Drivers of Nest Success and Stochastic Population Dynamics of the Common Eider (Somateria mollissima)

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DRIVERS OF NEST SUCCESS AND STOCHASTIC POPULATION DYNAMICS
OF THE COMMON EIDER (SOMATERIA MOLLISSIMA)

by

David T. Iles

A thesis submitted in partial fulfillment
of the requirements for the degree
of
MASTER OF SCIENCE
in
Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

2012
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ABSTRACT

Drivers of Nest Success and Stochastic Population Dynamics of the Common Eider (Somateria Mollissima)

by

David T. Iles, Master of Science
Utah State University, 2012

Anthropogenic perturbations to Arctic ecosystems have influenced large-scale climate processes, as well as finer-scale ecological relationships within and amongst populations of species. Life history theory predicts a trade-off between the temporal variation in a vital rate and its impact on population dynamics. Here, we examine the drivers of long-term variation in reproductive success in a sub-Arctic common eider (Somateria mollissima) colony, and evaluate the impacts of variation in reproductive success on eider population dynamics.

In Chapter 2, we develop a suite of nest survival models to evaluate the effects of variation in predator abundance, the availability and spatial distribution of alternative prey, and breeding season climate on annual common eider nest success. Eider nest success declined across the 41 years of study, but was also highly variable across years. Annual variation in nest success was driven by a complex interaction between predators and alternative prey, as well as breeding season climate. Our results suggest that
increased abundance of snow geese (alternative prey) may buffer annual fluctuations in arctic fox abundance, yet result in a long-term decline in eider nest success suggesting apparent competition via other predator species (e.g. gulls). The effect of breeding season climate was subtle compared to the influence of biotic factors and indicated that cold, wet conditions in early spring were correlated with decreased nest success, while warm, wet conditions in late spring increased eider nest success.

In Chapter 3 we develop a stochastic population model to evaluate the relative effects of variation and covariation amongst multiple vital rates on population dynamics, and determine the impact of long-term changes in the abundance of alternative prey on eider population dynamics. Consistent with life history predictions, we found that proportional changes in adult survival have the largest impact on population dynamics, yet high variation in the vital rates underlying fertility contribute more to actual variation in population growth. The eventual exodus of alternative prey from the eider colony reduced the long-term growth rate, primarily through negative impacts on mean nest success.

(105 pages)
PUBLIC ABSTRACT

Drivers of Nest Success and Stochastic Population Dynamics of the Common Eider (*Somateria Mollissima*)

by

David T. Iles

Human-caused climate alterations to Arctic ecosystems have resulted in a constellation of impacts on the biological relationships within them, yet the consequences of these changes on the population dynamics of many species are poorly understood. Thus, an understanding of the drivers of variation in population performance is needed to inform the management and conservation of imperiled species. Here, we use a long-term dataset for the common eider, an Arctic-breeding sea duck, to examine the drivers of annual variation in nest survival, and evaluate the effects of variation in vital rates on population growth. Our chapter 2 results suggested that increased abundance of local alternative prey may buffer annual fluctuations in arctic fox abundance, yet may stimulate populations of other nest predators (e.g. gulls), resulting in a long-term decline in nest success. Additionally, breeding season climate had a subtle effect on annual nesting success. In Chapter 3, we found that the population growth rate declined across the study, primarily due to changes nest success. Including correlations amongst vital rates altered the direction of effect of changes in vital rate variance. Thus, long-term studies are needed to accurately predict the effects of environmental change on populations, and a concerted effort should be made to monitor multiple parts of the life cycle simultaneously in order to correctly account for correlations amongst vital rates.
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David T. Iles
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CHAPTER 1

INTRODUCTION

Anthropogenic perturbations have disproportionately affected high-latitude ecosystems, with accompanying changes in both the mean and variability of climate processes (Vinnikov et al. 1999; Houghton et al. 2001). Corresponding effects in the phenology, distribution, and abundance of arctic species have resulted in widespread consequences for both population dynamics and community interactions in these systems (Walther et al. 2002; Abraham, Jefferies, & Alisauskas 2005; Post et al. 2009). However, for many populations the consequences of changes in the biotic and abiotic processes governing population dynamics remain unclear.

Life history theory predicts that selection in stochastic environments will buffer traits most strongly correlated with fitness against environmental stochasticity (Pfister 1998; Gaillard & Yoccoz 2003; Morris & Doak 2004; Morris et al. 2008; but see Koons et al. 2009). Since fitness in stochastic environments is directly related to the population growth rate, selection is expected to reduce temporal variability in the vital rates to which growth rate is most sensitive (Tuljapurkar 1990; Pfister 1998; Doak et al. 2005). Comparative studies both among and within species have consistently supported this prediction, suggesting that it is one of the key generalities of life history evolution (Pfister 1998; Gaillard, Festa-Bianchet, & Yoccoz 1998; Gaillard et al. 2000; Morris & Doak 2004; but see Koons et al. 2009). For example, the population growth rate of long-lived species is usually more sensitive to changes in adult survival than fertility. As a consequence, adult survival tends to be the most stable vital rate through time, yet
paradoxically, may influence actual population dynamics less than other vital rates that vary considerably (Gaillard et al. 1998).

These predictions appear to be supported in sea ducks, which have adopted a bet-hedging life history to compensate for highly variable reproductive success. For example, the common eider (*Somateria mollissima*) is a colonial-nesting sea duck that delays breeding for several years, has relatively high, stable adult survival, and is highly iteroparous (Goudie, Robertson, & Reed 2000). On the other hand, reproductive success appears to be highly variable through time, primarily due to the boom-bust nature of nest success and duckling survival (Coulson 1984; Goudie et al. 2000).

The common eider, along with many other sea duck species, has experienced long-term declines across much of its range, with some populations declining as much as 75-95% (Robertson & Gilchrist 1998). Sea ducks are important both ecologically and economically, and are critical components of subsistence harvest in northern communities (Gilchrist & Robertson 2000; Goudie et al. 2000). Thus, the factors governing sea duck populations are of concern to conservationists, waterfowl managers, and aboriginal communities. Yet, even for well studied species like the common eider, the demographic causes of these declines are poorly understood (Robertson & Gilchrist 1998; Ekroos et al. 2012). In particular, very few population models have been developed for sea ducks, owing to the difficulty of monitoring Arctic-breeding species throughout their life cycle. The relative importance of relationships among life cycle components and their underlying vital rates to population dynamics therefore remain unclear.
Periodically, avian and mammalian predators such as herring gulls (*Larus argentatus*), ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), arctic foxes (*Vulpes lagopus*), and increasingly, polar bears (*Ursus maritimus*), decimate coastal eider colonies, depredating large numbers of eggs, ducklings, and even attendant females (Goudie *et al.* 2000; Rockwell & Gormezano 2009). Accordingly, earlier thawing of the Arctic icepack (Vinnikov *et al.* 1999) may be influencing the phenology and composition of the predator community, and thus, the frequency of catastrophic reproductive failure in eider colonies (Skinner *et al.* 1998; Rockwell & Gormezano 2009).

In recent decades populations of snow geese (*Chen caerulescens*) have increased exponentially as a result of novel agricultural subsidies available to geese on wintering grounds and along migration routes (Jefferies, Rockwell, & Abraham 2004; Gauthier *et al.* 2005). Many populations of snow geese breed in colonies along arctic coasts, often in close proximity to colonies of other marine waterfowl. The unprecedented increase in availability of snow goose eggs and ducklings on arctic landscapes could therefore augment predator populations, with several (potentially opposing) impacts on common eider reproductive success. For example, if predator foraging is strictly frequency-dependent, the increased abundance of snow geese may “swamp out” predator effects on other nearby species. However, if increased availability of alternative prey bolsters predator populations, there may be negative consequences for other sympatric prey species, including common eiders.

