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HIGHLIGHTED STUDENT RESEARCH

The impact of sea ice conditions on breeding decisions is modulated by body condition in an arctic partial capital breeder

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Abstract

Determining how environmental conditions interact with individual intrinsic properties is important for unravelling the underlying mechanisms that drive variation in reproductive decisions among migratory species. We investigated the influence of sea ice conditions and body condition at arrival on the breeding propensity, i.e. the decision to reproduce or not within a single breeding season, and timing of laying in migrating common eiders (*Somateria mollissima*) breeding in the Arctic. Using Radarsat satellite images acquired from 2002 to 2013, we estimated the proportion of open water in the intertidal zone in early summer to track the availability of potential foraging areas for pre-breeding females. Timing of ice-breakup varied by up to 20 days across years and showed strong relationship with both breeding propensity and the timing of laying of eiders: fewer pre-breeding individuals were resighted nesting in the colony and laying was also delayed in years with late ice-breakup. Interestingly, the effect of sea ice dynamics on reproduction was modulated by the state of individuals at arrival on the breeding grounds: females arriving in low condition were more affected by a late ice-breakup. Open water accessibility in early summer, a likely proxy of food availability, is thus crucial for reproductive decisions in a (partial) capital breeder. Our predictive capacity in determining how Arctic-breeding seabirds respond to changes in environmental conditions will require incorporating such cross-seasonal cumulative effects.

Keywords Reproductive decisions · Breeding propensity · Individual state · Sea ice · Common eider

Introduction

The trade-off between current investment in reproduction and survival remains one of the most prominent topics in ecological and life history theory (Williams 1966; Stearns 1992; Ricklefs and Wikelski 2002; Sutherland et al. 2013; Kulaszewicz et al. 2016). Higher energy allocation to current reproduction is expected to limit the energy available for somatic needs, resulting in downstream consequences to both future reproductive success and survival in iteroparous species (Stearns 1989, 1992; Harshman and Zera 2007). The largest expected drivers of reproductive investment are: (a) access to resources (interplaying with environmental stochasticity) and (b) individual quality (Wilson and Nussey 2010). A great deal of research has been dedicated to investigating how these drivers govern life-history traits such as litter, clutch size, parental care or progeny survival (Williams 1966; Van Noordwijk and de Jong 1986; Brown and Shine 2002; Bustnes et al. 2002; Gagliano et al. 2007). However, early reproductive decisions such as breeding propensity (defined as the decision of whether to reproduce within a

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This interdisciplinary study revealed the interplay between environmental stochasticity (Arctic sea ice dynamic) and individual state that modulate reproductive decisions in a seabird species.

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single breeding season) have been less examined despite that it can also have tremendous impacts on subsequent survival and/or future reproduction (Faaborg et al. 2010; Cubaynes et al. 2011). For example, in many long-lived species, individuals can skip reproduction until the following reproductive episode to avoid breeding costs that may jeopardize their own survival (Rivalan et al. 2005; Souchay et al. 2014; Legagneux et al. 2016). Although breeding propensity is considered as a critical demographic parameter given its strong impact on both individual fitness and population growth (Cam et al. 1998; Sedinger et al. 2008), it is considered to be one of the most difficult reproductive parameters to properly estimate in vertebrates (Sedinger et al. 2001, 2011) since non-breeders are often entirely absent from breeding sites (Spendelow and Nichols 1989; Chastel 1995; Reed et al. 2004;). Consequently, there are few studies on the mechanisms that mediate reproductive decisions (Bond et al. 2008; Souchay et al. 2014). For migratory species, the state of an individual upon arrival in the breeding area is a prevailing parameter governing individual variation in reproductive decisions (Drent and Daan 1980; Clutton-Brock 1988; Blums et al. 2005; Descamps et al. 2011; Warren et al. 2014; Legagneux et al. 2016) and the probability of reproducing successfully should increase with a greater body condition at arrival (Rowe et al. 1994; Bêty et al. 2003; Hennin et al. 2016). Individual state and reproductive decisions also depend on environmental conditions, and the effect of environmental conditions on breeding decisions and survival can moreover be modulated by individual state or quality (Öst et al. 2003; Robert et al. 2012).

Most Arctic ecosystems are driven by or depend upon ice dynamics (Post et al. 2013) and these have changed extensively in recent decades in response to climate change and various anthropogenic activities (ACIA 2005). Changes in sea ice affect organisms that rely on ice cover for different life functions (Stirling et al. 2004; Gaston et al. 2009; Gilg et al. 2012). Several studies have shown the impacts of variation in ice conditions on reproductive parameters of migratory seabirds breeding in the Arctic (Gaston and Hipfner 1998; Gaston et al. 2005; Chaulk and Mahoney 2012). However, because of the general lack of knowledge on the underlying mechanisms generating variation in key reproductive decisions, no studies have to date examined the predicted interactive effects between ice dynamics and individual state prior to investment in reproduction on decisions such as breeding propensity and phenology.

Here, we use a long-term study (2002–2013) of Arctic-nesting common eiders (*Somateria mollissima*) to examine the interactive effects of individual body condition and sea ice conditions on reproductive decisions. This system is particularly useful for examining these questions because eiders can be captured at arrival from migration and prior to making breeding investment decisions (Hennin et al. 2015). Arctic-breeding eiders use a mixed capital-income reproductive strategy where they must gain enough body reserves prior breeding. Females rely partly on local resources acquired during the pre-breeding and laying period to build up body reserves (Sénéchal et al. 2011a) and produce their clutch (Descamps et al. 2011; Sénéchal et al. 2011a, b). Coastal habitats used by eiders are still largely ice-covered following their migratory arrival in the Eastern Arctic (Gilchrist pers. obs.). Consequently, the timing of ice-breakup should drive food access in the vicinity of the breeding colony possibly impacting rate of condition gain following arrival. Individual state at arrival in the colony largely determines reproductive decisions. For instance, by experimentally reducing body mass of pre-breeding female common eiders, a causal relationship was confirmed between body mass and breeding propensity (Legagneux et al. 2016) and between body mass and timing of breeding (Descamps et al. 2011). We focused this present work on the breeding propensity and breeding phenology of individuals in relation with sea ice condition. We anticipated that both the timing of sea ice breakup and individual body condition at arrival should influence reproductive decisions of female common eiders. Hence, we predicted that: (1) a late ice-breakup would result in a reduction in breeding propensity and delayed laying dates and, (2) females arriving in lower condition would: (a) have a lower breeding propensity and delayed laying dates, and (b) be more affected by a late ice-breakup. Finally, we tested for the effect of individual arrival date on breeding decisions.

