for early June and mid-June for each year, as well as the rate of snow loss within this period. Finally, using daily ice cover and concentration maps provided by the Canadian ice service (CIS) online ice archive database, we determined the first day within each year (2002–2008) that East Bay was free of ice (defined as <1/10 concentration of ice cover by the CIS). This is the best approximation we have for the earliest date each year that ducklings can depart with mothers with a reasonable expectation of open water. Unfortunately, precise data on ice thickness within East Bay during the pre-laying period are not available from the CIS, meaning we could not include spring ice thickness as a potential climatic variable in laying/hatching analyses.

Duckling survival estimates

We used the return rates of female ducklings to the colony as a proxy of their survival. Return rates are predicted to be a good estimate of survival given that first-year prospecting and first-time breeding females are highly faithful to their natal colony (Wakeley and Mendall 1976; Swennen 1990; Tiedemann et al. 1999). Ducklings leave the colony for the sea with their mother, and often with additional attending hens, immediately following hatching (Bustnes and Erikstad 1991; McKinnon et al. 2006). Since 2003, hundreds of ducklings have been banded ($n = 624$; both metal and an individual color band for later re-sighting at a distance) by funnelling departing hens and ducklings into wire mesh holding pens (i.e. traps) set up on beaches of the island; ducklings are released soon after at the water's edge. Since ducklings leave their nest just after hatching (<24–48 h; Gilchrist, unpublished data), date at capture is a good proxy of their hatching date. Band re-sighting efforts in subsequent years were conducted from the same blinds used to observe female reproductive activities, minimizing disturbance to eiders nesting on the island. Mean offspring recruitment probability in relation to relative hatching dates were calculated using banding data from ducklings hatched from 2003 to 2005 inclusive. Only these years were included since a post-laying outbreak of avian cholera from 2006 to 2008 significantly reduced

duckling recruitment (Descamps et al. 2009; Descamps et al., unpublished data), which would therefore significantly skew results if we included these data. However, these estimates of duckling survival are reliable for cohorts 2003 through 2008 considering that 92% of first re-sighting occurred at age 1, 2 or 3, and 76% at age 1 or 2 (Descamps et al., unpublished data).

Plasticity in laying date in response to climatic variability

Although (1) we are able to individually nasal-tag hundreds of individual females each breeding season and (2) re-sighting rates during arrival are high (McKinnon et al. 2006; Descamps et al. 2009), recapturing individual females and repeatedly tracking their reproductive output across successive years in a colony of up to 9,000 individuals is challenging. As such, among the thousands of breeding nasal-tagged females followed from 2002 to 2008, we have been able to follow only 18 females across at least two repeated laying date observations in two different years. Although this sample size precludes the ability to carry out an extensive analysis linking reproductive plasticity to fitness as has recently been used in long-term datasets of European species (Nussey et al. 2005; Garant et al. 2007; Brommer et al. 2008; Charmantier et al. 2008), it is nonetheless possible to examine individual differences in plasticity and accuracy in the timing of laying (Brommer et al. 2003). We report these relationships as a basis for future study of reproductive plasticity in response to climatic variability.

Statistical analyses

We used general linear mixed model (GLMM) analyses to examine variability in reproductive timing (inter-individual analyses) and relationships between climatic variables and reproductive timing (inter-annual analyses); year was included as a random effect using the restricted maximum likelihood (REML) method. We then used linear regression analyses to explore relationships between local climatic cues (temperature, snow cover, rate of snow loss, ice-free date of the bay) and (1) mean annual laying date, (2) mean annual hatching date, and (3) variation in the mean annual laying date. To test whether temperature acts on laying date via a threshold effect on reproduction, we also constrained the analyses to the mean RFG date. The same absolute temperature at the RFG stage across years would indicate that individuals must reach this temperature threshold before commencing follicle recruitment. Only first reproductive attempts were included in analyses of reproductive traits (indeed, second laying attempts after primary clutch failure are very rare in this colony). Climatic variables and mean annual laying and hatching dates were normally distributed (Shapiro–Wilk tests: all $p > 0.35$). As some mean annual temperatures were close to 0°C, we transformed them into Kelvin before calculating coefficients of variation (CoV) since the CoV is highly sensitive to small changes in the mean when it is close to zero, limiting its usefulness (Zar 2009). A mixed model analysis of variance was used for reaction norm analyses to test for differences between individuals in both the laying date temperature and laying date–ice-free date relationship; individual identity was set as a random effect and temperature/ice-free date as a fixed effect. A significant individual identity term indicates that individuals differ in the elevation of the laying date–climatic cue relationship (individuals differ in their absolute laying date in the average climate), and a significant interaction term between individual identity and the climatic cue indicates that the slopes of the laying date–climatic cue relationship are significantly different (individuals differ in their climate-related reproductive flexibility; Brommer et al. 2003). Statistical analyses were performed using JMP 7.0.2 (SAS Institute) and mean $\pm$ SE are reported.