Here, we use data collected across 41 years from a common eider colony at La Pérouse Bay, Manitoba, Canada to investigate the drivers of long-term variation in
common eider nest success, and to examine the impacts of variation in nest success and 
covariation amongst other vital rates on common eider population dynamics. In Chapter 
2, we combine one of the longest datasets of common eider breeding ecology in North 
America with historical time series data for arctic foxes, snow geese, and climate to 
examine the effect of annual changes in the biotic and abiotic environment on nest 
success. Specifically, we develop a suite of nest survival models to evaluate the effects 
of variation in predator abundance, the availability and spatial distribution of alternative 
prey, and breeding season climate on annual common eider nest success. These results 
will help characterize long-term variation in nest success, and provide valuable insights 
into the drivers thereof.

In Chapter 3, we combine our estimates of nest success with additional vital rates 
from the study population and develop a stochastic population model to evaluate the 
relative impacts of variation in multiple vital rates on common eider population 
dynamics. We then use a recently developed stochastic life table response experiment to 
determine the impact of long-term changes in the abundance of alternative prey on eider 
population dynamics, through effects on the statistical properties of the underlying vital 
rates. Additionally, we conduct our analyses under four correlation scenarios to examine 
the effect of covariation in vital rates on population dynamics.

References


CHAPTER 2
PREDATORS, ALTERNATIVE PREY, AND CLIMATE INFLUENCE THE ANNUAL
BREEDING SUCCESS OF A LONG-LIVED SEA DUCK

Summary

1. Perturbations to ecosystems have the potential to directly and indirectly affect species interactions, with subsequent impacts on population dynamics and the factors 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 long-term trends in common eider nesting success, as well as to investigate the effects of arctic fox abundance (a terrestrial nest predator), the local abundance and spatial distribution of lesser snow geese (an alternative prey source), and spring climate on nest success.

4. Eider nest success declined over the course of the study, but was also highly variable across years. These changes in nest success were largely driven by a complex interaction between predators and alternative prey, as well as breeding season climate. The arctic fox index was positively correlated with nest success prior to the snow goose exodus from the eider colony. In addition, the effect of foxes during this period was buffered by increased snow goose abundance, presumably through partial prey swamping. However, while sympatric snow geese buffered the fox effect, increased snow goose abundance in
the pre-exodus time period also led to a general decline in eider nest success, suggesting that apparent competition was operating via the effects of snow geese on the avian nest predator community. Following the snow goose exodus, the effect of arctic foxes on eider nest success was reversed. The effect of spring climate depended on the stage of the breeding season; cold, wet conditions in early spring were correlated with decreased nest success, while warm, wet conditions in late spring increased eider nest success. These effects may be related to the influence of temperature and precipitation on reproductive investment, accessibility of eider islands to nest predators, or alternative prey availability.

5. These results underscore the significance of both trophic interactions and abiotic factors in regulating highly variable vital rates, which may have important consequences for population dynamics and the conservation of declining species.

Introduction

Anthropogenic climate change has led to increased environmental variability, particularly in high-latitude regions where temperature ranges and precipitation regimes have changed disproportionately compared to those at low-latitudes (Houghton et al. 2001; Walther et al. 2002). Corresponding effects have been observed within high-latitude ecosystems, where climate-driven changes in phenology, distribution, and abundance of species have resulted in widespread ecological consequences (Walther et al. 2002; Post et al. 2009). These climate-driven perturbations have the potential to influence trophic interactions within ecological communities, with resulting impacts on
the population dynamics of many arctic species (Ims & Fuglei 2005; Kausrud et al. 2008; Post et al. 2009; Rockwell, Gormezano, & Koons 2011).

The common eider (*Somateria mollissima*) is an arctic, colonial nesting sea-duck, and has experienced long-term declines across much of its range, with some populations decreasing as much as 75% (Robertson & Gilchrist 1998). In addition to its role in wetland and marine ecosystems, the common eider is important both economically and for subsistence harvest in northern communities (Goudie et al. 2000). Reduced abundance of common eiders is of obvious concern to conservationists, waterfowl managers, and aboriginal communities. Yet despite the extensive research attention given to common eiders (Milne & Dau 1974; Goudie, Robertson, & Reed 2000), the demographic causes of these declines 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, including gulls (*Laridae* spp.), common ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), arctic foxes (*Vulpes lagopus*), wolves (*Canis lupus*), and polar bears (*Ursus maritimus*) have been known to decimate the annual reproductive output of common eider breeding colonies (Russell 1975; Goudie et al. 2000; Drent & Prop 2008; Rockwell & Gormezano 2009). However, the relative effect of changes in predator abundance on annual reproductive success remains unclear, as do the biotic and abiotic mechanisms that modulate predation pressure.
The presence of non-competitive, alternative prey has the potential to indirectly impact a focal species, like common eider, through impacts on shared predators. Traditional predation theory predicts that in shared prey systems, predation frequency on a focal species may increase as the abundance of alternative prey decreases (Cornell 1976; Allen & Greenwood 1988). Correspondingly, large-scale increases in the abundance of an alternative prey species may “swamp out” predator effects on a focal species (Abrams & Matsuda 1996; Kitzberger, Chaneton, & Caccia 2007). This frequency-dependent predation behavior is especially prevalent for opportunistic predators (Bantle & Alisauskas 1998; Elmhagen et al. 2000; Samelius & Alisauskas 2000; Gauthier et al. 2004), which may “prey-switch” to readily available alternative prey items in the absence of a preferred prey species. For example, while often considered specialist predators on arctic small mammals (Elmhagen et al. 2000), arctic foxes are known to opportunistically switch to alternative prey in years of low lemming availability, potentially causing widespread reproductive failure in ground-nesting waterfowl (e.g. Elmhagen et al. 2000; Bety et al. 2002; Gauthier et al. 2004).

While increased abundance of an alternative prey may “swamp out” predator effects under strict frequency-dependent predation, apparent competition theory (Holt 1977) predicts that increased abundance or availability of a prey species can invoke a numerical response in the predator community, thereby resulting in increased predation pressure on other shared prey species, especially when these additional prey species are preferred by predators (Holt & Lawton 1994; Bonsall & Hassell 1997; Chaneton & Bonsall 2000). In recent decades, populations of arctic and sub-arctic breeding snow
geese (*Chen caerulescens*) have increased exponentially, largely as a result of agricultural nutrient subsidies available to geese on wintering grounds and migration routes (Jefferies, Rockwell, & Abraham 2004; Gauthier *et al.* 2005). Snow geese are aggressive nest defenders, and since both male and female snow geese attend nests during incubation, they can successfully deter predators as large as arctic foxes (Samelius and Alisauskas 2006). Nevertheless, a small proportion of snow goose eggs are still depredated each year (0-20%; Rockwell unpublished). In contrast, male eiders do not remain with females during incubation and female common eiders rarely engage in aggressive nest defense, instead relying on cryptic plumage for anti-predator defense (Goudie *et al.* 2000). Thus, the considerable increase in the availability of snow goose eggs on arctic landscapes could augment some terrestrial predator populations, especially herring gulls that forage almost entirely on waterfowl eggs and offspring across the Hudson Bay Lowlands (Samelius & Alisauskas 1999; Sammler, Andersen, & Skagen 2008). A bolstered gull population benefitting from ample availability of snow goose prey could have negative consequences on other sympatric waterfowl species, including common eiders, which are much less aggressive and perhaps preferred by egg predators.

