Predators, alternative prey and climate influence annual breeding success of a long-lived sea duck

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Summary

1. Perturbations to ecosystems have the potential to directly and indirectly affect species interactions, with subsequent impacts on population dynamics and the vital rates that regulate them.

2. The few long-term studies of common eider breeding ecology indicate that reproductive success is low in most years, interrupted by occasional boom years. However, no study has explicitly examined the drivers of long-term variation in reproductive success.

3. Here, we use encounter history data collected across 41 years to examine the effects of arctic foxes (a terrestrial nest predator), local abundance and spatial distribution of lesser snow geese (an alternative prey source), and spring climate on common eider nest success.

4. Eider nest success declined over the course of the study, but was also highly variable across years. Our results supported the hypothesis that the long-term decline in eider nest success was caused by apparent competition with lesser snow geese, mediated by shared predators. This effect persisted even following a large-scale exodus of nesting geese from the eider colony. Nest success was also lowest in years of low arctic fox index, presumably driven by prey switching in years of low small mammal availability. However, increased snow goose abundance appeared to buffer this effect through prey swamping. The effect of spring climate depended on the stage of the breeding season; cold and wet and warm and dry conditions in early spring were correlated with decreased nest success, whereas warm and wet conditions in late spring increased eider nest success.

5. These results underscore the significance of both trophic interactions and climate in regulating highly variable vital rates, which likely have important consequences for population dynamics and the conservation of long-lived iteroparous species.

Key-words: apparent competition, arctic fox, climate, common eider, lesser snow goose, nest survival, predation, *Somateria mollissima sedentaria*

Introduction

Human alterations to both climate and landscapes have had extensive impacts on natural systems. Anthropogenic climate change has led to increased environmental variability, particularly in high-latitude regions where temperature and precipitation regimes have changed disproportionately compared with those at low latitudes (Houghton *et al.* 2001). Corresponding effects on phenology, distribution and abundance of species have resulted in widespread ecological consequences (Walther *et al.* 2002). Independently, changes in human land use can also impact geographically distant ecosystems, particularly if systems are linked by species migration. For example, changes in North American agricultural practices have led to a 10-fold increase in snow goose populations (*Chen caerulescens*), resulting in catastrophic degradation of the Arctic salt marshes where snow geese breed (Abraham, Jefferies & Alisauskas 2005). Together, these

perturbations have the potential to influence trophic inter-actions within ecological communities and impact the population dynamics of many arctic species (e.g. Post *et al.* 2009; Rockwell, Gormezano & Koons 2011).

The common eider (*Somateria mollissima*) is a colonial nesting sea duck, and has experienced long-term declines across much of its (sub-)Arctic breeding range (Robertson & Gilchrist 1998; Suydam *et al.* 2000; Merkel 2004). In addition to its role in coastal and marine ecosystems, the common eider is important both eco-nomically and for subsistence harvest in northern com-munities. Reduced abundance of common eiders is thus of concern to conservationists, waterfowl managers and aboriginal communities (Gilliland *et al.* 2009). Yet, despite the extensive research attention given to common eiders (e.g. Milne & Dau 1976; Goudie, Robertson & Reed 2000), the drivers of population dynamics are poorly understood.

The few long-term studies of common eider breeding ecology indicate that both nesting success and duckling survival are low in most years, interrupted by occasional years of high success (e.g. Milne 1974; Coulson 1984; Swennen 1989). In particular, avian and mammalian predators have been known to decimate the annual repro-ductive output of common eider breeding colonies (Milne 1974; Swennen 1989; Rockwell & Gormezano 2009). However, the relative effect of changes in predation pressure on annual reproductive success remains unclear, as do the biotic and abiotic mechanisms that modulate predator abundance and foraging behaviour.

The presence of non-competitive alternative prey has the potential to indirectly impact a focal species, like com-mon eider, through impacts on shared predators. For example, as specialist predators on small mammals (Elmhagen *et al.* 2000), annual arctic fox (*Vulpes lagopus*) production closely tracks fluctuations in spring small mammal abundance. However, in years of low small mammal availability, arctic foxes are known to opportu-nistically switch to alternative prey for late-spring and summer subsistence (Tannerfeldt, Angerbjörn & ArvidSon 1994), potentially causing widespread reproductive failure in ground-nesting waterfowl (e.g. Bêty *et al.* 2002; Gauthier *et al.* 2004).

Alternatively, apparent competition theory predicts that increased abundance of a focal prey species can invoke a numerical response in the predator community, thereby resulting in increased predation pressure on other prey species (Holt & Lawton 1994). Predator-mediated appar-ent competition is often most acute when the secondary prey species is more easily captured than the focal prey species (Chaneton & Bonsall 2000). In recent decades, populations of snow geese have increased exponentially, largely as a result of agricultural nutrient subsidies avail-able to geese on wintering grounds and migration routes (Jefferies, Rockwell & Abraham 2004; Gauthier *et al.* 2005). Considerable increase in the availability of snow goose eggs on Arctic breeding grounds could augment or

congregate some terrestrial predator populations, especially avian predators that forage intensively (and in some cases, almost exclusively) on waterfowl eggs and off-spring in northern ecosystems (Martin & Barry 1978; Campbell 1990; Samelius & Alisauskas 1999; Sammler, Andersen & Skagen 2008).

Adult snow geese aggressively defend their nests against arctic foxes and avian predators (Cooke, Rockwell & Lank 1995), and may be less susceptible to total clutch loss than common eiders. Nevertheless, a relatively constant proportion (< 10%) of snow goose eggs are depredated annually on the Hudson Bay Lowlands (most often resulting in partial clutch loss; Cooke, Rockwell & Lank 1995; Rockwell, Gormezano & Koons 2011). A bol-stered predator community benefitting from increased availability of snow goose prey could thus have negative consequences on sympatric common eiders that are more vulnerable to nest predation.

The abiotic environment also has the potential to mod-ulate the biotic factors that influence nest survival. For example, eider nesting may be delayed by as much as a month in years of late ice breakup (Robertson 1995), with potential consequences for reproductive investment (Love *et al.* 2010). Somatic energy losses resulting from delayed breeding may influence the frequency and length of incubation breaks taken by female eiders, increasing the susceptibility of nests to predation as well as the likeli-hood of nest abandonment (Criscuolo *et al.* 2002; Lehikoinen, Kilpi & Öst 2006; D'Alba, Monaghan & Nager 2010). Alternatively, high spring temperatures and precipitation may increase breeding propensity (Love *et al.* 2010) or decrease the accessibility of nesting islands to predators through conditions that raise river water levels (Robertson 1995).