Methods

Study area

The study was conducted at the East Bay Migratory Bird Sanctuary on Southampton Island, Nunavut, in the Canadian Arctic (64°02′N, 81°47′W; Fig. 1). East Bay supports the largest known nesting colony of common eiders in the Canadian Arctic occurring on Mitivik Island (up to 8000 pairs annually between 2002 and 2013). This small (400 × 800 m), low-lying (< 8 m) island is located in the middle of the bay at 5 km from the nearest coast. East Bay is characterized by landfast sea ice, defined as sea ice that forms and remains fixed along the coast (World Meteorological Organisation 1970; König Beatty 2007), which melts completely during the summer. This bay is shallow (< 30 m; Sénéchal & Bêty, unpublished data) and receives freshwater input from six rivers (Fig. 1). The flush of terrestrial water runoff in the spring accelerates local melting of seasonal sea ice in subarctic and arctic coastal ecosystems (Dean et al. 1994; Ingram et al. 1996; Granskog et al.

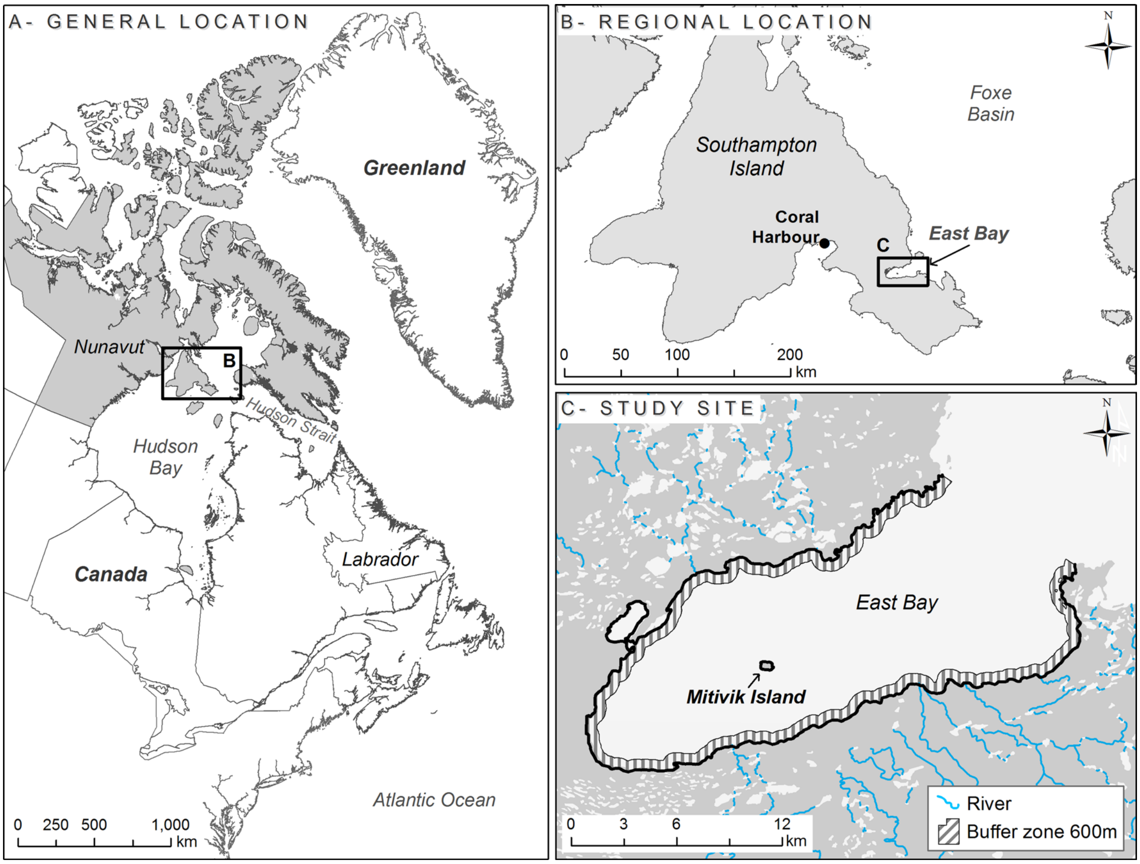

Fig. 1 Maps outlining the location of the study area. The common eider colony is located on Mitivik Island, in East Bay, on Southampton Island, Nunavut, Canada. The six rivers flowing into the bay and the tidal buffer zone of 600 metres used to determine the timing of ice-breakup (proportion of open water) are also shown (in C)

2011) and this likely explains the initial melting of sea ice at river mouths at East Bay.

During the non-breeding season, common eiders from this colony migrate through Hudson Strait to winter in either southwest Greenland (~ 60% of population) or on the Labrador and Newfoundland Coast (~ 40% of population; Mosbech et al. 2006). The first individuals to visit East Bay and surroundings arrive up to a month before the laying period begins and when the bay is still completely ice-covered (Mosbech et al. 2006; Bêty & Gilchrist, unpublished data). As the season progresses and the sea ice at river mouths thaws, eiders forage on benthic invertebrates in open water at these locations and in the nearby associated ice leads (Bêty & Gilchrist, unpublished data; Sénéchal et al. 2011b). The ice cover breaks up in July and the ice floes are pushed in and out of the bay by tides, winds and currents, and the bay is entirely ice-free by early August. Importantly, female eiders that time laying so that the hatching of ducklings occurs a few days prior to entirely ice-free conditions have the highest probability of duckling survival (Love et al. 2010).