The abiotic environment also has the potential to modulate the biotic factors that influence nest survival. For example, spring temperature and precipitation can influence small mammal abundance through conditions that create flooding (Kausrud *et al.* 2008), which in turn could influence the degree to which foxes affect eider nesting success. Spring climate may also influence annual predation pressure by differentially affecting the phenology of predators and/or the phenology of nest initiation in prey, creating an
ecological “mismatch” (Drever & Clark 2007; Both et al. 2009; Rockwell et al. 2011).

For example, nesting within gull colonies can be beneficial or detrimental to eider nest success, depending on the stage of the gull breeding season (Gotmark 1989). The arrival of eiders on the breeding grounds and subsequent nest initiation is highly dependent on spring ice breakup, and may be delayed by as much as a month in years of late ice breakup (Robertson 1995; Lehikoinen, Kilpi, & Ost 2006; D’Alba, Monaghan, & Nager 2010). If eider nesting coincides with the incubation period of nesting gulls, eiders may enjoy a protective benefit of aggressive nest defense by adult gulls. Conversely, if changes in spring climate result in earlier nesting by eiders without a parallel advance in nesting by gulls, this protective benefit could be absent or even reversed (Gotmark 1989).

Here, we use data collected across 41 years from the La Pérouse Bay eider colony to investigate the effect of annual changes in arctic fox abundance, local abundance and spatial distribution of nesting snow geese (an alternative prey species), and spring climate on common eider nesting success. We predict that the effect of arctic fox abundance on common eider nest success will depend on the availability of local alternative prey; in years of low alternative prey availability, nest success will decline. Accordingly, increased snow goose abundance near the common eider colony should offset negative interactions with arctic foxes through prey swamping, but may stimulate populations of other predators such as gulls, resulting in decreased common eider nest success over the long term. Moreover, we predict that spring climate will modulate the strength and direction of these relationships through effects on alternative prey abundance, predator and prey phenology, and nest attendance of the eiders themselves.
Materials and Methods

Study Area

Field work was conducted in the Mast and Wao Wao river deltas, which feed into La Pérouse Bay (58°43’N, 93°24’W), approximately 30km east of Churchill, Manitoba, Canada. The river outflows form braided deltas with numerous islands that a colony of 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, though much of the data has not been published (Table 2.1).

Our study represents the longest investigation of S. m. sedentaria breeding ecology and nesting success. Historically, the two main egg predators for the La Pérouse Bay eider colony have been arctic foxes and herring gulls (Larus argentatus) (Guild 1974; Schmutz et al. 1983; Watson, Robertson, & Cooke 1993; Robertson 1995). In addition, the eider colony was historically bordered by a small snow goose colony (Cooke, Rockwell, & Lank 1995; Robertson 1995). However, following the snow goose population explosion (Fig. 2.1) and subsequent habitat degradation in traditional nesting areas, the primary snow goose colony shifted away from the eider colony, with resulting declines in local snow goose nest densities (Ganter & Cooke 1998; Cooch, Rockwell, & Brault 2001; Fig 2.2).

Nest Observations

At the onset of nesting each year, nests were located using repeated foot searches of the known breeding areas. 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 dates of each nest were estimated based on the incubation age of the nest and the number of eggs in the clutch, with an estimated laying rate of 1 egg per day. Nests were rechecked at 6 to 10 day intervals to assess fate, and were considered successful if they hatched at least 1 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 database offers one of the longest and most complete datasets for examining changes in arctic fox abundance, with records that can be linked back to those kept by the historical Hudson’s Bay Company (Elton & Nicholson 1942). Churchill is located near the southernmost portion of the arctic fox range (Wrigley & Hatch 1976; Hersteinsson & MacDonald 1992), and near the northern border of Manitoba. Furthermore, Churchill is the largest of just a few small settlements in northern Manitoba (Manitoba Aboriginal and Northern Affairs 2011). As such, provincial records of arctic fox pelt harvests are more likely to represent local trends in arctic fox populations than pelt records for species occupying a larger provincial range (e.g. red fox).

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, and we use the residuals from this model as indices of fox abundance/recruitment in each year (i.e., corrected for number of trappers). Because annual pelt harvest data was 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 3 (the upper 3rd order limit was based on plots of the autocorrelation and partial autocorrelation functions; Cryer & Chang 2008). For use as a covariate in nest survival analyses, we standardized the fox indices using a z-transformation. Due to possible lags in reporting of furs (i.e. the residual number of furs in a year could reflect the relative fox abundance 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.

Another caveat to consider is that arctic fox reproduction is highly correlated with spring lemming abundance (Roth 2003), while subsequent juvenile survival is strongly influenced by summer food availability (Tannerfeldt, Angerbjorn, & Arvidson 1994). Fox pelts, however, are most valuable and thus 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 wiser adults (Smirnov 1968; Roth 2003). Fox pelt harvest during the winter might therefore be representative of a composite measure of adult fox abundance, as well as fox production and juvenile recruitment within a year. Thus, if years of low relative fox harvest represent low spring lemming availability (i.e., driving poor fox reproductive output), we predict that they will be
correlated with low eider nest survival because of adult foxes ‘switching’ to eider eggs as an alternative to lemmings (Bety et al. 2002).

**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 (Kerbes et al. 2006; Jefferies, Jano, & Abraham 2006). A state-space model incorporating both population process variation and observation error (Humbert et al. 2009) was then used to interpolate snow goose abundances in years when 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. The z-standardized snow goose population estimates were used in eider nest survival analyses to examine alternative-prey hypotheses.

In 1995, long-term snow goose nest density plots were established to examine trends in snow goose nest density in the traditional colony. In each year of study, snow goose nests (both active and depredated) were counted within each of five circular sub-plots, and average snow goose density for each plot was calculated (Fig. 2.2). Nest density data from these plots captured the tail-end of a large-scale snow goose exodus from the eider colony. Without sufficient data to examine local snow goose nest density dynamics prior to the establishment of the long-term nest density plots, we created a binary variable for use in analyses to examine the effect of the snow goose exodus on eider nest success. Figure 2.2 indicates that most nesting snow geese had left the area
nearest the eider colony by 1998. As such, years prior to 1998 were assigned a “pre-exodus” status, while 1998 and onwards were assigned a “post-exodus” status.

Spring Climate Data

Local climate variables (temperature and precipitation) hypothesized to influence common eider nest success through effects on predator phenology and female incubation constancy were obtained online from the Environment Canada Climate Data Archive (http://climate.weatheroffice.gc.ca). Because we hypothesized that these effects may act differently depending on the stage of the breeding season, daily climate averages were divided into two periods: early breeding season (May 1 – June 10) and late breeding season (June 11 – July 15). 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 climate from mid to late incubation (late June/early July). Additionally, we considered more parsimonious climate models in which daily climate 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 et al. 1983). Rather than exclude 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 (Table 2.2). 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 analyzed nest survival data using the RMark package in program R (Laake & Rexstad 2008). Competing generalized linear models of DSR were fit using maximum likelihood, and relative support was evaluated using Schwarz’s information criterion (SIC; Schwarz 1978), rather than AICc (Akaike 1973; Burnham & Anderson 2010), which tends to favor over-parameterized models when sample size is large (Hooten 1995; Taper & Gogan 2002).