Results

Climate-related flexibility in reproductive decisions

Inter-annual variability in mean daily temperature and snow cover in May and June was large (temperature: $F_{6,214} = 10.6$, $p < 0.001$; Fig. 1a; snow cover: $F_{6,850} = 13.7$, $p < 0.0001$; Fig. 1b). Inter-annual variation in laying dates was also large ($F_{6,751} = 40.4$, $p < 0.0001$; Table 1), and laying date was highly correlated with hatching date across individuals ($r^2 = 0.92$, $F_{1,308} = 3{,}572.8$, $p < 0.0001$, $\beta = 0.95$; Table 2), indicating little flexibility in incubation duration. The warmer the temperature in mid-June, the earlier the mean laying date (Table 2; Fig. 2a); however, temperature in early June showed no correlation with laying date (Table 2). The temperature at the start of the rapid follicular growth (RFG) stage was negatively related to both mean annual laying and hatching date (Table 2; Fig. 2b). Additionally, temperatures in mid-June predicted open water (ice-free) conditions at East Bay ($r^2 = 0.77$, $F_{1,6} = 16.4$, $p = 0.009$, ice-free date $= 209.8 - 2.33 \times$ mid-June temperature) and both the mean annual laying date and the mean annual hatching date were strongly correlated with the annual first day of ice-free conditions at East Bay (Table 2; Fig. 2c). Neither snow cover, nor the rate of snow loss, predicted laying or hatching date (Table 2) or ice-free conditions (early June snow cover: $r^2 = 0.009$, $p = 0.88$; mid-June snow cover: $r^2 = 0.03$, $p = 0.80$; rate of snow loss: $r^2 = 0.13$,

Table 1 Reproductive timing in Arctic common eiders (*Somateria mollissima*) breeding at East Bay, Nunavut, Canada (2002–2008)

Study year	Mean laying date (days after June 1)	n_{laying}	Mean hatching date (days after July 1)	n_{hatch}
2002	29.4 ± 0.99	55	24.3 ± 1.09	26
2003	29.6 ± 0.62	90	24.8 ± 1.22	38
2004	34.3 ± 0.60	150	32.0 ± 0.54	76
2005	25.5 ± 0.49	150	20.3 ± 0.50	77
2006	23.8 ± 0.52	154	17.6 ± 0.53	66
2007	30.8 ± 0.45	154	25.1 ± 0.61	63
2008	26.7 ± 0.52	96	22.0 ± 0.56	38

n_{laying} and n_{hatch} indicate the annual number of nasal-tagged females that laid eggs and hatched ducklings, respectively, in the colony and were then followed; mean ± SEM are shown

$p = 0.61$. Moreover, there was no relationship between the first day of zero snow cover and the earliest laying date ($r^2 = 0.07$, $F_{1,6} = 0.40$, $p = 0.55$); indeed, in only 2 years (2007 and 2008) did any birds (only three individuals) ever begin laying before all snow had disappeared: 2/153 birds in 2007 (2 days prior) and 3/96 birds in 2008 (1 day prior).

Climatic variation, reproductive timing and fitness

Warmer springs had higher variation in spring temperatures ($r^2 = 0.72$, $F_{1,6} = 13.1$, $p = 0.01$, $\beta = 0.00073$; Fig. 3a). This variability strongly predicted variability in mean laying date ($r^2 = 0.92$, $F_{1,6} = 56.9$, $p = 0.0006$, $\beta = 1.54$; Fig. 3b) and, as such, laying was more protracted in warmer springs ($r^2 = 0.59$, $F_{1,6} = 7.2$, $p = 0.04$, $\beta = -0.0067$) due to more individuals laying after than before the mean as mid-June temperature increased (i.e., increasing positive skew in the laying date distribution as mid-June temperature increased: $r^2 = 0.56$, $F_{1,6} = 6.46$, $p = 0.052$, $\beta = 0.069$; Fig. 3c).