Eider reproductive data

Each year (2002–2013), we captured female eiders (87–335 females annually) in flight as they passed over the nesting colony during their pre-breeding period in early June using large salmon gill nets suspended by cables. The trapping period lasted 3 to 4 weeks every year. We thus assumed that capture date was a good proxy of arrival date at the colony (Descamps et al. 2010). Individuals were weighed using a Pesola scale (± 2.5 g), banded (with both metal and alphanumeric colour bands) and marked with a unique temporary plastic nasal tag combination (Descamps et al. 2011). Body mass at capture was used as a proxy of female body condition (a measure of the individual state) at arrival since it has been demonstrated to be an adequate index of endogenous reserves (Descamps et al. 2011). Previous studies at our colony have further demonstrated that a body mass threshold around 2000 g is required to initiate follicle development (Sénéchal et al. 2011a; Hennin et al. 2015).

We collected reproductive data (e.g. timing of nest initiation) by monitoring the colony from eight permanent concealed observation blinds which facilitated consistent inter-annual behavioural observations. From these blinds, we could monitor marked eiders using spotting scopes. Because nasal-tagged females were easily identified at distance and since we monitored the colony twice daily for several hours, we could accurately identify and track individuals. We estimated the breeding propensity of female eiders as follows: individuals captured and resighted on a nest in the colony were classified as breeders, while individuals that were caught and banded, but not resighted on a nest, were considered non-breeders (total number of females nasal-tagged at banding: $N = 1751$, 2002–2013). Since female eiders are highly philopatric (i.e. faithful to their natal and breeding area; Coulson 1984; Swennen 1990) and given that our colony is geographically isolated from the closest large colony (> 200 pairs being > 200 km away), females not resighted on a nest on Mitivik Island have a lower chance to be breeding elsewhere, and were thus categorized as non-breeders. Laying dates were calculated using only the first nesting attempt of nasal-tagged females ($N = 780$). Renesting following early nest failure is rare at East Bay (< 3.4% over 12 years, Gilchrist, unpublished data). Only four individuals were recaptured twice in our dataset, we decided not to include a random factor to account for this pseudo-replication because we obtain similar results with and without those recaptured birds. A similar approach was recently used to measure breeding propensity in the colony (Legagneux et al. 2016).

To reduce disturbance to the colony, only brief visits to perform egg candling were made to improve the estimation of laying dates. The observation effort was highly comparable between years considering the small size of the island and the eight blinds dispersed strategically throughout the colony, and this contributed to a high detection probability of nasal-tagged females. We could not use the reproductive data for 2010 in our analyses because of a high rate of accidental nasal tag loss associated with the use of the wrong type of monofilament used to attach the tags. Although adding the 2010 reproductive data did not extensively change the observed pattern, we decided to withdraw this year to reduce potential bias.

Monitoring of ice-breakup

Information on sea ice conditions at East Bay for the period of interest (20 May to 31 July) was derived from RADARSAT images acquired from the Canadian Ice Service (see methods in electronic supplementary material (1). To examine the timing of ice-breakup at river mouths in early June, we calculated the proportion of open water (percentage of open water, hereafter OW%) in a zone along the shoreline. This zone included the river mouths where eiders are known to forage during the pre-breeding and laying periods. To represent this area, we created a 600-m buffer zone extending offshore from the shoreline (1:250,000 digital vector; National Topographic Data Base, NTDB, Natural Resources Canada, https://geogratis.ca/, last accessed October 2014). We tested different buffer sizes from 200 to 1000 m with a 200-m step (the minimum resolution of our images). We limited the maximum buffer width to 1000 metres because we were interested by the sea ice melt at river mouths only (Sénéchal et al. 2011a). We used a 600-m buffer (the closest value to the median). All buffers were highly correlated ($r = 0.987$, $p < 0.001$).

To generate an estimate of the OW%, we extracted the pixels of the radar images contained in the buffer using the *Extract by mask* Tool from the *Spatial Analyst Extension* in ArcGIS. The percentage of water pixels out of the total pixels of the buffer was then calculated to obtain the OW% for a given day. Once calculated for all images, we created a time series of OW% for each year (see electronic supplementary material, figure S1) and identified the day associated with a given OW% to quantify the annual timing of ice-breakup at river mouths. We tested multiple OW% (ranging from 1 to 10% or 0.4 to 4 km^2, respectively) to assess which OW% was most correlated to eider reproductive parameters and ice conditions. The OW% of 1% was selected as the best predictor of the timing of ice-breakup at river mouths because this was the minimal surface measurable with our satellite images and a small OW% represents a great access to benthic foraging habitats. The OW% of 1% is therefore referred to as the timing of ice-breakup at river mouths in our study.

Statistical analysis

We tested the effect of both, (a) timing of ice-breakup at river mouths and (b) female body condition at arrival on the breeding propensity and the timing of laying of common eiders. Mixed models were used to quantify variation in breeding propensity and timing of laying because we had two hierarchical levels: eiders and ice-related parameters. We also statistically assessed year-differences of the time series (Pinheiro and Bates 2000). We included the arrival date at the colony as a covariate in our models to control for its effect on body condition at arrival and given that this parameter appears to directly influence eider breeding decisions at this colony (Descamps et al. 2011; Hennin et al. 2016). We also tested for a quadratic effect for arrival date because if a general decrease in breeding propensity over time is the norm, we expected that birds could also pay a cost of arriving too early on the breeding ground (Nilsson 1994; Bêty et al. 2004). We performed mixed logistic regressions using a binomial family to examine breeding propensity (0 = non-breeder, 1 = breeder) using *glmer* function from the *lme4* package and *AICcmodavg* package (Mazerolle 2016) in

R 2.15.3 (R Development Core Team). For the timing of laying, we used linear mixed models using *lme* function from the *nlme* package. The dispersion parameter for the breeding propensity model when considering a quasi-binomial distribution was close to 1 ($\hat{c} = 0.98$) indicating that there was no significant over-dispersion in our model. For all models, the timing of ice-breakup at river mouths [ICE-BREAKUP], the arrival date at the colony [ARRIVAL], and the individual body condition of female at arrival [CONDITION] were included as fixed factors while year was included as a random factor. We considered individuals as sampling units to take into account the variable response of individuals to explanatory variables rather than mean annual values. We examined the correlation matrices of explanatory variables to avoid multi-colinearity. No explanatory variables were strongly correlated ($r < 0.5$; Supplementary Table S2). We included all possible biologically relevant two-way interactions between covariates. For a retained significant interactions (*), the corresponding main effects were included in the model. Models combining various factors were ranked based on Akaike's Information Criterion corrected for sample size (AICc) to find the most parsimonious model (lowest AICc value; Burnham and Anderson 2004). To evaluate the global fit for the models, we calculated a pseudo-R^2 based on the likelihood ratio using *r.squaredLR* function for the logistic model (breeding propensity). We also estimated the marginal and conditional pseudo-R^2 using the *r.squaredGLMM* function for the linear mixed model (both functions from package *MuMIn*; Barton 2016). All values are presented as mean ± s.e.m.