To evaluate general trends in annual nest survival across the study, we constructed a null model (time-invariant), a linear time-trend model, and a quadratic year effect model, and evaluated relative support for each using SIC. 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). As a basis for evaluating goodness-of-fit for the best performing models (see below) we also constructed a fully-saturated temporal model in which DSR was estimated separately for each year of study.

We then developed models to explain temporal variation in DSR. To facilitate analysis of a reasonable number of models representing our biological hypotheses and to avoid model dredging, we stratified our model construction and selection into two categories: biotic models (containing predator and alternative prey covariates), and
abiotic models (containing early/late spring precipitation and temperature covariates). The covariates from the best performing models within each modeling category (as determined by SIC) were then combined in models with plausible additive and interactive terms to examine the interplay between biotic and abiotic variables. Upon selection of the best approximating model, we added a term to evaluate the effect of visitor disturbance on nest survival, and evaluated support for this last model using SIC. We used a plural approach for model inference; to make inference on specific covariates and interactions we assessed the direction of effects (+ or -), whether effects were unique or multi-collinear representations of the same underlying process, the precision of parameter estimation, and the relative evidence for each model (Cooch & White 2006; Burnham & Anderson 2010). Finally, average nest success within a year was calculated based on the product of daily survival rate across 28 days (4 days of laying + 24 days of incubation; DSR$_{28}$), while 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:

$$D_I = 1 - \left( \frac{\text{dev}_I}{\text{dev}_N} \right),$$

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. 2011). We then calculated the ratio of deviance reduction for each model.
relative to the fully-saturated temporal model (the maximum possible reduction in deviation attributable to temporal processes):

\[ R = \frac{D_I}{D_{FS}} \]  

(2)

where \( D_I \) and \( D_{FS} \) is the deviance reduction of 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.

**Results**

A total of 5661 nests were considered in this analysis, including 1349 nests with encounter histories that were simulated from published summary estimates (Table 2.2). On average, nests were visited 3.81 times. In every year of study, predation was the main cause of nest failure. Nest abandonment was attributed to only 4.96% of total failed nests, and ranged annually from 0% to 25% of failed nests (abandonment was included as failure in the dataset unless caused by, e.g., attempts at trapping a female on the nest, in which case the observation was right-censored).

Of the general time trend models we considered, the linear trend fit better than the null and quadratic models, indicating that DSR (and thus nest success) declined across the years of study (Table 2.3; \( \beta_{\text{year, trend}} \) 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 0.0009 to 0.95 (Figs. 2.3 & 2.4). 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 ($\beta_{\text{VisitDay}}$ for DSR = -0.82, 95% CI = -0.95 to -0.69; Fig. 2.3). We thus corrected for these effects in all subsequent analyses.

The model selection results for the biotic and abiotic covariates are detailed in Tables 2.4, 2.5, and 2.6. 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 2.4). The top model from the initial biotic model selection tier suggested an important interaction between snow goose abundance and the snow goose exodus, an interaction between snow goose abundance and the fox index that only operated during the pre-exodus time period, and an interaction between fox index and the snow goose exodus (Table 2.5). 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 of the effects of the top ranked biotic and abiotic models, except for the interaction between late spring precipitation and temperature (Table 2.6). The model selection results indicated that an interaction between fox index and spring precipitation did not improve the model fit enough to warrant inclusion in the model (Tables 2.7 & 2.8). The best-performing biotic-abiotic model explained 0.87 of the deviance accounted for by the fully-saturated temporal model, indicating that it was a good fit to the data (Table 2.9).

The estimated coefficients for covariates in the top model are summarized in Tables 2.7 and 2.8. Annual fox index strongly influenced common eider nest survival, and this effect was highly dependent on the availability of alternative prey. Prior to the
snow goose exodus from the eider colony, fox index was positively correlated with nest survival. In addition, the effect of foxes on eider nest success appeared to lessen as the local snow goose abundance increased (see Fox-by-Goose interaction term in Table 2.8, Fig. 2.5; pre-exodus). After the goose exodus from the traditional nesting areas, however, the fox index was negatively correlated with eider nest survival, and the effect of foxes was no longer modulated by snow goose abundance (Fig. 2.5, Table 2.8).

In general, increased goose abundance in proximity to the eider colony appeared to negatively affect eider nest success. Following goose exodus from the eider nesting area, however, this effect was reversed; the growing snow goose colony farther down the coast resulted in increased eider nest success (Table 2.8), though this effect was subtle in comparison to the effect of geese when they were nesting in proximity to the eider colony (Fig. 2.5).

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, wet conditions in early spring were negatively correlated with nest survival (Fig. 2.6). In the late breeding season, both temperature and precipitation were positively correlated with daily survival rate (Fig. 2.6, Table 2.8). Thus, temperature tended to be positively correlated with nest success in both the early and late spring, while the effect of precipitation and its interaction with temperature depended on the stage of the breeding season.
Discussion

Previous studies of common eider reproductive success suggest that both annual nest survival and duckling survival are poor in most years, interrupted by occasional “boom” years, making both highly variable through time (Milne 1974; Coulson 1984; Swennen 1989). Congruent with this previous research, 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. 2.3). Overall, there appeared to be a general decrease in annual nest survival across the study, with the most recent years having the lowest nest success (nearly 0) recorded in the literature.

The apparent negative trend in nest success, and accompanying variation around the trend, is the result of a complex interaction between predators, alternative prey (in this system, small mammals and snow geese), and spring climate. Specifically, we found that the effect of arctic foxes on common eider nest success was modulated by the abundance and spatial distribution of lesser snow geese, a major alternative prey source for nest predators. Prior to the snow goose exodus, the positive correlation between fox index and common eider nest success supports the hypothesis that in years of low small mammal abundance (and thus low fox index), adult foxes switch to predation on ground-nesting waterfowl. In addition, high densities of snow geese nesting in proximity to eiders appeared to offset these negative impacts, presumably through prey-swamping or active aggression by the geese against predators (the Goose x Fox interaction term in Table 2.8 counteracts the fox effect in the pre-exodus time period; Robertson 1995). This
result is perhaps not surprising; fluctuations in arctic fox productivity are regulated by early spring small mammal availability rather than ground nesting birds (Roth 2003; Gauthier et al. 2004). As such, arctic foxes do not likely respond numerically to increased abundance of ground-nesting waterfowl, and were thus quickly swamped out by the exponential increase in lesser snow geese surrounding the eider colony.

In contrast to the positive effect of fox index in the pre-exodus time period, common eider nest survival was negatively affected by the fox index in the post-exodus time period (more so than any other parameter; Table 2.8). As noted above, our measure of annual fox index is based on fur harvest data from the following winter, which are likely driven by a combination of previous spring fox production and subsequent juvenile survival over the summer. While annual fox production is dependent upon early spring small mammal abundance, subsequent juvenile survival is highly influenced by summer food availability (Tannerfeldt et al. 1994). Thus, we might expect a high degree of prey-switching by arctic foxes both in years of low fox production, and in years of high spring fox production followed by the combination of a crash in small mammal abundance (e.g., due to flooding of lowland habitats) and exodus of the snow geese from the common eider colony.