Here, we use data collected across 41 years from the La Pérouse Bay common eider colony to investigate the biotic and abiotic drivers of inter-annual changes in com-mon eider nesting success. We predict that (1) years of low arctic fox recruitment (driven by an absence of small mammal prey) will be associated with low eider nest suc-cess, due to prey switching by adult arctic foxes (Fig. 1a and b). (2) Increased abundance of lesser snow geese (*C. c. caerulescens*) in the region may have stimulated avian predator populations that are able to respond numerically to changes in snow goose abundance, result-ing in decreased common eider nest success over the long term via apparent competition (Fig. 1c and d). Further-more, because arctic foxes generally do not respond numerically to increases in goose abundance, we predict that the effect of foxes on common eiders will decline as snow goose populations increase due to prey swamping of foxes by geese (Fig. 1c). Moreover, we predict that (3) in general, spring temperature and precipitation will be positively correlated with common eider nest success through their combined effects on eider reproductive investment and accessibility of nesting islands to predators.
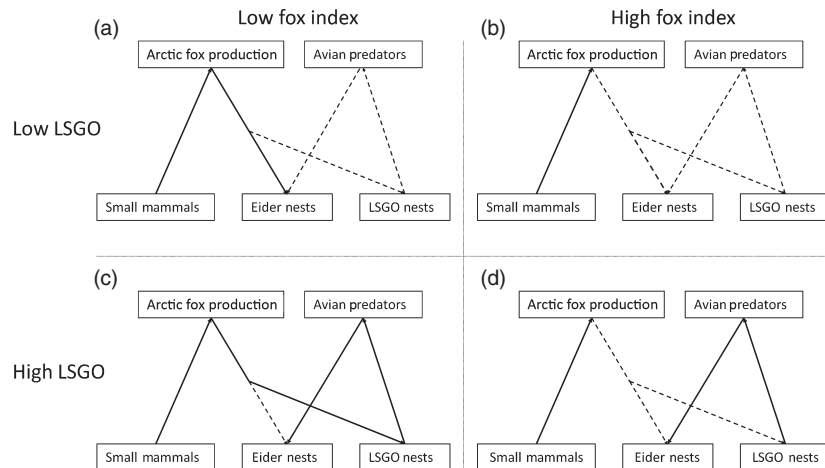
Fig. 1. Diagrammatic representation of our hypotheses about the interactive effect of fox index and snow goose abundance on common eider nest success. Solid arrows represent strong effects of trophic interactions (expected to negatively affect focal prey populations); dashed arrows represent weak effects of trophic interactions (expected to have more subtle effects on focal prey populations). (a) Low small mammal abundance results in low arctic fox production (reflected by the arctic fox index), causing arctic foxes to switch to foraging on ground-nesting waterfowl. Low snow goose abundance is not yet affecting common eiders through apparent competition. (b) High availability of small mammals increases arctic fox index, reducing trophic interactions between foxes and waterfowl. (c) Increased snow goose abundance bolsters avian predator populations, resulting in apparent competition with common eiders. High snow goose availability buffers the negative effect of foxes on common eiders in low fox productivity years through prey swamping. (d) High small mammal abundance reduces prey switching by arctic foxes, but snow geese still cause reductions in common eider nest success through apparent competition.

Materials and methods

STUDY AREA

Breeding habitat for common eiders in northern Manitoba is mainly restricted to the coast of Hudson Bay and the distributaries that flow into it. Field work was conducted in the Mast and Wao Wao river deltas, which feed into La Pérouse Bay (58°43′ N, 93°24′ W), *c.* 30 km east of Churchill, Manitoba, Canada. The river outflows form braided deltas with numerous islands that several hundred pairs of Hudson Bay common eiders (*S. m. sedentaria*) use annually for breeding and nesting (for further details see Schmutz, Robertson & Cooke 1983). The breeding ecology of this colony has been studied in 23 of the last 41 years (Iles 2012). As such, our study represents the longest investigation of *S. m. sedentaria* breeding ecology and nesting success. Furthermore, unlike many other common eider populations, *S. m. sedentaria* that breed along the southwest coast of Hudson Bay are unharvested and unmanaged, therefore providing a rare opportunity to 'isolate' the ecological processes governing reproductive success.

Historically, the two main egg predators for the La Pérouse Bay eider colony have been arctic foxes and herring gulls (*Larus smithsonianus*; Guild 1974; Schmutz, Robertson & Cooke 1983). In addition, the nesting habitat was shared with a small snow goose colony (Robertson 1995; Fig. 2). However, following the snow goose population explosion (Fig. 3) and subsequent habitat degradation of the goose brood-rearing areas, the snow goose colony shifted away from the eider colony, with resulting declines of up to 67% of local snow goose nest densities (see Lesser Snow Goose Data below; Ganter & Cooke 1998; Cooch, Rockwell & Brault 2001; Iles 2012). Importantly, the degradation of grass and sedge meadow brood-rearing areas leading to the eventual snow goose exodus from the eider colony did not affect common eider nesting habitat (Jefferies, Jano & Abraham 2006).

NEST OBSERVATIONS

At the onset of nesting each year, eider nests were located using repeated searches of the known breeding areas. Nest searches (and rechecks of discovered nests) were conducted on 6–10-day intervals. Upon discovery, nests were marked with a small wooden stake (popsicle stick) and the location was recorded with a GPS, or mapped onto a grid in years prior to GPS use. Clutch size was recorded upon each visit, and in most years observers recorded incubation age of nests using either egg candling (Weller 1956) or floating (Westerkov 1950). Initiation date of each nest was estimated based on the incubation age of the nest and the number of eggs in the clutch, with an estimated laying rate of one egg per day (Watson, Robertson & Cooke 1993). Nests were rechecked at 6–10-day intervals to assess fate, and were considered successful if they hatched at least one egg, determined by either presence of ducklings or fresh egg membranes in the nest. The nest was recorded as unsuccessful if all eggs were missing from a nest upon revisit and no signs of hatch were present.