The highest duckling survival probability occurred in females that timed laying to match duckling hatching 3 days prior to fully ice-free conditions at East Bay (Fig. 4), i.e., best explained by a quadratic function ($r^2 = 0.46$, $F_{2,15} = 6.48$, $p = 0.009$, mean recruitment = $0.198 - 0.012 \times$ deviation from ice-free date $- 0.002 \times$ deviation from ice-free date^2). The linear relationship was marginally significant, but had much less explanatory power ($r^2 = 0.21$ $F_{1,16} = 4.37$, $p = 0.053$; mean recruitment = $0.132 - 0.011 \times$ deviation from ice-free date).

Climate-related reproductive plasticity

The laying date of females from which we had at least two breeding attempts across years was earlier in warmer springs and earlier ice-free dates (temperature: $t = -2.88$, $p = 0.007$, $\beta = -1.34 \pm 0.48$, $n = 36$; Fig. 5a; ice-free date: $t = 2.96$, $p = 0.007$, $\beta = 0.47 \pm 0.16$, $n = 36$; Fig. 5b), as was seen at the population level (Table 2; Fig. 2). There was a strong individual effect for both mean mid-June temperature and ice-free date which explained an additional 33.7 and 36.4% of the variance, respectively, (temperature: female: $F_{17,35} = 2.39$, $P < 0.05$; female × temperature: $F_{17,35} = 1.29$, $p = 0.25$; $n = 36$, $r^2 = 73\%$; ice-free date: female: $F_{17,35} = 2.27$, $P < 0.05$; female × ice-free date: $F_{17,35} = 1.70$, $p = 0.54$; $n = 36$, $r^2 = 72\%$). The difference between the earliest and latest laying date elevation was over 8.6 days. The range in predicted laying dates in the average environment, i.e., calculated for each individual using average spring temperature, was -5.3 to $+10.7$ days. Predicted relative laying date (deviation from the first day of ice-free conditions) indicates that 28% (5/18) of the females would have lower duckling recruitment probability than birds laying at the population mean date based on the recruitment-timing of reproduction relationship presented in Fig. 4.

Table 2 Relationships between local climatic variables and reproductive timing in Arctic common eiders breeding at East Bay, Nunavut, Canada (2002–2008)

Climatic variable	Mean laying date				Mean hatching date			
	R^2	$F_{1,6}$	p	β	R^2	$F_{1,6}$	p	β
Mean temperature early June	0.11	0.65	0.46	−0.52	0.06	0.31	0.600	−0.46
Mean temperature mid-June	**0.59**	**7.29**	**0.04**	**−1.22**	**0.66**	**9.93**	**0.025**	**−1.61**
Mean temperature RFG	**0.75**	**15.4**	**0.01**	**−1.41**	**0.82**	**23.5**	**0.005**	**−1.84**
Mean snow cover early June	0.08	0.49	0.52	−0.13	0.07	0.41	0.630	−0.16
Mean snow cover mid-June	0.02	0.12	0.76	−0.05	0.01	0.06	0.870	−0.06
Rate of snow loss	0.22	1.02	0.57	−1.71	0.24	1.21	0.390	−2.12
Date of ice-free conditions	**0.64**	**8.73**	**0.03**	**0.47**	**0.78**	**17.4**	**0.009**	**0.66**