Tannerfeldt and Angerbjorn (1998) note that coastal arctic fox populations tend to be less cyclic, and in some cases even acyclic, when compared to inland populations due to the availability of persistent marine resources along coasts. Furthermore, several studies have documented general dietary shifts by arctic foxes from small mammals to more abundant alternative prey, including ground-nesting waterfowl, even when
lemmings remain abundant (e.g. Stickney 1991; Bantle & Alisauskas 1998; Samelius & Alisauskas 2000). Interestingly, previously common cycles in the northern Manitoba arctic fox index appear to have ceased in recent years (Fig. 2.1). Thus, a general switch in preferred prey in recent years may account for both the discrepancy in the effect of fox index in the two time periods and the dampening of cycles in the fox index over time.

Our results could also be related to apparent competition. Although increased local abundance of snow geese swamp out the effect of arctic foxes (which do not likely respond numerically to increases in snow goose abundance), several studies have documented both behavioral and numerical responses of avian predator populations to increased snow goose abundance (Samelius & Alisauskas 1999; Bety et al. 2002; Sammler et al. 2008). Importantly, the herring gull population in Western Hudson Bay that forages almost exclusively on waterfowl eggs and ducklings (and goslings) has experienced long-term increases in abundance in response to the snow goose population explosion (Sammler et al. 2008). As such, an augmented avian predator community is likely responsible for the negative correlation between common eider nest survival and snow goose abundance. Furthermore, as predicted by apparent competition theory, following the snow goose exodus this effect was reversed. In the post-exodus time period, the majority of the nesting snow goose population had moved down the coast, presumably drawing avian predators away from the much smaller eider colony, and resulting in the positive, though much more subtle effect on eider nest success.

Unfortunately, there are no long term data available for our study area to disentangle the interaction between spring fox production and summer small mammal...
availability, or to evaluate long-term dietary patterns in local arctic fox populations. It therefore remains unclear whether the strong negative effect of fox index on nesting success in the post-exodus time period is driven by complex trophic interactions, a general switch in preferred arctic fox prey, a combination of the two, or another unexamined factor. Nevertheless, this study provides compelling evidence that nest success is strongly influenced by an interaction between predators and alternative prey, and underscores the importance of long-term monitoring efforts at multiple trophic levels.

Finally, we also found that spring climate influences common eider nest survival, and that climate during specific stages of the breeding season is important. Cold and wet conditions during the early spring were correlated with decreased nest survival. Nest initiation for common eiders is delayed in cold, wet springs until islands become ice free, with accompanying effects on reproductive investment (Lehikoinen et al. 2006; Chaulk & Mahoney 2011). In cold, wet years, damming by landfast ice at the mouth of the river delta may result in flooding conditions in the eider nesting areas upstream, further delaying nesting. Furthermore, predation pressure by herring gulls on eider nests is most intense prior to gull nest initiation (Gotmark 1989; Robertson 1995), which may be delayed more by severe spring conditions than that of cold-hardy common eiders. As a result, it is possible that cold, wet conditions in early spring result in decreased reproductive investment by common eiders, which when coupled with the delayed nesting phenology of predatory gulls relative to eiders, result in decreased nest survival.

Both temperature and precipitation were positively correlated with nest survival during the mid to late spring (June 11-July 15). While gull predation is a major cause of
nest failure during early incubation, the accessibility of nesting islands to mammalian predators (particularly arctic foxes) in mid-late incubation is an important determinant of nesting success (Robertson 1995). Accordingly, precipitation during this period may reduce the accessibility of eider islands to arctic foxes by altering river conditions. As opposed to early spring, temperature in the mid-late breeding 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, vegetative nest cover affects the detection and accessibility of nests by predators, with accompanying impacts on nest survival (Schmutz et al. 1983; Gotmark 1988).

Although often considered an extreme capital breeder (Meijer & Drent 2008), recent evidence suggests that female common eiders sometimes feed extensively just before and during egg laying, thereby supplementing energy reserves for follicular development and incubation (Rigou & Guillemette 2010). Following egg-laying, female common eiders maintain one of the highest incubation constancy levels of any waterfowl species (Afton & Paulus 1992). However, nesting females still take occasional incubation breaks to drink water, and in cases of prolonged incubation and severe depletion of fat reserves, they will feed during incubation breaks to recoup energy losses (Criscuolo et al. 2002). Accordingly, spring and summer climate could affect incubation constancy, the ability of females to offset energy losses with nearshore foods (if these areas are not covered by landfast ice), and ultimately the length of time nests are left unattended and exposed to predation.
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). In general, our results suggest that warmer temperatures in both early and late spring are correlated with higher nest survival. This agrees with the findings of D’Alba et al. (2010), who found a positive relationship between the abundance of new recruits and spring temperatures 2 years earlier (the hatch year for new recruits). However, we also found an important interaction between temperature and precipitation, dependent upon the stage of the breeding season, which complicates direct predictions of the effect of climate trends on nest survival.

This study makes use of the longest term dataset for breeding sea ducks in North America to examine the annual biotic and abiotic covariates that regulate variation in nest survival. Nevertheless, within-season factors and nest-specific characteristics likely play a role in regulating nest survival as well, and an examination of these factors would help clarify the mechanisms responsible for the results of this study. Specifically, we expect that the timing of mean snow goose hatch within a season will strongly influence common eider nest success, and further, that this effect will depend on the local abundance of snow geese. Furthermore, if early season nest predation on common eiders is strongly influenced by the presence of pre-breeding gulls, we expect that nest survival will depend on the laying date of individual nests relative to the mean for that year. Finally, while our analysis suggests that average spring temperature and precipitation influence nest survival, an examination of the interaction between spring climate and
laying-date (generally termed the “Mismatch hypothesis;” Drever & Clark 2007) can provide important insights into the fitness consequences of climate change.

Annual nest success appears to be highly variable through time, but the consequences of this variability on common eider population dynamics remain unclear. Demographic theory suggests that in long-lived iteroparous species such as common eiders, population growth rate tends to be most sensitive to changes in adult survival and least sensitive to changes in reproductive vital rates (Caswell 2001). 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 (Goudie et al. 2000; Wilson et al. 2007; Hario, Mazerolle, & Saurola 2009).

Although population growth rate in common eiders may be least sensitive to changes in reproductive vital rates, high variability in these rates compared to adult survival may actually cause more change in population growth. Thus, our next step will be to develop a population model for common eiders in our region and investigate the consequences of observed variability in nesting success, and the drivers of this variability, on population dynamics. Such research will be needed to help guide the conservation of this declining species amidst changing environmental conditions.
References


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


Table 2.1. Historical studies of *S. m. sedentaria* nesting ecology at La Pérouse Bay, Manitoba.

<table>
<thead>
<tr>
<th>Investigator</th>
<th>Years of Study</th>
<th>Peer-reviewed publications based on data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ben Guild</td>
<td>1972-1973</td>
<td></td>
</tr>
<tr>
<td>Ken Abraham</td>
<td>1976-1977</td>
<td></td>
</tr>
<tr>
<td>Chris Davies</td>
<td>1984-1986</td>
<td></td>
</tr>
<tr>
<td>David Iles</td>
<td>2009-2011</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.2. Years in which encounter histories were simulated. Apparent nest success estimates were transformed into a corrected Mayfield DSR based on the Johnson-Green correction (Johnson 1991); n denotes the sample size of nests found.