ARCTIC FOX DATA

The Manitoba Conservation Furbearer data base offers one of the longest and most complete data sets for examining changes in arctic fox demographics, with records that can be linked back to those kept by the historical Hudson's Bay Company (Elton & Nicholson 1942). As the arctic fox range in Manitoba is mainly restricted to the Hudson Bay coast (Hersteinsson & MacDonald 1992), provincial records of arctic fox pelt harvests are likely a reflection of local trends in arctic fox demography.
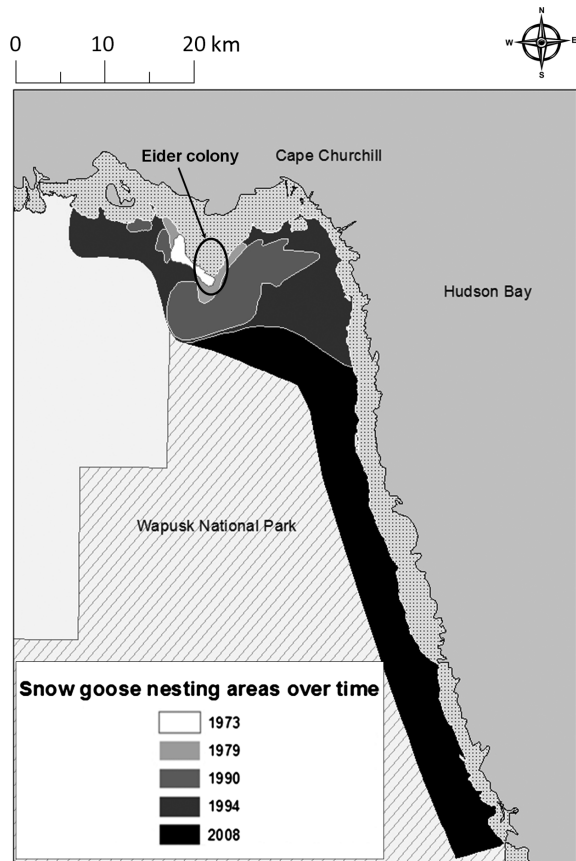
Fig. 2. Map of the temporal distribution of snow geese along the Cape Churchill Peninsula coast in relation to the eider breeding colony. Common eider nests are distributed between two rivers (the Mast and Wao Wao rivers; not pictured in this map), primarily within the boundary described in this figure. By 2011, nesting densities of snow geese within the traditional colony (near the eider colony) had declined by *c.* 67% of those observed in the mid 1990s.
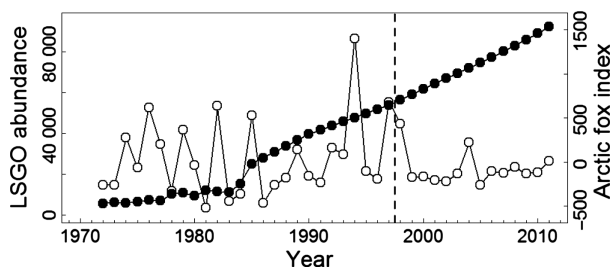

Fig. 3. Estimated lesser snow goose (LSGO) abundance (solid circles) in the Cape Churchill Peninsula region and arctic fox index (open circles) in northern Manitoba over the course of our study (1972–2011). Dashed vertical line separates the pre-exodus and post-exodus time periods.

To account for variation in the annual arctic fox harvest data caused by socioeconomics, we fit linear models that included the number of registered trap lines, inflation-corrected price of pelts in the current or previous year, as well as plausible interaction terms. The best model (registered trap lines) was chosen based on model-selection criteria described below (see Nest Survival Analyses), and we use the residuals from this model as indices of fox

prevalence in each year (i.e. corrected for annual number of trappers; Fig. 3). Because annual pelt harvest data were only available until 2009, we forecasted the fox index for 2010 and 2011 using the most parsimonious parameterization of autoregressive moving average (ARMA) models up to order three (the upper 3rd order limit was based on plots of the autocorrelation and partial autocorrelation functions; Cryer & Chan 2008). A detailed description of model selection and time-series analyses used to calculate fox index is included in Appendix S1.

Estimates of annual arctic fox index ranged between −520 and 1398 across the study. For use as a covariate in nest survival analyses, we standardized the fox indices (as well as other covariates; see below) using a z-transformation. This transformation reduces model convergence errors associated with model fitting in the RMark environment (see Nest Survival Analyses), and allowed us to assess the relative magnitude of effects in our models on comparable scales. Due to possible lags in reporting of furs (i.e. the residual number of furs in a year could reflect fox prevalence in the previous year), we considered both the current fox index and the previous year's fox index as potential covariates in our analyses of nest survival.

Arctic fox reproduction is highly correlated with spring lemming abundance (Roth 2003), while subsequent juvenile survival is strongly influenced by summer food availability (Tannerfeldt, Angerbjörn & ArvidSon 1994). Fox pelts, however, are most valuable and thus foxes are most heavily trapped the following winter (Roth 2003). Moreover, the majority of fox harvest consists of juveniles because of their higher vulnerability to being trapped relative to experienced adults (Smirnov 1968; Roth 2003). As a result, fox pelt harvest is likely more representative of annual juvenile recruitment to the winter (which itself is driven by spring and summer food availability; Bêty *et al.* 2002; Roth 2003) rather than an index of adult abundance. Accordingly, our measure of fox index was highly correlated with published estimates of local fox den occupancy (Roth 2003; slope in linear regression = 20·67, *P* = 0·049, adjusted R^2 = 0·85). Thus, without long-term data to evaluate changes in small mammal abundance and fox production directly, we regarded the arctic fox fur-harvest index as an indirect measure of spring and summer small mammal abundance with which to evaluate our predator and alternative prey hypotheses related to common eider nest success (see Introduction and Fig. 1).

LESSER SNOW GOOSE DATA

Lesser snow goose abundance in the Cape Churchill Peninsula region was estimated based on aerial photograph surveys of nesting pairs along the coast (Jefferies, Jano & Abraham 2006; Kerbes *et al.* 2006). A state-space model incorporating both population process variation and observation error (Humbert *et al.* 2009) was then used to interpolate snow goose abundance for 23 of the last 46 years in which surveys were not conducted. Finally, to project population estimates for years after the last aerial survey in 2006 (the state-space model could only be used to estimate abundance between aerial survey years), we used the most recent estimate of population growth rate attained from the state-space model (Fig. 3). Snow goose abundance ranged from 3882 to 92 056 across the study. Z-standardized snow goose population estimates were used in eider nest survival analyses to examine alternative prey hypotheses (see Introduction and Fig. 1).

Data from long-term snow goose nest density plots captured the tail end of a large-scale snow goose exodus from the eider colony (to the east and south; Fig. 2), resulting in a local decline of *c*. 67% of nesting snow geese by 1998 (Iles 2012). Without sufficient data to examine local snow goose nest density dynamics prior to the establishment of the long-term nest density plots in 1995, we created a binary variable for use in analyses to examine the effect of the spatial snow goose exodus on eider nest success; years prior to 1998 were assigned a 'pre-exodus' status, while 1998 and onwards were assigned a 'post-exodus' status. The inclusion of an exodus covariate in a subset of our candidate models allowed us to address our predictions related to apparent competition between snow geese and common eiders in more detail by examining the effects of both changes in snow goose abundance and spatial location on common eider nest survival.

CLIMATE DATA

Local climate variables (temperature and precipitation) hypothesized to influence common eider nest success through effects on predator phenology and female reproductive investment were obtained online from the Environment Canada Climate Data Archive (http://climate.weatheroffice.gc.ca). Because we hypothesized that climate variables may influence nest survival differently depending on the stage of the breeding season, seasonal weather averages were divided into two periods: early-breeding season (May 1–June 10) and late-breeding season (June 11–July 15). For example, while certain early-season climate characteristics may influence nest survival through impacts on reproductive investment by adult common eiders, different late-season climate factors may influence the accessibility of eider islands to predators, vegetation growth (and thus nest concealment), or the survival and abundance of alternative prey (i.e. lemmings). The early-breeding season period captured environmental variation during the pre-laying period (early-mid May) until early to mid incubation (early June). The late-breeding season period examined the role of weather conditions from mid to late incubation (late June–early July). In addition, we considered more parsimonious climate models in which daily weather was averaged over the entire breeding season (May 1–July 15), rather than split into two time periods (early–late incubation). Covariates were standardized using a z-transformation.