Bold signifies significance at $p < 0.05$. See "Methods" for explanations of climatic variables
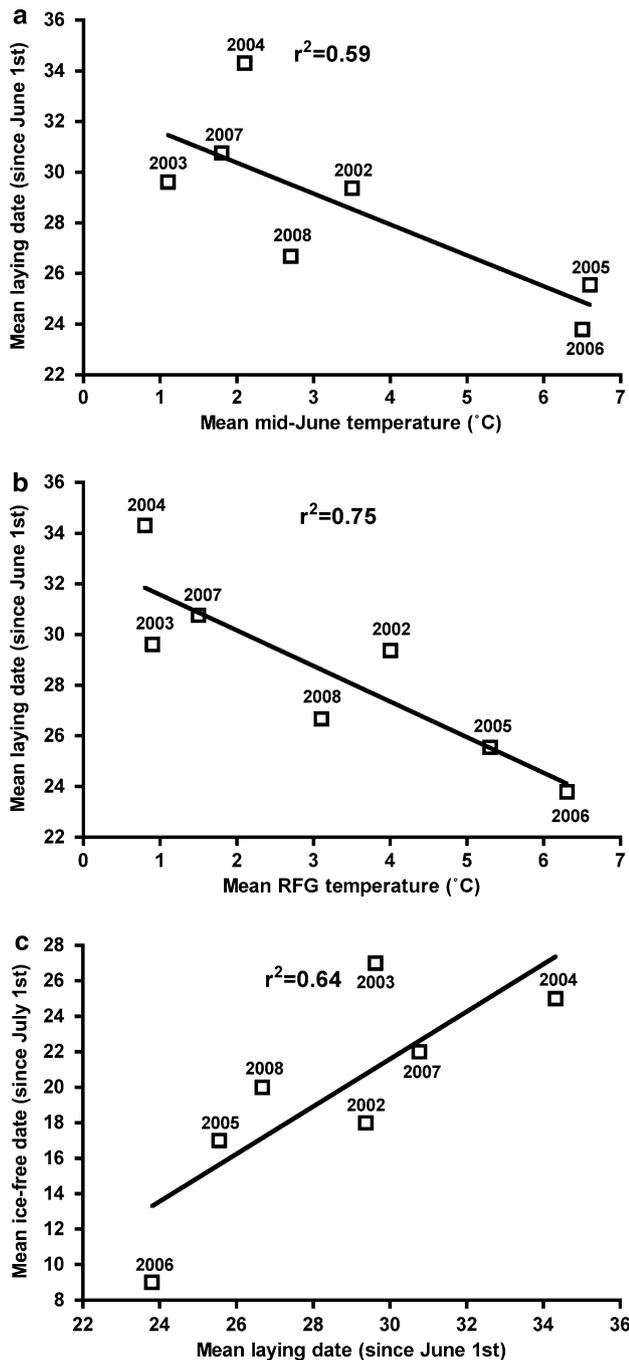
Fig. 2 Relationship between **a** the mean temperature in mid-June and the mean annual laying date, **b** the mean temperature at the RFG stage (see "Methods") and the mean annual laying date, and **c** the mean annual laying date and the first day of ice-free conditions at the East Bay eider colony, Southampton Island, Nunavut, Canada. Laying date is expressed in days from June 1 and ice-free date from July 1

Fig. 3 Relationships between variability in both June temperature and laying date: **a** mid-June temperature and variation (CoV) in the temperature, **b** variability in mid-June temperature and variability in mean laying date, and **c** mid-June temperature and degree of positive skew in the population laying date at the East Bay eider colony, Southampton Island, Nunavut, Canada; see "Methods" for the calculation of the CoV and results for explanation of skew