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>Apparent N.S.</th>
<th>Corrected DSR</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1972</td>
<td>110</td>
<td>0.7446</td>
<td>0.9807</td>
<td>Guild (1974)</td>
</tr>
<tr>
<td>1973</td>
<td>78</td>
<td>0.6030</td>
<td>0.968</td>
<td>Guild (1974)</td>
</tr>
<tr>
<td>1978</td>
<td>401</td>
<td>0.4514</td>
<td>0.9518</td>
<td>Schmutz et al. (1983)</td>
</tr>
<tr>
<td>1979</td>
<td>396</td>
<td>0.6995</td>
<td>0.9769</td>
<td>Schmutz et al. (1983)</td>
</tr>
<tr>
<td>1980</td>
<td>364</td>
<td>0.6978</td>
<td>0.9767</td>
<td>Schmutz et al. (1983)</td>
</tr>
</tbody>
</table>
Table 2.3. Nest survival model comparison of time trend and visitor effect models. npar = the number of parameters in a model, ΔSIC = difference in SIC points between a respective model and the top model.

<table>
<thead>
<tr>
<th>Model</th>
<th>npar</th>
<th>ΔSIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linear Year Effect + Visitor</td>
<td>3</td>
<td>0.0</td>
</tr>
<tr>
<td>Quadratic Year Effect + Visitor</td>
<td>4</td>
<td>7.1</td>
</tr>
<tr>
<td>Linear Year Effect</td>
<td>2</td>
<td>202.4</td>
</tr>
<tr>
<td>Quadratic Year Effect</td>
<td>3</td>
<td>208.9</td>
</tr>
<tr>
<td>Null + Visitor Effect</td>
<td>2</td>
<td>386.5</td>
</tr>
<tr>
<td>Null</td>
<td>1</td>
<td>609.8</td>
</tr>
</tbody>
</table>
Table 2.4. Nest survival model comparison of abiotic covariates. “ES” = early spring (May 1 - June 10), “LS” = late spring (June 11 - July 15), “S” = entire breeding period (May 1 – July 15), “precip” = total daily precipitation, “temp” = average daily temperature, npar = the number of parameters in a model, ΔSIC = difference in SIC points between a respective model and the top model.

<table>
<thead>
<tr>
<th>Model</th>
<th>npar</th>
<th>ΔSIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>ES_precip × ES_temp + LS_temp × LS_precip</td>
<td>7</td>
<td>0.0</td>
</tr>
<tr>
<td>ES_precip × ES_temp + LS_temp</td>
<td>5</td>
<td>19.5</td>
</tr>
<tr>
<td>ES_precip × ES_temp + LS_temp + LS_precip</td>
<td>6</td>
<td>28.2</td>
</tr>
<tr>
<td>ES_precip × ES_temp</td>
<td>4</td>
<td>116.7</td>
</tr>
<tr>
<td>ES_precip × ES_temp + LS_precip</td>
<td>5</td>
<td>124.8</td>
</tr>
<tr>
<td>LS_precip × LS_temp + ES_precip</td>
<td>5</td>
<td>145.2</td>
</tr>
<tr>
<td>ES_precip + LS_precip</td>
<td>3</td>
<td>239.3</td>
</tr>
<tr>
<td>ES_precip</td>
<td>2</td>
<td>258.8</td>
</tr>
<tr>
<td>ES_precip + ES_temp</td>
<td>3</td>
<td>266.0</td>
</tr>
<tr>
<td>ES_temp × LS_temp</td>
<td>4</td>
<td>284.1</td>
</tr>
<tr>
<td>LS_precip × LS_temp</td>
<td>4</td>
<td>319.1</td>
</tr>
<tr>
<td>LS_precip × LS_temp + ES_temp</td>
<td>5</td>
<td>322.7</td>
</tr>
<tr>
<td>S_precip × S_temp</td>
<td>4</td>
<td>343.3</td>
</tr>
<tr>
<td>LS_precip + LS_temp</td>
<td>3</td>
<td>370.3</td>
</tr>
<tr>
<td>LS_precip</td>
<td>2</td>
<td>394.2</td>
</tr>
<tr>
<td>ES_temp + LS_temp</td>
<td>3</td>
<td>420.1</td>
</tr>
<tr>
<td>LS_temp</td>
<td>2</td>
<td>439.7</td>
</tr>
<tr>
<td>ES_temp</td>
<td>2</td>
<td>440.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>--------------</td>
<td>---</td>
<td>------</td>
</tr>
<tr>
<td>Null</td>
<td>1</td>
<td>462.5</td>
</tr>
<tr>
<td>$S_{\text{precip}} + S_{\text{temp}}$</td>
<td>3</td>
<td>464.9</td>
</tr>
</tbody>
</table>
Table 2.5. Nest survival model comparison of biotic covariates. “fox” = arctic fox index in current year, “foxlastyear” = arctic fox index in the previous year, “CCP” = annual lesser snow goose abundance on the Cape Churchill Peninsula, “pre_exodus/post_exodus” = dummy variables (1 or 0) to indicate time period before/after goose exodus from traditional nesting colony. ΔSIC = difference in SIC points between a respective model and the top model. Full interactions between model covariates are denoted by ×, partial interactions (denoted by :) are only fit for non-zero levels of binary covariates (e.g. when pre-exodus = 1). The number of parameters in a given model is denoted by ‘npar’.

<table>
<thead>
<tr>
<th>Model</th>
<th>npar</th>
<th>ΔSIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCP × pre_exodus + CCP:fox;pre_exodus + fox × pre_exodus</td>
<td>7</td>
<td>0.0</td>
</tr>
<tr>
<td>CCP × pre_exodus + CCP × fox + fox × pre_exodus</td>
<td>7</td>
<td>5.6</td>
</tr>
<tr>
<td>CCP × post_exodus + post_exodus × fox</td>
<td>6</td>
<td>118.8</td>
</tr>
<tr>
<td>CCP:pre_exodus + CCP:fox;pre_exodus + fox × pre_exodus</td>
<td>6</td>
<td>146.4</td>
</tr>
<tr>
<td>CCP × fox + post_exodus × fox</td>
<td>6</td>
<td>189.9</td>
</tr>
<tr>
<td>CCP + post_exodus × fox</td>
<td>5</td>
<td>356.6</td>
</tr>
<tr>
<td>post_exodus × fox</td>
<td>4</td>
<td>395.3</td>
</tr>
<tr>
<td>CCP × fox</td>
<td>4</td>
<td>399.4</td>
</tr>
<tr>
<td>CCP × post_exodus + CCP × fox</td>
<td>6</td>
<td>410.4</td>
</tr>
<tr>
<td>CCP × pre_exodus + CCP:fox;pre_exodus + fox:pre_exodus</td>
<td>6</td>
<td>509.9</td>
</tr>
<tr>
<td>CCP × pre_exodus + CCP:fox;pre_exodus + fox</td>
<td>6</td>
<td>516.7</td>
</tr>
<tr>
<td>CCP</td>
<td>2</td>
<td>613.8</td>
</tr>
<tr>
<td>CCP + fox</td>
<td>3</td>
<td>622.3</td>
</tr>
<tr>
<td>CCP + post_exodus</td>
<td>3</td>
<td>623.1</td>
</tr>
<tr>
<td>CCP × post_exodus</td>
<td>4</td>
<td>633.4</td>
</tr>
<tr>
<td>Model</td>
<td>(Intercept)</td>
<td></td>
</tr>
<tr>
<td>------------------------------------------------</td>
<td>-------------</td>
<td></td>
</tr>
<tr>
<td>CCP + post_exodus + CCP:post_exodus</td>
<td>4</td>
<td>633.4</td>
</tr>
<tr>
<td>CCP + pre_exodus + CCP:pre_exodus</td>
<td>4</td>
<td>633.4</td>
</tr>
<tr>
<td>post_exodus</td>
<td>2</td>
<td>756.0</td>
</tr>
<tr>
<td>post_exodus + foxlastyear</td>
<td>3</td>
<td>761.7</td>
</tr>
<tr>
<td>post_exodus × foxlastyear</td>
<td>4</td>
<td>763.3</td>
</tr>
<tr>
<td>post_exodus + fox</td>
<td>3</td>
<td>766.3</td>
</tr>
<tr>
<td>fox</td>
<td>2</td>
<td>1016.4</td>
</tr>
<tr>
<td>Null</td>
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<td>1018.6</td>
</tr>
<tr>
<td>foxlastyear</td>
<td>2</td>
<td>1023.1</td>
</tr>
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</table>
Table 2.6. Biotic/abiotic nest survival models (final tier of model comparison); top model from which further inference was made is in bold. The top biotic and abiotic models, and the null model have additionally been included for comparison. “fox” = arctic fox index in current year, “foxlastyear” = arctic fox index in the previous year, “CCP” = annual lesser snow goose abundance on the Cape Churchill Peninsula, “pre_exodus/post_exodus” = dummy variables (1 or 0) to indicate time period before/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 , $\Delta$SIC = difference in SIC points between a respective model and the top model. Full interactions between model covariates are denoted by $\times$, partial interactions (denoted by :) are only fit for non-zero levels of binary covariates (e.g. when pre-exodus = 1). The number of parameters in a given model is denoted by ‘npar’.