Results

The sea ice melting patterns at the river mouths at East Bay showed inter-annual variability with years characterized by a rapid and early ice-breakup process (2005–2006) or a long and late ice-breakup punctuated by refreezing events (2004–2009; see electronic supplementary material, figure S1). The timing of ice-breakup at river mouths (i.e. date of 1% of open water at river mouths—OW1%) varied over three weeks over the 12-year study period, from 10 June in 2006 to 01 July in 2009 (see electronic supplementary material, Table S1).

Common eider reproductive parameters showed significant inter-annual variation from 2002 to 2013. The probability that female eiders initiated reproduction (breeding propensity) varied from 60% in 2005 and 2006 to only 33% in 2009 (average of annual means = 45% ± 14.2). The median laying date varied from 23 June in 2006 to 04 July in 2004 (average of annual medians = 29 June ± 0.21 day), i.e. within a narrower timeframe (< 2 weeks) overlapping the period of OW1% (see electronic supplementary material, Table S1). The timing of ice-breakup at the river mouths itself predicted annual variation in both mean breeding propensity ($R^2 = 0.35$, $F_{1,9} = 6.463$; see Fig. 2a) and median laying dates ($R^2 = 0.67$, $F_{1,9} = 21.62$; see Fig. 3a).

The most parsimonious model explaining individual variation in breeding propensity retained four explanatory variables including an interaction between the timing of ice-breakup and the arrival body condition of females (Table 1; other candidate models had a ΔAIC > 8). To illustrate the significant interaction between body condition and sea ice breakup, we used a cut-off at 2,000 g, a

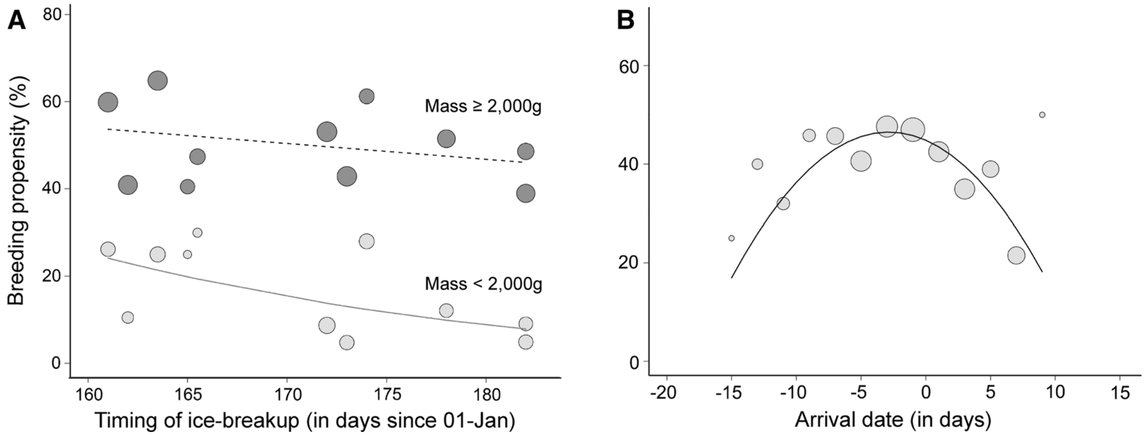

Fig. 2 The breeding propensity (%) of female common eiders in relation to **a** the timing of spring ice-breakup (day of 1% of open water—see methods) and **b** the arrival date at the colony. In **a** females were separated in two categories based on their arrival body mass (≥ or < 2000 g—see methods for justification) to illustrate the interaction between timing of ice-breakup and arrival body condition (see Table 2). Grey circle sizes are proportional to log$N$. Arrival dates are expressed in days relative to the annual mean arrival date. Logistic (**a**) and quadratic (**b**) regressions are fitted for significant (solid line) and non-significant (dotted line) relationships

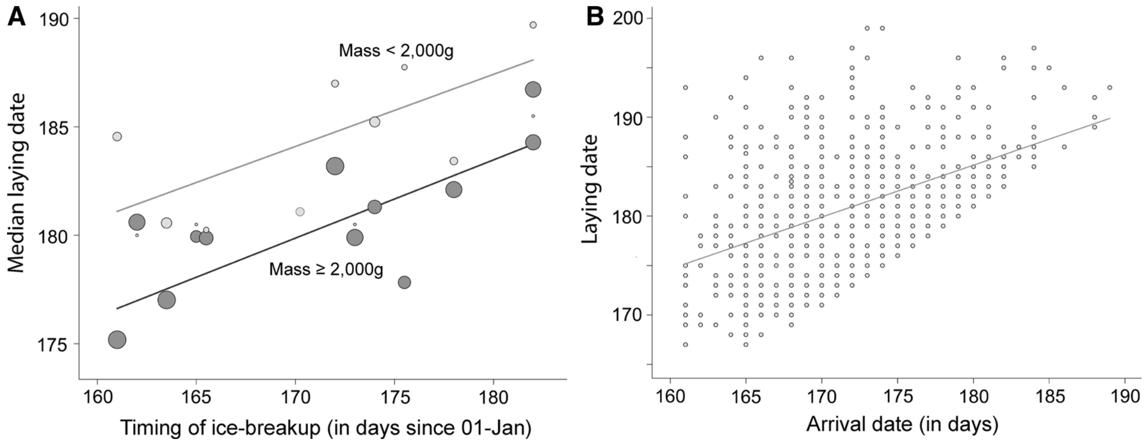

Fig. 3 The laying date of female common eiders in relation to **a** the timing of ice-breakup at river mouths (day of 1% of open water—see methods) and **b** the arrival date at the colony. In **a** females were separated in two categories based on their arrival body mass (≥ or < 2,000 g) and grey circles sizes are proportional to log N. Linear regressions (solid line) are fitted for breeding propensity and timing of ice breakup and arrival