Discussion

In common eiders nesting in the largest known Arctic colony in Canada, temperature in mid-June was a good predictor of laying date, hatching date and the occurrence of ice-free conditions in the surrounding bay. Mean hatching date was closely associated with the first day of ice-free conditions, and ducklings that hatched just prior to fully ice-free conditions had the highest return probability. These results are biologically relevant since eider
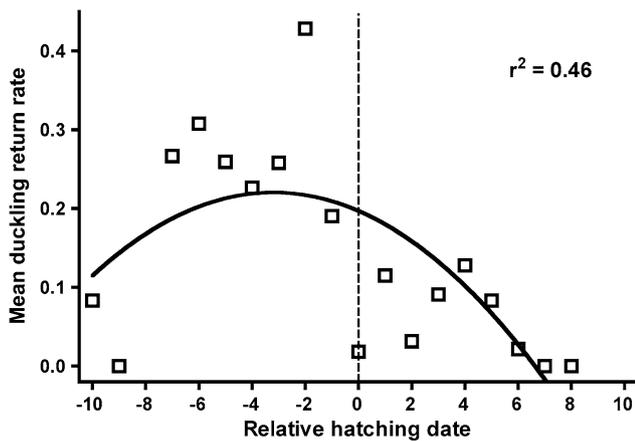
Fig. 4 The proportion of female common eider ducklings returning to the breeding colony as adults in relation to their relative hatching date within a given year (0 = first day of ice-free condition within each year) at the East Bay eider colony, Southampton Island, Nunavut, Canada
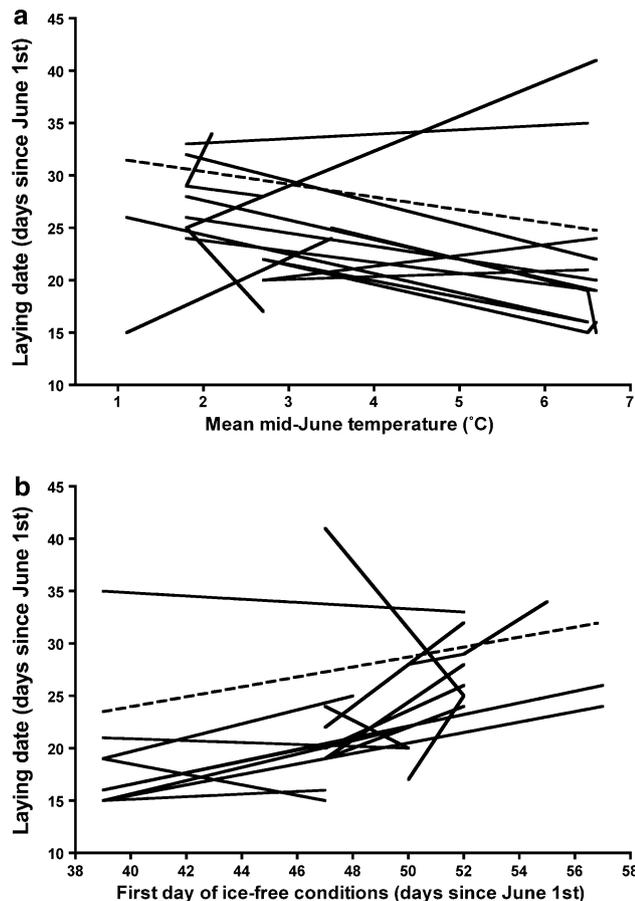
Fig. 5 Individual flexibility in laying date decisions amongst 18 female common eiders breeding in successive years in response to variation in **a** mid-June temperature and **b** the timing of ice-free conditions at the East Bay eider colony, Southampton Island, Nunavut, Canada. *Stippled lines* are the mean population responses. Laying date and day of first ice-free conditions are expressed in days from June 1

ducklings forage independently from their mothers and therefore have an immediate need for open water to maximize the amount of time spent acquiring resources for growth (and future reproductive returns; Christensen 1999; Goudie et al. 2000). Interestingly, neither ice-breakup nor reproductive timing in eiders was related to spring snow cover. Moreover, although snow cover is likely more of a constraint on, rather than a cue to, the timing of laying, snow cover did not appear to limit the timing of laying as snow disappeared well before almost all birds began laying.

Links between climate and the timing of reproduction

Our data suggest that local pre-laying temperature influences the strategy to time laying to match duckling hatching to ice-free conditions. That warmer springs were correlated with earlier laying dates and earlier ice-breakup suggests a threshold temperature that drives the commencement of follicle recruitment; indeed, recent evidence suggests that temperature can act as a causal cue for the timing of breeding (Visser et al. 2009). If so, we would expect a similar threshold temperature across years in an analysis constrained to temperature cues at the RFG stage. However, eiders initiated egg formation at a range of absolute temperatures suggesting that, while females likely use temperature to time reproduction, they obviously use additional cues to fine-tune their decisions (i.e., birds do not respond to a threshold temperature and likely integrate information from multiple cues). Additional cues could include ice thickness, ice flex as the tide comes in and out of East bay, ice-breakup at local river mouths and even the amount of time already passed in the season. Furthermore, variation in temperature could simultaneously influence (1) the quantity/quality of pre-laying resources by altering access to several river mouths that open into East Bay which are important for condition gain during pre-breeding (Sénéchal 2009; Sénéchal et al., submitted; Descamps et al., submitted), and (2) the timing of ice-free conditions. Access to pre-laying resources are an important consideration since waterfowl only partly depend on body stores to finance their reproduction and must gain condition (hyperphagia) during pre-laying by acquiring local resources (Bêty et al. 2003; Sénéchal 2009; Sénéchal et al., submitted). In this case, temperature could be related to the timing of laying via changes in access to pre-laying resources, rather than variation in the cue itself. As such, although it initially appears that temperature plays a simplistic direct role in the timing of reproduction, multiple cues and environmental responses related to temperature may be involved in fine-tuning decisions about the timing of laying. Data on seasonal variation in the rate of condition gain during the pre-laying period, as well as the

number and duration of foraging trips, will improve our understanding of whether temperature directly or indirectly influences the timing of laying.