NEST SURVIVAL ANALYSIS

Of the 23 years in which the colony was studied, 18 years had repeated, visit-specific information from which nest daily survival rates could be estimated. In the earliest years of the study, only the apparent nest success estimates were available from published literature (Schmutz, Robertson & Cooke 1983). Rather than excluding these years from analyses, we transformed apparent nest success estimates into corrected daily survival rates (DSR; Green 1989; Johnson 1991), and representative encounter histories were simulated based on the estimated average DSR and the reported sample size for these years (Iles 2012). Data from these simulations were then used in inter-annual models of nest DSR to elucidate the dominant drivers of annual variation in nest success.

We analysed nest survival data using the RMark package (Laake & Rexstad 2012) in program R (version 2·13·0). Competing generalized linear models of DSR were fit using maximum likelihood, and relative support was evaluated using Schwarz's information criterion (SIC; Schwarz 1978; Taper & Gogan 2002).

Before evaluating the underlying drivers of nest success, we examined general temporal trends in annual nest survival across the study by constructing a null model (time-invariant), a linear time-trend model, and a fully saturated temporal model in which DSR was estimated separately for each year of study. We constructed each of these models with and without a term for visitor disturbance, which could affect annual estimates of nest survival (e.g. Bolduc & Guillemette 2003). The visitor disturbance term therefore allowed us to examine if the daily survival rate of each nest changed as a function of whether the nest was visited on that day, and allowed us to correct for visitor impacts on nest success.

Next, we developed models to explain annual variation in DSR with mechanistic covariates. To facilitate analysis of a reasonable number of models representing our biological hypotheses and to avoid model dredging, we first stratified our model construction and selection into two initial categories: biotic models (containing predator and alternative prey covariates), and abiotic models (containing early–late spring precipitation and temperature covariates). The support for models within each category was evaluated with SIC.

We then developed a set of models (each with a term for visitor effects) that included additive and plausible interactive effects of the biotic and abiotic variables that performed best in the preceding analyses. In addition to evaluating the relative evidence for each model with SIC, we also evaluated the direction (+ or −) and precision of parameter estimates in the top model(s) (Burnham & Anderson 2002; Cooch & White 2012). Finally, average nest success within a year was calculated based on the product of estimated daily survival across 28 days (assuming a modal clutch size with 4 days of laying + 24 days of incubation; $NS = DSR^{28}$), and precision in nest success was calculated from the logit-scale coefficients using the delta method (Seber 1982).

To evaluate the goodness-of-fit of our best-performing models, we first calculated Zheng's (2000) deviance reduction measure:

$$D_1 = 1 - \left(\frac{\text{dev}_1}{\text{dev}_N}\right) \qquad \text{eqn 1}$$

where dev_I is the deviance of the model of interest and dev_N is the deviance of the null model (in our case, constant daily survival rate across all years). This method is appropriate for generalized linear models, and evaluates a model's proportional reduction in deviance relative to the null model (Zheng 2000; Adler & HilleRisLambers 2008; Aubry *et al.* 2010). We then calculated the ratio of deviance reduction (*R*; not to be confused with the coefficient of determination R^2) for each model relative to the fully saturated temporal model (the maximum possible reduction in deviance attributable to annual variation):

$$R = \frac{D_1}{D_{FS}} \qquad \text{eqn 2}$$

where D_I and D_{FS} are the deviance reductions in the model of interest and the fully saturated temporal model respectively. The relative deviance reduction *R* is therefore 1 for the fully saturated temporal model and 0 for the null model. There are no formal goodness-of-fit tests appropriate for the generalized linear models used in this analysis (Cooch & White 2012). As such, *R* only

represents a measure of each model's fit to the data relative to the temporally saturated model.

Results

A total of 5661 nests were considered in this analysis from 23 years of study. On average, nests were visited 3·8 times. In every year of study, predation was the main cause of nest failure. Nest abandonment was attributed to only 5·0% of total failed nests, and ranged annually from 0 to 25% of failed nests (abandonment was included as failure in the data set unless it was human induced, e.g. attempts at trapping a female on the nest, in which case the observation was right censored).

A linear trend fit better than the null model, indicating that DSR (and thus nest success) declined across the years of study (β_{trend} for DSR = −0·032, 95% CI = −0·035 to −0·029). The temporally saturated fixed year effect model indicated that annual nesting success varied considerably, ranging from 0·00089 to 0·95 (Fig. 4). The model selection results also indicated that survival was lower on days in which the nest was visited than when it was not, suggesting that observer effects negatively affected nest survival estimates ($\beta_{VisitDay}$ for
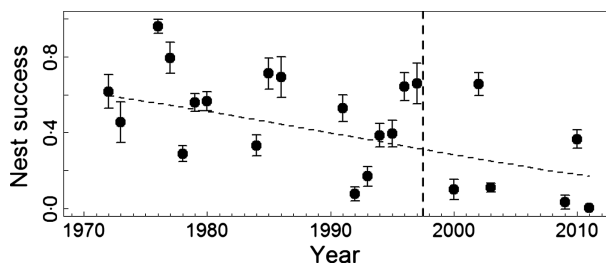

Fig. 4. Annual nest survival estimates (DSR[28]) of common eiders from the fixed year effect model taking into account visitor effects (black circles). Bars represent 95% confidence intervals. Dashed line represents fitted values for the linear time trend. Dashed vertical line separates the pre-exodus and post-exodus time periods.

DSR = −0·82, 95% CI = −0·95 to −0·69; Table S.3·1 in Appendix S3). We thus corrected for these effects in all analyses.

In the initial abiotic tier of model selection, the best-performing model included an interaction between early-spring temperature and precipitation and an interaction between late-spring temperature and precipitation (Table 1, $R = 0·32$). The top model from the initial biotic model selection tier suggested an important interaction between snow goose abundance and fox index, as well as an additive effect of the snow goose exodus on common eider nest success (Table 1, $R = 0·42$). These top models and their effects were then considered in additive and interactive models to examine the combined influence of the biotic and abiotic environment on eider nest survival. The highest ranked model from the final set of candidate models included all effects contained in the top-ranked biotic and abiotic models, except for the effect of the snow goose exodus (Table 1; for an expanded list of model selection results see Appendix S2). The best-performing biotic–abiotic model explained 0·69 of the deviance accounted for by the fully saturated temporal model, indicating that it explained a large proportion of annual variation in the nest survival data.