Table 1 (a) Variables, number of parameters, Akaike information criterion, ΔAICc, Akaike weights (*ω*) and pseudo-R^2 for the four most parsimonious models explaining variation in breeding propensity of common eiders breeding at East Bay, Nunavut, Canada (2002–2013)

(a) Selected models for breeding propensity

Variables	*k*	AICc	AAICc	*ω*	Pseudo-R^2
Ice-breakup × condition + arrival date + arrival date^2	7	2112.18	0	0.98	0.22
Ice-breakup × condition + arrival date	6	2120.53	8.02	0.02	0.22
Condition + arrival date + arrival date^2	5	2123.53	11.36	0	0.21
Ice-breakup +condition + arrival date + arrival date^2	6	2124.38	12.2	0	0.21
Null	2	2389.39	277.21	0	0.03

(b) First-ranked model parameter

Parameters	Ice-breakup	Condition	Ice-breakup × Condition	Arrival date	Arrival date^2	Intercept
β	− 3.20E−01	− 2.19E−02	1.51E−04	− 7.84E−02	− 7.80E−02	59.73
SE	8.75E−02	6.78E−03	4.02E−05	1.39E−02	1.40E−02	14.94
P	< 0.001	0.0012	0.0002	< 0.0001	< 0.0001	< 0.0001

(b) First-ranked model parameter estimates, standard error (SE) and *p*-value

Logistic mixed models with year as a random factor. Models with ΔAICc > 20 were discarded from the Table. In the presence of an interaction between two factors, each individual factor was also retained in the model

Ice-breakup Ice-breakup at river mouth, *Condition* Body condition (mass) at arrival, *Arrival date* Relative arrival date

condition threshold required to initiate egg production in female common eider (Sedinger et al. 2011a; see methods). This interaction revealed that breeding propensity varies according to the timing of ice-breakup only for females arriving in lower body condition (< 2000 g; $\beta_{\text{ICE-BREAKUP}} = -\ 0.063 \pm 0.027$; $N = 399$; Fig. 2a) compared to females arriving in higher condition (≥ 2000 g; $\beta_{\text{ICE-BREAKUP}} = -\ 0.013 \pm 0.0148$; $N = 1218$; Fig. 2a). We also found support for a quadratic relationship between arrival date and breeding propensity (Table 1), with a lower probability for females arriving either relatively early or late compared to the yearly median arrival date ($\beta_{\text{ARRIVAL-DATE}}^{2} = -\ 0.078 \pm 0.014$; Table 1; Fig. 2b).

The most parsimonious model explaining variation in laying date of common eiders included three explanatory variables (Table 2). Earlier laying dates were related with an earlier timing of ice-breakup at river mouths in June ($\beta_{\text{ICE-BREAKUP}} = 0.199 \pm 0.066$, $N = 780$; Fig. 3a), individuals arriving earlier at the colony ($\beta_{\text{ARRIVAL-DATE}} = 4.20 \pm 0.044$; Fig. 3b) and those arriving in higher body condition ($\beta_{\text{CONDITION}} = -\ 0.0084 \pm 0.0011$; Fig. 3a). However, we found no evidence of an interactive effect between the timing of

Table 2 (a) Variables, number of parameters, Akaike information criterion, ΔAICc, Akaike weights (ω), and marginal and conditional pseudo-$R^2$for the two most parsimonious models explaining variation in the timing of laying of common eiders breeding at East Bay, Nunavut, Canada (2002–2013)

a) Selected models for timing of laying

Variables	k	AICc	ΔAICc	ω	m-R^2	c-R^2
Ice-breakup + condition + arrival date	6	4758.37	0	0.75	0.31	0.37
Ice-breakup × condition + arrival date	7	4760.55	2.17	0.25	0.31	0.37
Null	3	4886.69	128.32	0	0	0.23

(b) First-ranked model parameter

Parameters	Ice-breakup	Condition	Arrival date	Intercept
β	1.99E−01	− 8.45E−03	4.20E+00	93.19
SE	6.62E−02	1.11E−03	4.43E−02	12.68
P	0.013	< 0.001	< 0.001	< 0.01

(b) First-ranked model parameter estimates, standard error (SE) and p-value

Linear mixed models with year as a random factor. Models with ΔAICc > 20 were discarded from the Table. In the presence of an interaction between two factors, each individual factor was also retained in the model

Ice-breakup ice-breakup at river mouth, *Condition* body condition (mass) at arrival, *Arrival date* relative arrival date

ice-breakup and arrival body condition on individual laying date $\beta = -1.80\text{e}{-}04 \pm 1.60\text{e}{-}04$; Table 2; Fig. 3a).

Discussion

We provided evidence that breeding decisions in common eiders nesting at East Bay in Eastern Arctic depend on the interaction between individual energetic state at arrival and the timing of ice-breakup (a proxy of food availability). To our knowledge, this study is the first to examine the influence of such interactions on breeding propensity, a key reproductive parameter affecting population dynamics in long-lived species. Indeed, female breeding propensity was as low as 33% and the laying date was delayed by as much as 12 days in years of late ice-breakup compared to the earliest ice-breakup year. The influence of sea ice dynamics was dependent on the state of individuals at arrival on the breeding grounds: females arriving in a lower body condition were more strongly affected by late ice-breakup. These interacting effects were only detected for breeding propensity but sea ice conditions also influenced the timing of breeding. Our findings highlight the importance of the timing and the body condition of individuals at arrival on breeding decisions for species that rely partly on stored resources during the breeding season (Descamps et al. 2011).