Fitness consequences for the timing of reproduction

Climatic warming is selecting for earlier laying in some European passerines, as females attempt to maintain the match between climate-induced resource abundance and offspring requirements (Nussey et al. 2005; Charmantier et al. 2008). In eiders, the highest female duckling survival probability was apparently not achieved by the earliest-laying individuals, but by individuals that timed laying to match duckling hatching to ice-free conditions (to be precise, maximum survival was attained by hatching 3 days before full ice-free conditions; Fig. 4). This curve–linear relationship between the timing of laying and reproductive success has been previously reported for both Arctic and temperate species (Findlay and Cooke 1982; Lepage et al. 2000; references in Dunn 2004). The laying date which maximizes duckling return rate can be predicted by: (1) the correlation between spring temperature and ice-free date, (2) the correlation between laying and hatching dates and ice-free date, and (3) the fact that open water is important for duckling fitness (see previous paragraph). Our data indicate that very early-laying females may not maximize duckling recruitment in 'average' years. This could be due to many factors including ducklings facing severe foraging conditions if ice has not yet fully left the bay (see Lepage et al. 2000 for a comparison in a terrestrial-foraging bird) or increased predation risk due to a lack of a predator-swamping. Late-laying females also experienced reduced duckling return rates which could conceivably occur via limited foraging time for ducklings in the short seasonal post-natal environment, being at a higher risk to harsh fall storm exposure, and/or increased predation risk. A potential climate-induced reduction of reproductive success in late-laying birds could be amplified if these birds are also of lower quality (i.e., young and inexperienced, those in poor arrival condition), which may further reduce reproductive success (see Öst et al. 2008).

We found a positive relationship between spring temperature and its variability, and this variability was positively related to variability in laying date. The most parsimonious explanation is that more low-quality females (see above) had the opportunity to commence laying in warmer years (see Reed et al. 2004 for an example in snow geese). Indeed, the decision of when to reproduce is likely only second in importance to whether or not to reproduce in a given year for females of a long-lived avian species with low annual fecundity, breeding in a seasonal environment (Arnold and Rohwer 1991; Erikstad et al. 1993; Dunn 2004). As such, we would therefore expect more

birds (presumably of lower quality; see Bêty et al. 2003) to lay later in the season in warmer years. This idea is supported by an increase in the positive skew of the population laying distribution with increasing mid-June temperatures; that is, more birds laid after the population mean than before in warmer springs. It is therefore possible that warmer climatic conditions may be correlated with increased nesting attempts in eiders (see also Rönkä et al. 2005; Lehikoinen et al. 2006; Jónsson et al. 2009; D'Alba et al. 2010). However, it should be cautioned that an increase in the absolute number of laying female eiders in warmer years does not necessarily equate to an increase in colony productivity, since we do yet know (1) whether additional females are of low or high quality, or (2) how warmer breeding seasons effect downstream reproductive stages (i.e., incubation, hatching and duckling growth/survival). Indeed, work in snow geese has revealed that warmer springs negatively influence traits related to gosling fitness (Dickey et al. 2008).

Climate-related reproductive plasticity

Repeated-measures data on the reproductive decisions of individuals are used to examine individual variation in phenological responses to climate change and consequences of plasticity on fitness (Nussey et al. 2005; Both et al. 2006; Reed et al. 2006, 2009; Charmantier et al. 2008; Brommer et al. 2008). Our repeated-measures dataset is presently too small to examine the effects of plasticity on fitness; nevertheless, it provides useful information about the degree of individual reproductive plasticity in response to climatic variability. Most of the 18 females examined had a similar degree of climate-induced reproductive plasticity (similar slopes), but significantly different laying date choices in the average environment (different elevations), in their laying date–temperature relationships (Fig. 5). These results are in-line with those of Erikstad et al. (1993) indicating that laying date is repeatable within individuals and that over a third of the variation is due to among-individual effects (see "Results"). The source of this among-individual variation is difficult to determine, but may be due to differences in individual quality (i.e., age, experience or intrinsic quality). These results are also similar to a British population of great tits (Parus major) where females are relatively invariant (little to no inter-individual variation in plasticity), and the mean population response is highly adaptive despite the presence of individual variation in the ability to accurately predict the optimal date to initiate laying (Garant et al. 2007; Charmantier et al. 2008). Our results suggest that climatic variation has likely selected for flexibility in phenology in our population of eiders, at least in relation to the present degree of climatic variation.

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