The estimated coefficients for covariates in the top model are summarized in Appendix S3. The increase in snow goose abundance along the Cape Churchill Peninsula during the study negatively affected eider nest success, and accounts for the decline in eider nest success across the study (β_{Goose} = −0·82; Fig. 5). This is consistent with our hypothesis that snow geese negatively influence common eider nest success through apparent competition. Furthermore, the inclusion of effects of the eventual snow goose exodus from the eider colony did not improve model fit enough to warrant inclusion in the top model (Table S.2·1 in Appendix S2).

Annual fox index also influenced common eider nest survival, and this effect was highly dependent on the abundance of nesting snow geese. At the beginning of the study (low snow goose abundance), the effect of fox index was highly positive (β_{Fox} = 0·23; Fig. 5). This supports

Table 1. Comparison of top models from each tier of model selection. A linear year effect and null model are also included for comparison

Model	Type	npar	Dev	Δ(SIC)	R
Goose × Fox + ES$_{temp}$ × ES$_{precip}$ + LS$_{temp}$ × LS$_{precip}$ + VisitDay	Biotic–Abiotic	11	16680·3	0·0	0·69
Goose × Fox + Exodus + VisitDay	Biotic	6	17101·7	365·9	0·42
ES$_{precip}$ × ES$_{temp}$ + LS$_{temp}$ × LS$_{precip}$ + VisitDay	Abiotic	8	17259·5	545·9	0·32
Linear Year Effect + VisitDay	Linear	3	17363·1	594·0	0·25
VisitDay	Null	2	17760·8	980·5	0·00

"Goose" = annual lesser snow goose abundance on the Cape Churchill Peninsula, "Fox" = arctic fox index in current year, "Exodus" = dummy variable (1 or 0) to indicate time period before and after goose exodus from traditional nesting colony, "ES" = early spring (May 1–June 10), "LS" = late spring (June 11–July 15), "precip" = average daily precipitation, "temp" = average daily temperature, "VisitDay" = effect of a nest visit on daily survival. Model headings are as follows: "Type" = type of covariates included in model, "npar" = number of parameters in model, "Dev" = model deviance, "ΔSIC" = difference in SIC points between a respective model and the top model, "R" = relative model reduction in deviance, compared to fully saturated temporal model (not included in this table).
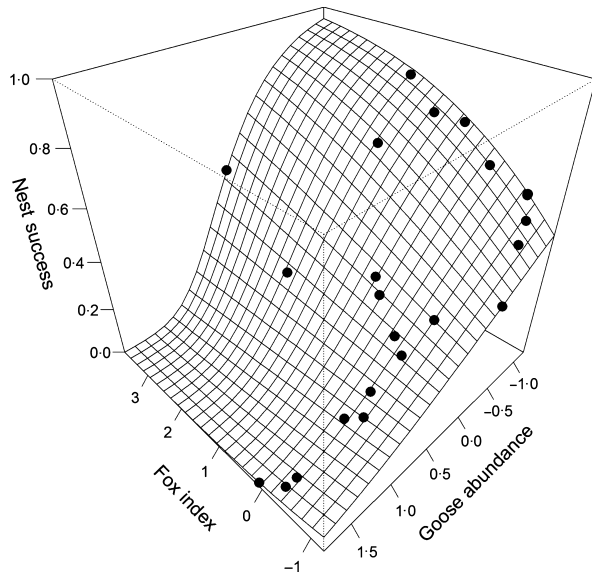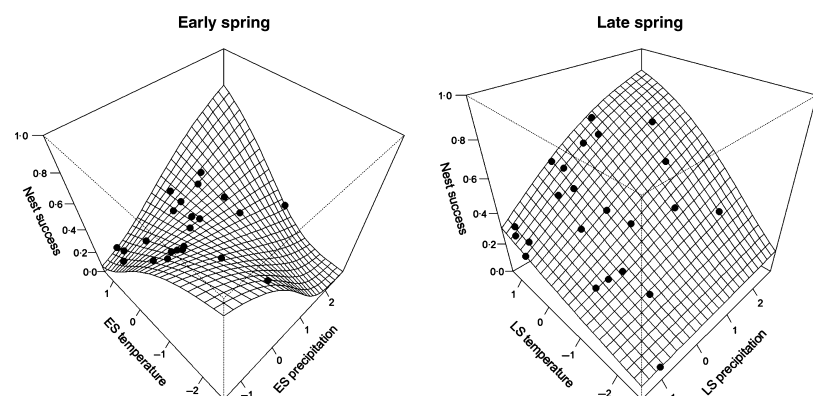
Fig. 5. The interactive effect of the fox index and lesser snow goose abundance on common eider nest success. Both covariates were z-transformed. Axes are scaled to the min and max values observed across the study, and all other parameters in the model were fixed at their mean values. Solid points represent combinations of covariates that were actually observed).

our hypothesis that in years of low fox index (and thus low small mammal availability), arctic foxes switch to consuming waterfowl eggs. However, with the increase in snow goose abundance along the Cape Churchill Peninsula coast, the effect of fox index declined ($\beta_{\text{Goose} \times \text{Fox}} = -0.28$; Fig. 5).

Spring climate in both the early- and late-breeding season influenced common eider nest success. An interaction between early-spring temperature and precipitation suggested that cold and wet, as well as warm and dry conditions in early spring were associated with decreased nest survival, while warm, wet conditions during this period were associated with high nest success (Fig. 6). In the late-breeding season, both temperature and precipitation were positively correlated with daily survival rate (Fig. 6, Table S.3·1 in Appendix S3).

Discussion

Similar to previous long-term studies of common eiders (Milne 1974; Coulson 1984; Swennen 1989), our estimates of annual nest success varied considerably across the 23 years of our study; in some cases, the difference in annual nest success between adjacent years was as large as 0·5 (Fig. 4). Overall, we observed a notable decline in annual nest survival across the study, with the most recent years having among the lowest nest success (nearly 0) recorded in the literature (Goudie, Robertson & Reed 2000).

The apparent negative trend in nest success, and accompanying variation around the trend, was the result of a complex interaction between predators, alternative prey (in this system, snow geese and possibly small mammals), and breeding season climate. The strong, negative effect of snow goose abundance suggests that the long-term decline in common eider nest success across the study was caused by apparent competition with snow geese. Several studies have documented both behavioural and numerical responses of avian predator populations to increased snow goose abundance (Samelius & Alisauskas 1999; Bêty et al. 2002; Sammler, Andersen & Skagen 2008). The herring gull population in western Hudson Bay that forages almost exclusively on waterfowl eggs and ducklings (and goslings) may have increased or congregated in response to the snow goose population explosion (Sammler, Andersen & Skagen 2008). Importantly, common eider nesting habitat was not directly affected by destructive snow goose foraging that degraded the adjacent salt marshes (Iles 2012). As such, an augmented avian predator community is likely responsible for the negative correlation between common eider nest survival and snow goose abundance.