Our results indicate that breeding propensity was influenced by environmental conditions in seabirds and suggest that failure to breed under unpredictable local conditions may be an adaptive strategy to avoid costs to future reproduction and survival (Bonnet et al. 2002; Cubaynes et al. 2011; Robert et al. 2012). Female eiders arriving in a lower energetic state were more influenced (in terms of breeding decisions) by the timing of ice-breakup compared to females arriving in a better condition. Individuals arriving in a lower state, potentially as a result of severe moult, winter or early spring conditions (Descamps et al. 2010; Harms et al. 2015), are less likely to invest in reproduction if additional severe environmental conditions (such as late ice-breakup that restricts access to foraging) are encountered on the breeding grounds (Lehikoinen et al. 2006). In Monteiro's Storm-Petrels (*Oceanodroma monteiroi*) for instance, reproductive costs (measured through a reduction in survival) typically occurred in years of low food availability and affected only individuals of lower quality (Robert et al. 2012). Not surprisingly then, favourable conditions on the breeding grounds can offset the carry-over effects of previously unfavourable environmental conditions (Legagneux et al. 2012). For female eiders arriving in a positive energetic state (i.e., over the threshold required to start developing follicles, ca. 2000 g; Sénéchal et al. 2011a; Hennin et al. 2015), the timing of sea ice breakup did not significantly affect the breeding propensity. Overall, our measure of breeding propensity could potentially be under-estimated if poor quality individuals decided to breed elsewhere than in the study colony. However, this is very unlikely since eider females are highly philopatric to their breeding ground (Coulson 1984; Swennen 1990).

Among most bird species, early arrival on the breeding grounds is generally associated with early egg-laying (Dalhaug et al. 1996; Tombre and Erikstad 1996; Bêty et al. 2003) and may ultimately lead to a higher breeding success (Lepage et al. 2000; Newton 2006). Nonetheless, pre-breeding feeding sites may be limited when birds arrive too early in spring (Reed et al. 2004; Madsen et al. 2007) and hence potential costs of early arrival can counteract the apparent reproductive benefit. Few empirical studies have quantified potential costs of early arrival across multiple years varying in key environmental parameters (Bêty et al. 2004). Our data show that the earliest arriving female eiders had lower breeding propensity than females arriving around the median arrival date. Individuals arriving first (i.e. late May) at our study site typically faced extensive ice cover in most years (see electronic supplementary material, figure S1, table S1) that would constrain their ability to access benthic marine prey resources. We also detected a decline in the breeding propensity over the season. As food accessibility should increase over time as the ice recedes, we suggest that this response cannot be generated by constraints in body condition gain alone, but could possibly reflect an effect of age given that young females often arrive later compared to experimented ones (Cristol 1995), and also be an adaptive strategy given the seasonal decline in the survival of juveniles (Daan et al. 1988). Indeed, duckling survival decreases sharply late in the season at our site (Love et al. 2010), making it less profitable for females to invest in reproduction regardless of their body condition. Individuals arriving late and that are unable to reach the minimum condition threshold in a short pre-breeding interval would be predicted to skip reproduction (Rowe et al. 1994). Such interplay between these two parameters was recently documented in our population: both timing of arrival and individual physiological state in pre-breeding females predicted laying dates (Hennin et al. 2016).

Direct and indirect effects of variation in sea ice conditions on the reproduction of polar seabirds have been observed through changes in diet and increased foraging costs (Gaston et al. 2005; Mallory and Forbes 2007; Emmerson and Southwell 2008), delayed laying date (Gaston and Hipfner 1998; Gaston et al. 2005; Chaulk and Mahoney 2012; Descamps et al. 2015) and increased predation risk (Chaulk et al. 2007; Iverson et al. 2014). However, understanding the mechanistic links between variation in sea ice and reproductive parameters is complex because it involves the body condition of the birds which is partly determined by conditions experienced outside the breeding ground (carry-over effects) and by the food availability close to the breeding ground. Thus, the actual linkages often remain unclear for most species (Gaston et al. 2005; Lehikoinen et al. 2006; Love et al. 2010; Chaulk and Mahoney 2012). In our study system, the timing of ice-breakup at river mouths represents the first access to local prey resources available to eiders after their arrival from migration and prior to egg-laying (Sénéchal et al. 2011a, b). Hence, a late ice-breakup likely induces extra foraging and travelling costs as birds seek foraging opportunities at longer distances. This could interfere with the pre-breeding energetic dynamics of female eiders by slowing down their rate of condition gain compared to years with earlier ice-breakup.

In the context of ongoing global change, forecasting the effects of changes in sea ice conditions is challenging for migratory species breeding at high latitudes where abiotic conditions are known to be undergoing rapid and pronounced change (Post et al. 2013). Local cues used to time migration and breeding may be less reliable in a changing environment (Walther et al. 2002; Visser et al. 2009). Moreover, despite the potential benefits of an early ice-breakup, warmer temperatures can indirectly and negatively impact the breeding decisions, nesting success and offspring survival of seabirds. Indeed, it has recently been shown that the increase in the duration of the ice-free period is directly linked to increases in polar bear (*Ursus maritimus*) predation at bird colonies (Rockwell and Gormezano 2009; Iverson et al. 2014), including the eider colony at East Bay (Iverson et al. 2014). Measuring and predicting the overall effect of changes in sea ice dynamics on seabird reproductive decisions and predation risks is often challenging and warrants research to identify the long-term impacts at the population level and should be expanded to other marine and terrestrial species.

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Author contributions FJG, JB and SB conceived the research question, the project and the analysis. FJG and PL conducted field work and GG provided long-term monitoring breeding data.FJG and PL analyzed the data. FJG, PL and JB wrote the manuscript; other authors provided editorial advice.