<table>
<thead>
<tr>
<th>Model</th>
<th>npar</th>
<th>$\Delta$SIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + ES_precip $\times$ ES_temp + LS_precip + LS_temp</td>
<td>12</td>
<td>0.0</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + ES_precip $\times$ ES_temp + LS_precip + LS_temp + ES_precip $\times$ fox</td>
<td>13</td>
<td>1.9</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + ES_precip $\times$ ES_temp + LS_precip $\times$ LS_temp</td>
<td>13</td>
<td>10.9</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + LS_precip $\times$ LS_temp + ES_precip</td>
<td>11</td>
<td>89.1</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + LS_precip $\times$ LS_temp + ES_temp + ES_precip</td>
<td>12</td>
<td>91.8</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + ES_precip $\times$ ES_temp + LS_temp</td>
<td>11</td>
<td>100.2</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + LS_temp $\times$ LS_precip</td>
<td>10</td>
<td>106.6</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + LS_precip $\times$ LS_temp + ES_temp</td>
<td>11</td>
<td>117.3</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + ES_precip $\times$ ES_temp + ES_precip $\times$ fox</td>
<td>11</td>
<td>133.3</td>
</tr>
<tr>
<td>CCP $\times$ pre_exodus + CCP:fox:pre_exodus + fox $\times$ pre_exodus + ES_precip $\times$ ES_temp + ES_precip $\times$ fox</td>
<td>11</td>
<td>199.3</td>
</tr>
<tr>
<td>Expression</td>
<td>Degree</td>
<td>AIC</td>
</tr>
<tr>
<td>------------------------------------------------</td>
<td>--------</td>
<td>-------</td>
</tr>
<tr>
<td>$CCP \times \text{pre_exodus} + CCP:\text{fox:pre_exodus} + \text{fox} \times \text{pre_exodus} + \text{ES_precip} \times \text{fox}$</td>
<td>9</td>
<td>229.5</td>
</tr>
<tr>
<td>$CCP \times \text{pre_exodus} + CCP:\text{fox:pre_exodus} + \text{fox} \times \text{pre_exodus} + \text{ES_temp} \times \text{ES_precip}$</td>
<td>10</td>
<td>237.4</td>
</tr>
<tr>
<td>$CCP \times \text{pre_exodus} + CCP:\text{fox:pre_exodus} + \text{fox} \times \text{pre_exodus}$</td>
<td>7</td>
<td>256.1</td>
</tr>
<tr>
<td>$\text{ES_precip} \times \text{ES_temp} + \text{LS_temp} \times \text{LS_precip}$</td>
<td>7</td>
<td>812.2</td>
</tr>
<tr>
<td>Null</td>
<td>1</td>
<td>1274.7</td>
</tr>
</tbody>
</table>
Table 2.7. DSR beta coefficients from the top biotic-abiotic model with visitor effects included. “ES” = early spring (May 1 - June 10), “LS” = late spring (June 11 - July 15). Estimate = beta coefficient of effect on a logit scale, SE = standard error of coefficient, LCL/UCL = lower/upper 95% confidence limits. Full interactions between model covariates are denoted by ×, partial interactions (denoted by :) are only fit for non-zero levels of binary factors (e.g. when Pre-exodus = 1).

<table>
<thead>
<tr>
<th>Beta Coefficient</th>
<th>Estimate</th>
<th>SE</th>
<th>LCL</th>
<th>UCL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.8242</td>
<td>0.2915</td>
<td>-1.3955</td>
<td>-0.2528</td>
</tr>
<tr>
<td>Goose Abundance</td>
<td>1.0747</td>
<td>0.1498</td>
<td>0.7810</td>
<td>1.3683</td>
</tr>
<tr>
<td>Pre-exodus</td>
<td>4.3459</td>
<td>0.2990</td>
<td>3.7600</td>
<td>4.9319</td>
</tr>
<tr>
<td>Fox Index</td>
<td>-5.6488</td>
<td>0.3259</td>
<td>-6.2876</td>
<td>-5.0100</td>
</tr>
<tr>
<td>ES Precipitation</td>
<td>-0.0809</td>
<td>0.0328</td>
<td>-0.1452</td>
<td>-0.0165</td>
</tr>
<tr>
<td>ES Temperature</td>
<td>-0.0254</td>
<td>0.0335</td>
<td>-0.0911</td>
<td>0.0403</td>
</tr>
<tr>
<td>LS Precipitation</td>
<td>0.2943</td>
<td>0.0321</td>
<td>0.2315</td>
<td>0.3571</td>
</tr>
<tr>
<td>LS Temperature</td>
<td>0.2756</td>
<td>0.0239</td>
<td>0.2287</td>
<td>0.3226</td>
</tr>
<tr>
<td>Visit Day</td>
<td>-0.9021</td>
<td>0.0634</td>
<td>-1.0264</td>
<td>-0.7778</td>
</tr>
<tr>
<td>Goose Abundance : Pre-exodus</td>
<td>-1.7342</td>
<td>0.1633</td>
<td>-2.0543</td>
<td>-1.4140</td>
</tr>
<tr>
<td>Fox Index x Pre-exodus</td>
<td>5.7806</td>
<td>0.3230</td>
<td>5.1475</td>
<td>6.4137</td>
</tr>
<tr>
<td>ES Precipitation x ES Temperature</td>
<td>0.2773</td>
<td>0.0334</td>
<td>0.2118</td>
<td>0.3429</td>
</tr>
<tr>
<td>Goose Abundance x Fox Index : Pre-exodus</td>
<td>-0.2537</td>
<td>0.0385</td>
<td>-0.3291</td>
<td>-0.1782</td>
</tr>
</tbody>
</table>
Table 2.8. DSR beta coefficient effects during pre- and post-snow goose exodus time periods. “ES” = early spring (May 1 - June 10), “LS” = late spring (June 11 - July 15). Estimate = beta coefficient of effect on a logit scale, SE = standard error of coefficient.