Importantly, the effect of snow geese on common eiders was not dampened or reversed by the eventual exodus of snow geese from the eider colony. We offer two potential explanations for this result. First, as of 2011, the highest densities of snow geese along the CCP coast are located less than 15 km from the traditional nesting areas (spanning up to 75 km away; Fig. 2; Aubry et al. in press).

Fig. 6. The effect of spring temperature and precipitation on common eider nest success. Early spring (ES) = May 1–June 10, Late spring (LS) = June 11–July 15, temperature = mean daily temperature, precipitation = total daily precipitation. All covariates were z-transformed. Axes are scaled to the min and max values observed across the study; all other parameters in the model were fixed at their mean values. Solid points represent combinations of covariates that were actually observed.

These distances are unlikely to provide a barrier to the avian predator species responsible for apparent competitive effects between eiders and snow geese. Second, the rivers that provide willow islands for nesting eiders also have an abundance of large rocks surrounded by water that provide ideal gull nesting habitat. Although long-term time-series data on gull nest densities are not available, the breeding population of herring gulls within the eider colony appears to have grown precipitously in parallel with the geese. In 1972–1976, there were less than 10 gull nests within the rivers surrounding the eider colony, while in 2012 we found over 70 in the same area (KFA and DTI unpublished data). These results suggest that the effects of apparent competition may persist for decades after local densities of a shared prey have declined.

We did, however, find that the effect of arctic foxes on common eider nest success was modulated by the abundance of lesser snow geese. At the beginning of the study, with low snow goose abundance, arctic fox index was positively correlated with common eider nest success. This supports the hypothesis that in years of low fox production (and thus low small mammal abundance) arctic foxes switch to predation on ground-nesting waterfowl, and is consistent with the findings of other studies (e.g. Bêty *et al.* 2002; Gauthier *et al.* 2004). The increasing abundance of snow geese along the CCP coast appeared to buffer the effects of arctic foxes, presumably through partial prey swamping (Robertson 1995). This result is perhaps not surprising; fluctuations in arctic fox productivity are more so regulated by early spring small mammal availability than nest availability (Roth 2003; Gauthier *et al.* 2004). As such, arctic foxes generally do not respond numerically to increased abundance of ground-nesting waterfowl, but their effective predation pressure on eiders can be buffered by the availability of lesser snow geese surrounding the eider colony (Figs 3 and 5).

We also found an influence of season-specific climate on common eider nest survival. Cold and wet as well as dry and warm conditions during the early spring were associated with decreased nest survival, whereas warm and wet conditions were associated with increased nest survival during the mid to late spring (June 11–July 15). Nest initiation for common eiders is delayed in cold, wet springs until islands become ice free and flooding subsides, with accompanying effects on reproductive investment (Lehikoinen, Kilpi & Öst 2006; Chaulk & Mahoney 2012). Diminished investment in cold, wet years by incubating eider hens may expose their nests to increased avian predation when taking more frequent incubation breaks in an effort to recoup somatic energy losses accrued during reproductive delay (Criscuolo *et al.* 2002).

On the other hand, spring conditions that allow for early-nest initiation (e.g. warm and dry conditions) and thus an extended breeding season may increase the breeding propensity of low-quality females. For example, Love *et al.* (2010) showed that nest initiation profiles were more positively skewed in warm years, suggesting increased breeding effort by lower quality breeders. An increased proportion of low-quality breeders that are subject to higher rates of nest failure could decrease average nest success while simultaneously increasing net reproductive output in a given year, and may partly explain the negative association we found between average nest success and warm and dry climate in early spring.

Although gull predation is a major cause of nest failure during early incubation, the accessibility of nesting islands to mammalian predators (particularly arctic foxes) is an important determinant of nesting success later in the season (Robertson 1995). Accordingly, more precipitation during late spring may reduce the accessibility of eider islands to arctic foxes by raising water levels in the river. As opposed to early spring, temperature in the mid-late nesting season is unlikely to directly affect reproductive investment. However, the growth rate of plants, and thus nest concealment, depends on temperature (Myneni *et al.* 1997). In turn, seasonal changes in vegetative nest cover may affect the detection and accessibility of nests by avian and mammalian predators, with accompanying positive impacts on nest survival (Schmutz, Robertson & Cooke 1983; Götmark & Ahlund 1988; but see Öst & Steele 2010).

Climate models predict an increase in the mean and variance of both temperature and precipitation in high-latitude regions (Houghton *et al.* 2001; Post *et al.* 2009). Our results suggest that warmer and wet conditions in early spring and warmer temperatures in late spring will improve common eider nest survival. This agrees with the findings of D'Alba, Monaghan & Nager (2010), who found a positive relationship between the abundance of new recruits to a breeding population of common eiders and spring temperatures 2 years earlier (the hatch year for new recruits). However, our results also indicate that the effect of climate may change throughout a season. Consequently, we caution that finer scale climate predictions may be needed to accurately estimate the effect of climate perturbations on natural populations.

Our models explained a large amount of the annual variability in common eider nest survival over the course of our study (69%), and an integration of intra-annual covariates with inter-annual covariates could further improve predictive abilities. For example, within-season factors (e.g. timing of snow goose hatch, gull nesting phenology, onshore arrival of polar bears) and nest-specific characteristics (e.g. laying dates, vegetation phenology and female age) likely play a role in regulating nest survival as well. An examination of these factors would help clarify the mechanisms responsible for our findings, especially those related to the effect of breeding season climate on eider nest success.

Our study provides compelling evidence that eider nest success is strongly influenced by an interaction between predators and alternative prey, and establishes this population of eiders among the list of species adversely affected by the growth of lesser snow goose populations, and

ultimately, by landscape change in mid-continent North America (Abraham, Jefferies & Alisauskas 2005; Jefferies, Jano & Abraham 2006). The importance of trophic interactions and/or climate in regulating highly variable vital rates have been demonstrated for other populations of common eiders (e.g. Coulson 1984; Swennen 1989; Love *et al.* 2010), as well as other long-lived sea birds (e.g. black-legged kittiwakes, Murphy, Springer & Roseneau 1991; snow petrels, Chastel, Weimerskirch & Jouventin 1993; greater scaup, Flint *et al.* 2006; black scoters, Schamber, Broerman & Flint 2010). However, while it is clear that reproductive output in this population is highly variable through time and driven by a complex interplay of environmental factors, the consequences of this variability on population dynamics are not known.

Demographic theory suggests that in long-lived iteroparous species, population growth rate tends to be most sensitive to changes in adult survival and least sensitive to changes in reproductive vital rates (Pfister 1998). However, selection is expected to buffer the traits most strongly correlated with fitness against environmental change, thereby reducing their variability through time (Gaillard & Yoccoz 2003; but see Koons *et al.* 2009). This prediction appears to be supported in long-lived sea ducks, which have adopted a bet-hedging life history strategy to compensate for years of low annual reproductive output with relatively high and stable adult survival (Wilson *et al.* 2007).