References

ACIA (2005) Impacts of warming climate: Arctic climate impact assessment. Cambridge University Press, Cambridge

Barton K (2016) MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn. Accessed 08 Oct 2016

Bêty J, Gauthier G, Giroux JF (2003) Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. Am Nat 162:110–121

Bêty J, Giroux JF, Gauthier G (2004) Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behav Ecol Soc 57:1–8

Blums P, Nichols JD, Hines JE, Lindberg MS, Mednis A (2005) Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. Oecologia 143:365–376

Bond JC, Esler D, Williams TD (2008) Breeding propensity of female harlequin ducks. J Wild Manage 72:1388–1393

Bonnet X, Lourdais O, Shine R, Naulleau G (2002) Reproduction in a typical capital breeder: costs, currencies, and complications in the aspic viper. Ecology 83:2124–2135

Brown GP, Shine R (2002) Reproductive ecology of a tropical natricine snake, *tropidonophis mairii* (colubridae). J Zool 258:63–72

Burnham KP, Anderson DR (2004) Multimodel inference—understanding AIC and BIC in model selection. Sociol Meth Res 33:261–304

Bustnes JO, Erikstad KE, Bjørn TH (2002) Body condition and brood abandonment in common eiders breeding in the high arctic. Waterbirds 25:63–66

Cam E, Hines JE, Monnat JY, Nichols JD, Danchin E (1998) Are adult non breeders prudent parents? The kittiwake model. Ecology 79:2917–2930

Chastel O (1995) Influence of reproductive success on breeding frequency in four southern petrels. Ibis 137:360–363

Chaulk KG, Mahoney ML (2012) Does spring ice cover influence nest initiation date and clutch size in common eiders? Polar Biol 35:645–653

Chaulk KG, Robertson GJ, Montevecchi WA (2007) Landscape features and sea ice influence nesting common eider abundance and dispersion. Can J Zool 85:301–309

Clutton-Brock TH (1988) Reproductive success: Studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, IL, USA

Coulson JC (1984) The population dynamics of the eider duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. Ibis 126:525–543

Cristol DA (1995) Early arrival, initiation of nesting, and social status: an experimental study of breeding female red-winged blackbirds. Behav Ecol 6:87–93

Cubaynes S, Doherty PF, Schreiber EA, Gimenez O (2011) To breed or not to breed: a seabird's response to extreme climatic events. Biol Lett 7:303–306

Daan S, Dijkstra C, Drent R, Meijer T (1988) Food supply and the annual timing of avian reproduction. In: Proceedings of the International Ornithological Congress, vol 19. University of Ottawa Press, Ottawa, pp 392–407

Dalhaug L, Tombre IM, Erikstad KE (1996) Seasonal decline in clutch size of the barnacle goose in Svalbard. Condor 98:42–47

Dean KG, Stringer WJ, Ahlnas K, Searcy C, Weingartner T (1994) The influence of river discharge on the thawing of sea ice, mackenzie river delta: albedo and temperature analyses. Polar Res 13:83–94

Descamps S, Yoccoz NG, Gaillard J-M, Gilchrist HG, Erikstad KE, Hanssen SA, Cazelles B, Forbes MR, Bêty J (2010) Detecting population heterogeneity in effects of north atlantic oscillations on seabird body condition: get into the rhythm. Oikos 119:1526–1536

Descamps S, Bêty J, Love OP, Gilchrist HG (2011) Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. Funct Ecol 25:671–681

Descamps S, Tarroux A, Varpe Ø, Yoccoz NG, Tveraa T, Lorentsen SH (2015) Demographic effects of extreme weather events: snow storms, breeding success, and population growth rate in a long-lived Antarctic seabird. Ecol Evol 5:314–325

Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252

Emmerson L, Southwell C (2008) Sea ice cover and its influence on Adelie penguin reproductive performance. Ecology 89:2096–2102

Faaborg J, Holmes RT, Anders AD, Bildstein KL, Dugger KM, Gauthreaux SA, Heglund P, Hobson KA, Jahn AE, Johnson DH, Latta SC, Levey DJ, Marra PP, Merkord CL, Nol E, Rothstein SI, Sherry TW, Sillett TS, Thompson FR, Warnock N (2010) Recent advances in understanding migration systems of new world land birds. Ecol Monogr 80:3–48

Gagliano M, McCormick MI, Meekan MG (2007) Survival against the odds: ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. Proc R Soc B 274:1575–1582

Gaston AJ, Hipfner M (1998) The effect of ice conditions in northern Hudson bay on breeding by thick-billed murres (*uria lomvia*). Can J Zool 76:480–492

Gaston AJ, Gilchrist HG, Mallory ML (2005) Variation in ice conditions has strong effects on the breeding of marine birds at prince leopold island, Nunavut. Ecography 28:331–344

Gaston AJ, Bertram DF, Boyne AW, Chardine JW, Davoren G, Diamond AW, Hedd A, Montevecchi WA, Hipfner JM, Lemon MJF (2009) Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. Environ Rev 17:267–286

Gilg O, Kovacs KM, Aars J, Fort J, Gauthier G, Grémillet D, Ims RA, Meltofte H, Moreau J, Post E, Schmidt NM, Yannic G, Bollache L (2012) Climate change and the ecology and evolution of arctic vertebrates. Ann N Y Acad Sci 1249:166–190

Granskog MA, Kuzyk ZZA, Azetsu-Scott K, Macdonald RW (2011) Distributions of runoff, sea-ice melt and brine using δ 18 O and salinity data—a new view on freshwater cycling in Hudson Bay. J Mar Syst 88:362–374

Harms NJ, Legagneux P, Gilchrist HG, Bêty J, Love OP, Forbes MR, Bortolotti GR, Soos C (2015) Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an arctic migratory bird. Proc R Soc B 282:20142085

Harshman LG, Zera AJ (2007) The cost of reproduction: the devil in the details. Trends Ecol Evol 22:80–86

Hennin HL, Legagneux P, Bêty J, Williams TD, Gilchrist HG, Baker TM, Love OP (2015) Pre-breeding energetic management in a mixed-strategy breeder. Oecologia 177:235–243

Hennin HL, Bêty J, Legagneux P, Williams TD, Gilchrist HG, Love OP (2016) Energetic physiology mediates individual optimization of breeding phenology in a migratory arctic seabird. Am Nat 188:434–445

Ingram RG, Wang J, Lin C, Legendre L, Fortier L (1996) Impact of freshwater on a subarctic coastal ecosystem under seasonal sea ice (southeastern Hudson Bay, Canada). I. Interannual variability and predicted global warming influence on river plume dynamics and sea ice. J Mar Syst 7:221–231

Iverson SA, Gilchrist HG, Smith PA, Gaston AJ, Forbes MR (2014) Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian arctic. Proc R Soc B 281:20133128

König Beatty C (2007) Arctic landfast sea ice. PhD dissertation, Department of Mathematics, New York University, NY, USA