Although population growth rate in long-lived, iteroparous species may be least sensitive to changes in reproductive vital rates, high variability in these rates compared to adult survival may actually contribute more to observed changes in population growth and abundance (Gaillard & Yoccoz 2003). Thus, our next step will be to develop population models to investigate the consequences of observed variability in reproductive success, and the drivers of this variability, on population dynamics. Such research will provide valuable insight into the ecological processes governing populations amidst changing environmental pressures.

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References

Abraham, K.F., Jefferies, R.L. & Alisauskas, R.T. (2005) The dynamics of landscape change and snow geese in mid-continent North America. *Global Change Biology*, **11**, 841–855.

Adler, P.B. & HilleRisLambers, J. (2008) The influence of climate and species composition on the population dynamics of ten prairie forbs. *Ecology*, **89**, 3049–3060.

Aubry, L.M., Cam, E., Koons, D.N., Monnat, J.Y. & Pavard, S. (2010) Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. *Journal of Animal Ecology*, **80**, 375–383.

Aubry, L.M., Rockwell, R.F., Cooch, E.G., Brook, R., Mulder, C. & Koons, D.N. (In press) Environmental causes and the demographic consequences of changes in lesser snow goose gosling condition. *Global Change Biology*.

Bêty, J., Gauthier, G., Korpimäki, E. & Giroux, J.F. (2002) Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. *Journal of Animal Ecology*, **71**, 88–98.

Bolduc, F. & Guillemette, M. (2003) Human disturbance and nesting success of common eiders: interaction between visitors and gulls. *Biological Conservation*, **110**, 77–83.

Burnham, K. P. & Anderson, D. R. (2002) *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer, New York.

Campbell, B.H. (1990) Factors affecting the nesting success of Dusky Canada Geese on the Copper River Delta, Alaska. *The Canadian Field Naturalist*, **104**, 567–574.

Chaneton, E.J. & Bonsall, M.B. (2000) Enemy-mediated apparent competition: empirical patterns and the evidence. *Oikos*, **88**, 380–394.

Chastel, O., Weimerskirch, H. & Jouventin, P. (1993) High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*. *Oecologia*, **94**, 278–285.

Chaulk, K.G. & Mahoney, M.L. (2012) Does spring ice cover influence nest initiation date and clutch size in common eiders? *Polar Biology*, **35**, 645–653.

Cooch, E.G., Rockwell, R.F. & Brault, S. (2001) Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. *Ecological Monographs*, **71**, 377–400.

Cooch, E.G. & White, G. eds. (2012) *Program MARK, A Gentle Introduction*, 12th edn. http://www.phidot.org/software/mark/docs/book. Accessed 16/10/2011.

Cooke, F., Rockwell, R.F. & Lank, D.B. (1995) *The Snow Geese of La Pérouse Bay: Natural Selection in the Wild*. Oxford University Press, USA.

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

Criscuolo, F., Gabrielson, G.W., Gendner, J.P. & Le Maho, Y. (2002) Body mass regulation during incubation in female common eiders *Somateria mollissima*. *Journal of Avian Biology*, **33**, 83–88.

Cryer, J.D. & Chan, K.S. (2008) *Time Series Analysis: With Applications in R*, 2nd edn. Springer, New York, NY.

D'Alba, L., Monaghan, P. & Nager, R.G. (2010) Advances in laying date and increasing population size suggest positive responses to climate change in common eiders *Somateria mollissima* in Iceland. *Ibis*, **152**, 19–28.

Elmhagen, B., Tannerfeldt, M., Verucci, P. & Angerbjörn, A. (2000) The arctic fox (*Alopex lagopus*): an opportunistic specialist. *Journal of Zoology*, **251**, 139–149.

Elton, C. & Nicholson, M. (1942) The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology*, **11**, 215–244.

Flint, P.L., Grand, J.B., Fondell, T.F. & Morse, J.A. (2006) Population dynamics of greater scaup breeding on the Yukon-Kuskokwin Delta, Alaska. *Wildlife Monographs*, **162**, 1–22.

Gaillard, J.M. & Yoccoz, N.G. (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.

Ganter, B. & Cooke, F. (1998) Colonial nesters in a deteriorating habitat: site fidelity and colony dynamics of Lesser Snow Geese. *Auk*, **115**, 642–652.

Gauthier, G., Bêty, J., Giroux, J.F. & Rochefort, L. (2004) Trophic interactions in a high arctic snow goose colony. *Integrative and Comparative Biology*, **44**, 119–129.

Gauthier, G., Giroux, J.F., Reed, A., Béchet, A.A. & Bélanger, L. (2005) Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands? *Global Change Biology*, **11**, 856–868.

Gilliland, S.G., Gilchrist, H.G., Rockwell, R.F., Robertson, G.J., Savard, J.-P.L., Merkel, F. & Mosbech, A. (2009) Evaluating the sustainability of harvest among northern common eiders *Somateria mollissima* borealis in Greenland and Canada. *Wildlife Biology*, **15**, 24–36.

Götmark, F. & Ahlund, M. (1988) Nest predation and nest site selection among eiders *Somateria mollissima*: the influence of gulls. *Ibis*, **130**, 111–123.

Goudie, R. I., Robertson, G.J. & Reed, A. (2000) Common eider (*Somateria mollissima*). *The Birds of North America Online* (ed. A. Poole). Cornell Lab of Ornithology, Ithaca. http://bna.birds.cornell.edu/bna/species/546. Accessed 16/10/2011.

Green, R.E. (1989) Transformation of crude proportions of nests that are successful for comparison with Mayfield estimates of nest success. *Ibis*, **131**, 305–306.

Guild, B.L. (1974) The Breeding Biology of the Hudson Bay Eider at La Pérouse Bay, Manitoba. M.S. thesis. Wright State University, Dayton.

Hersteinsson, P. & MacDonald, D.W. (1992) Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos*, **64**, 505–515.

Holt, R.D. & Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology, Evolution, and Systematics*, **25**, 495–520.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J. & Xiaosu, D., eds. (2001) *Climate Change 2001: The Scientific Basis: Contributions of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

Humbert, J.Y., Mills, L.S., Horne, J.S. & Dennis, B. (2009) A better way to estimate population trends. *Oikos*, **118**, 1940–1946.

Iles, D.T. (2012) Drivers of nest success in common eiders and impacts on population dynamics. M.S. thesis, Utah State University, Logan, UT.

Jefferies, R.L., Jano, A.P. & Abraham, K.F. (2006) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, **94**, 234–242.