Kulaszewicz I, Wojczulanis-Jakubas K, Jakubas D (2016) Trade-offs between reproduction and self-maintenance (immune function and body mass) in a small seabird, the little auk. J Avian Biol 48:371–379

Legagneux P, Fast PLF, Gauthier G, Bêty J (2012) Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proc R Soc B 279:876–883

Legagneux P, Hennin H, Williams TD, Gilchrist HG, Love OP, Bêty J (2016) Food shortage reduces breeding propensity regardless of pre-laying physiological investment in a partial capital breeder. J Avian Biol 47:001–007

Lehikoinen A, Kilpi M, Öst M (2006) Winter climate affects subsequent breeding success of common eiders. Glob Change Biol 12:1355–1365

Lepage D, Gauthier G, Menu S (2000) Reproductive consequences of egg-laying decisions in snow geese. J Anim Ecol 69:414–427

Love OP, Gilchrist HG, Descamps S, Semeniuk CAD, Bêty J (2010) Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an arctic marine bird. Oecologia 164:277–286

Madsen J, Tamstorf M, Klaassen M, Eide N, Glahder C, Riget F, Nyegaard H, Cottaar F (2007) Effects of snow cover on the timing and success of reproduction in high-arctic pink-footed geese *Anser brachyrhynchus*. Polar Biol 30:1363–1372

Mallory ML, Forbes MR (2007) Does sea ice constrain the breeding schedules of high arctic northern fulmars? Condor 109:894–906

Mazerolle MJ (2016) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-0. https://cran.r-project.org/package=AICcmodavg. Accessed 10 Oct 2016

Mosbech A, Gilchrist G, Merkel F, Sonne C, Flagstad A, Nyegaard H (2006) Year-round movements of northern common eiders *Somateria mollissima borealis* breeding in arctic canada and west greenland followed by satellite telemetry. Ardea 94:651–665

Newton I (2006) Can conditions experienced during migration limit the population levels of birds? J Ornith 147:146–166

Nilsson JÅ (1994) Energetic bottle-necks during breeding and the reproductive cost of being too early. J Anim Ecol 63:200–208

Öst M, Ydenberg R, Kilpi M, Lindström K (2003) Condition and coalition formation by brood-rearing common eider females. Behav Ecol 14:311–317

Pinheiro JC, Bates DM (2000) Mixed effects models in s and s-plus. Springer, New York

Post E, Bhatt US, Bitz CM, Brodie JF, Fulton TL, Hebblewhite M, Kerby J, Kutz SJ, Stirling I, Walker DA (2013) Ecological consequences of sea-ice decline. Science 341:419–524

Reed ET, Gauthier G, Giroux JF (2004) Effects of spring conditions on breeding propensity of greater snow goose females. Anim Biodiv Cons 27:35–46

Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. Trends Ecol Evol 17:462–468

Rivalan P, Prevot-Julliard AC, Choquet R, Pradel R, Jacquemin B, Girondot M (2005) Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. Oecologia 145:564–574

Robert A, Paiva VH, Bolton M, Jiguet F, Bried J (2012) The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. Ecology 93:1944–1952

Rockwell R, Gormezano L (2009) The early bear gets the goose: climate change, polar bears and lesser snow geese in western Hudson bay. Polar Biol 32:539–547

Rowe L, Ludwig D, Schutler D (1994) Time, condition, and the seasonal decline of avian clutch size. Am Nat 143:698–722

Sedinger JS, Lindberg MS, Chelgren ND (2001) Age-specific breeding probability in black brant: effects of population density. J Anim Ecol 70:798–807

Sedinger JS, Chelgren ND, Ward DH, Lindberg MS (2008) Fidelity and breeding probability related to population density and individual quality in black brent geese *Branta bernicla nigricans*. J Anim Ecol 77:702–712

Sedinger JS, Schamber JL, Ward DH, Nicolai CA, Conant B (2011) Carryover effects associated with winter location affect fitness, social status, and population dynamics in a long-distance migrant. Am Nat 178:E110–E123

Sénéchal É, Bêty J, Gilchrist H, Hobson K, Jamieson S (2011a) Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. Oecologia 165:593–604

Sénéchal É, Bêty J, Gilchrist HG (2011b) Interactions between lay date, clutch size, and postlaying energetic needs in a capital breeder. Behav Ecol 22:162–168

Souchay G, Gauthier G, Pradel R (2014) To breed or not: a novel approach to estimate breeding propensity and potential trade-offs in an arctic-nesting species. Ecology 95:2745–2756

Spendelow JA, Nichols JD (1989) Annual survival rates of breeding adult roseate terns. Auk 106:367–374

Stearns SC (1989) Trade-offs in life-history evolution. Funct Ecol 3:259–268

Stearns SC (1992) The evolution of life history. Academic press, London

Stirling I, Lunn NJ, Iacozza J, Elliott C, Obbard M (2004) Polar bear distribution and abundance on the southwestern Hudson bay coast during open water season, in relation to population trends and annual ice patterns. Arctic 57:15–26

Sutherland WJ, Freckleton RP, Godfray HCJ, Beissinger SR, Benton T, Cameron DD et al (2013) Identification of 100 fundamental ecological questions. J Ecol 101:58–67

Swennen C (1990) Dispersal and migratory movements of eiders *Somateria mollissima* breeding in the Netherlands. Ornis Scand 21:17–27

Tombre IM, Erikstad KE (1996) An experimental study of incubation effort in high-arctic barnacle geese. J Anim Ecol 65:325–331

Van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137–142

Visser ME, Holleman LJM, Caro SP (2009) Temperature has a causal effect on avian timing of reproduction. Proc R Soc B 276:2323–2331

Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Warren JM, Cutting KA, Takekawa JY, De La Cruz SE, Williams TD, Koons DN (2014) Previous success and current body condition determine breeding propensity in lesser scaup: evidence for the individual heterogeneity hypothesis. Auk 131:287–297

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of lack's principle. Am Nat 100:687–690

Wilson AJ, Nussey DH (2010) What is individual quality? An evolutionary perspective. Trends Ecol Evol 25:207–214

World Meteorological Organization (1970) WMO sea-ice nomenclature, terminology, codes and illustrated glossary. Secretariat of the WMO, Geneva