Jefferies, R.L., Rockwell, R.F. & Abraham, K.F. (2004) Agricultural food subsidies, migratory connectivity and large-scale disturbance in arctic coastal systems: a case study. *Integrative and Comparative Biology*, **44**, 130–139.

Johnson, D. (1991) Further comments on estimating nest success. *Ibis*, **133**, 205–207.

Kerbes, R.H., Meeres, K.M., Alisauskas, R.T, Caswell, F.D., Abraham, K.F. & Ross, R.K. (2006) Surveys of nesting mid-continent lesser snow geese and Ross's geese in Eastern and Central Arctic Canada, 1997-98. Technical Report Series, No. 447, Canadian Wildlife Service, Prairie and Northern Region.

Koons, D.N., Pavard, S., Baudisch, A. & Metcalf, J.E. (2009) Is life-history buffering or lability adaptive in stochastic environments? *Oikos*, **118**, 972–980.

Laake, J. & Rexstad, E. (2012) *RMark – An Alternative Approach to Building Linear Models in MARK. Program MARK: 'A Gentle Introduction'*, 11th edn (eds E. Cooch & G. C. White), pp. C-1–C-115. http://www.phidot.org/software/mark/docs/book. Accessed 16/10/2011.

Lehikoinen, A., Kilpi, M. & Öst, M. (2006) Winter climate affects subsequent breeding success of common eiders. *Global Change Biology*, **12**, 1355–1365.

Love, O.P., Gilchrist, H.G., Descamps, S., Semeniuk, C.A.D. & 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.

Martin, M. & Barry, T.W. (1978) Nesting behavior and food habits of parasitic jaegers at Anderson River Delta, Northwest Territories. *The Canadian Field Naturalist*, **92**, 45–50.

Merkel, F.R. (2004) Evidence of population decline in common eiders breeding in western Greenland. *Arctic*, **57**, 27–36.

Milne, H. (1974) Breeding numbers and reproductive rate of eiders at the Sands of Forvie National Nature Reserve, Scotland. *Ibis*, **116**, 135–152.

Milne, H. & Dau, C. P. (1976) A bibliography of eiders. Faune Bull. no. 20. Department of Tourism, Fish and Wildlife Division, Government of Québec, Québec, Canada.

Murphy, E.C., Springer, A.M. & Roseneau, D.G. (1991) High annual variability in reproductive success of kittiwakes (*Rissa tridactyla l.*) at a colony in western Alaska. *Journal of Animal Ecology*, **60**, 515–534.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. (1997) Increased plant growth in the northern latitudes from 1981 to 1991. *Nature*, **386**, 698–702.

Öst, M. & Steele, B.B. (2010) Age-specific nest-site preference and success in eiders. *Oecologia*, **162**, 59–60.

Pfister, C.A. (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 213–218.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Hoye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M. & Aastrup, P. (2009) Ecological dynamics across the arctic associated with recent climate change. *Science*, **325**, 1355–1358.

Robertson, G.J. (1995) Factors affecting nest site selection and nesting success in the common eider *Somateria mollissima*. *Ibis*, **137**, 109–115.

Robertson, G.J. & Gilchrist, H.G. (1998) Evidence of population declines among common eiders breeding in the Belcher Islands, Northwest Territories. *Arctic*, **51**, 378–385.

Rockwell, R.F. & Gormezano, L.J. (2009) The early bear gets the goose: climate change, polar bears and lesser snow geese in Western Hudson Bay. *Polar Biology*, **32**, 539–547.

Rockwell, R.F., Gormezano, L.J. & Koons, D.N. (2011) Trophic matches and mismatches: can polar bears reduce the abundance of nesting snow geese in western Hudson Bay? *Oikos*, **120**, 696–709.

Roth, J.D. (2003) Variability in marine resources affects arctic fox population dynamics. *Journal of Animal Ecology*, **72**, 668–676.

Samelius, G. & Alisauskas, R.T. (1999) Diet and growth of glaucous gulls at a large arctic goose colony. *Canadian Journal of Zoology*, **77**, 1327–1331.

Sammler, J.E., Andersen, D.E. & Skagen, S.K. (2008) Population trends of tundra-nesting birds at Cape Churchill, Manitoba, in relation to increasing goose populations. *The Condor*, **110**, 325–334.

Schamber, J.L., Broerman, F.J. & Flint, P.L. (2010) Reproductive ecology and habitat use of Pacific black scoters (*Melanitta nigra americana*) nesting on the Yukon-Kuskokwim Delta, Alaska. *Waterbirds*, **33**, 129–271.

Schmutz, J.K., Robertson, R.J. & Cooke, F. (1983) Colonial nesting of the Hudson Bay eider duck. *Canadian Journal of Zoology*, **61**, 2424–2433.

Schwarz, G. (1978) Estimating the dimension of a model. *Annals of Statistics*, **6**, 461–464.

Seber, G.A. (1982) *The Estimation of Annual Abundance and Related Parameters*, 2nd edn. MacMillan, New York.

Smirnov, V.S. (1968) Analysis of arctic fox population dynamics and methods of increasing the arctic fox harvest. *Problems of the North*, **11**, 81–101.

Suydam, R., Dickson, D.L., Fadely, J.B. & Quakenbush, L.T. (2000) Population declines of king and common eiders of the Beaufort Sea. *Condor*, **102**, 222–227.

Swennen, C. (1989) Gull predation upon eider *Somateria mollissima* ducklings: destruction of elimination of the unfit? *Ardea*, **77**, 21–44.

Tannerfeldt, M., Angerbjörn, A. & ArvidSon, B. (1994) The effect of summer feeding on juvenile arctic fox survival – a field experiment. *Ecography*, **17**, 88–96.

Taper, M.L. & Gogan, P.J.P. (2002) The Northern Yellowstone elk: density dependence and climatic conditions. *The Journal of Wildlife Management*, **66**, 106–122.

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

Watson, M.D., Robertson, G.J. & Cooke, F. (1993) Egg-laying time and laying interval in the common eider. *The Condor*, **95**, 869–878.

Weller, M.W. (1956) A simple field candler for waterfowl eggs. *The Journal of Wildlife Management*, **20**, 111–113.

Westerkov, K. (1950) Methods for determining the age of game bird eggs. *The Journal of Wildlife Management*, **14**, 56–67.

Wilson, H.M., Flint, P.L., Moran, C.L. & Powell, A.N. (2007) Survival of breeding pacific common eiders on the Yukon-Kuskokwim Delta, Alaska. *The Journal of Wildlife Management*, **71**, 403–410.

Zheng, B. (2000) Summarizing the goodness of fit of generalized linear models for longitudinal data. *Statistics in Medicine*, **19**, 1265–75.

Supporting Information

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

Appendix S1. Description of methods used to calculate arctic fox index.

Appendix S2. Detailed results of the final tier of model selection, including both biotic and abiotic covariates.

Appendix S3. Logit-scale daily survival rate beta coefficients from top biotic-abiotic model.