<table>
<thead>
<tr>
<th>Coefficient</th>
<th>Pre-exodus</th>
<th></th>
<th>Post-exodus</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>SE</td>
<td>Estimate</td>
<td>SE</td>
</tr>
<tr>
<td>Intercept</td>
<td>3.5218</td>
<td>0.0470</td>
<td>-0.8242</td>
<td>0.2915</td>
</tr>
<tr>
<td>Goose Abundance</td>
<td>-0.6595</td>
<td>0.0598</td>
<td>1.0747</td>
<td>0.1498</td>
</tr>
<tr>
<td>Fox Index</td>
<td>0.1318</td>
<td>0.0245</td>
<td>-5.6488</td>
<td>0.3259</td>
</tr>
<tr>
<td>ES Precipitation</td>
<td>-0.0809</td>
<td>0.0328</td>
<td>-0.0809</td>
<td>0.0328</td>
</tr>
<tr>
<td>ES Temperature</td>
<td>-0.0254</td>
<td>0.0335</td>
<td>-0.0254</td>
<td>0.0335</td>
</tr>
<tr>
<td>LS Precipitation</td>
<td>0.2943</td>
<td>0.0321</td>
<td>0.2943</td>
<td>0.0321</td>
</tr>
<tr>
<td>LS Temperature</td>
<td>0.2756</td>
<td>0.0239</td>
<td>0.2756</td>
<td>0.0239</td>
</tr>
<tr>
<td>ES Precipitation x ES Temperature</td>
<td>0.2773</td>
<td>0.0334</td>
<td>0.2773</td>
<td>0.0334</td>
</tr>
<tr>
<td>Goose Abundance x Fox Index</td>
<td>-0.2537</td>
<td>0.0385</td>
<td>0.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>Visit</td>
<td>-0.9021</td>
<td>0.0634</td>
<td>-0.9021</td>
<td>0.0634</td>
</tr>
</tbody>
</table>
Table 2.9. Ratio of annual variability in nest survival explained by the best performing biotic, abiotic, and combination of biotic and abiotic (biotic-abiotic) models. npar = number of parameters in model, “Dev” = residual deviance, “R” = deviance reduction ratio, calculated using equations (1) and (2). By definition, the fully saturated year effect model explains the maximum possible amount of annual variability in nest survival and the null model explains the minimum. All models in this table correct for visitor effects.

<table>
<thead>
<tr>
<th>Model</th>
<th>npar</th>
<th>Dev</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fully Saturated</td>
<td>24</td>
<td>16198.65</td>
<td>1</td>
</tr>
<tr>
<td>Biotic-Abiotic</td>
<td>13</td>
<td>16408.03</td>
<td>0.866</td>
</tr>
<tr>
<td>Biotic</td>
<td>8</td>
<td>16684.84</td>
<td>0.689</td>
</tr>
<tr>
<td>Abiotic</td>
<td>8</td>
<td>17285.81</td>
<td>0.304</td>
</tr>
<tr>
<td>Null</td>
<td>2</td>
<td>17760.77</td>
<td>0</td>
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</table>
Fig. 2.1. Estimated lesser snow goose (LSGO) abundance (solid circles) in the Cape Churchill Peninsula region from 1964 to 2011 and arctic fox index (open circles) in northern Manitoba from 1970 – 2011.
Fig. 2.2. Snow goose nesting densities (nests/ha) in the traditional core of the colonial nesting area nearest the eider colony.
Fig. 2.3. Annual nest survival estimates (DSR^{28}) 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.
Fig. 2.4. Estimates of annual nest success (DSR$^{28}$) from the saturated year effect model (solid circles) and the top biotic-abiotic model (open triangles). Bars represent 95% confidence intervals. Both models are corrected for visitor effects.
Fig. 2.5. The interactive effect of the fox index and lesser snow goose abundance in the pre- and post-exodus time periods on eider nest success. Axes are scaled to the min/max values for each time period (pre-/post-exodus), and all other parameters in the model are fixed at the mean value for the respective time period. The directions of the Fox index and LSGO abundance axes are reversed in the post-exodus panel to allow for complete visualization of curvature in the response surface. The additive and interactive effects were estimated across the complete range of the data, and the two panels are presented for visualization of the interaction (solid points represent combinations of covariates that were actually observed).
Fig. 2.6. 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. Axes are scaled to the min/max values observed across the study; all other parameters in the model are fixed at their mean values. Points represent combinations of covariates that were actually observed.
CHAPTER 3

EFFECTS OF A SHIFT IN ALTERNATIVE PREY ON THE STOCHASTIC
POPULATION DYNAMICS OF A LONG-LIVED SEA DUCK

Summary

1. Life history theory predicts a trade-off between temporal variability in a vital rate and its relative impact on population dynamics. This prediction appears to be supported in sea ducks, which compensate for variable reproductive success with high, stable adult survival.

2. Annual variation in nest success is strongly influenced by an interaction between predators and alternative prey, and to a lesser extent, climate. However, the relative effects of variation and covariation amongst multiple vital rates (and the drivers thereof) governing population dynamics are poorly understood.

3. Here, we develop a population model to evaluate the relative effect of environmental stochasticity and covariation amongst vital rates on common eider population dynamics. We then examine the effect of a large-scale shift in local alternative prey abundance using a recently developed stochastic life table response experiment (SLTRE), and decompose differences in the stochastic growth rate before and after this shift into contributions from individual vital rates.

4. Consistent with life history predictions, changes in adult survival disproportionately affect common eider population dynamics, and was the most stable vital rate through time. However, adult survival contributed less to variation in population growth than nest success and duckling survival, which both vary considerably.
5. The stochastic growth rate declined across the study, primarily due to a decrease in mean nest success following a large-scale exodus of local alternative prey (lesser snow geese). Furthermore, the degree of correlation amongst vital rates influenced the magnitude of the decline in population growth.

6. Our results indicate that both variation and covariation in vital rates need to be considered to accurately predict the population-level consequences of perturbations to vital rates. Future studies that link the environmental drivers of variation in vital rates to population processes will provide important insights into the effect of perturbations to arctic systems on population dynamics.

**Introduction**

Comparative studies of life history among and within populations have generally supported the theoretical prediction that selection will buffer the traits most strongly correlated with fitness (and similarly, population growth rate) against environmental stochasticity (Pfister 1998; Gaillard & Yoccoz 2003; Morris & Doak 2004, but see Koons et al. 2009). For example, the population dynamics of long-lived organisms are usually more sensitive to relative changes in the survival of adults than to changes in fertility, yet as a consequence, adult survival tends to be the most stable vital rate through time. Thus, the life history parameters to which growth rate is most sensitive may influence actual population dynamics less than other vital rates that vary considerably (Gaillard et al. 2000).

These life history predictions appear to be supported in sea ducks, which have adopted a bet-hedging life history strategy. Long-lived sea ducks compensate for years
of low and highly variable reproductive success with relatively high, stable adult survival (Coulson 1984). However, recent evidence suggests that sea duck populations have experienced long-term declines across much of their range (Goudie, Robertson, & Reed 2000; Rönkä et al. 2011). Even for well-studied species (e.g. the common eider; *Somateria mollissima*), the demographic causes of these declines are poorly understood (Ekroos et al. 2012, but see Gilliland et al. 2009).

Matrix projection models offer powerful tools with which to examine the relative effect of changes in demographic parameters on population dynamics in both deterministic and stochastic frameworks. They allow for both prospective analyses, which explore the functional relationship between demographic parameters and population dynamics, and retrospective analyses that evaluate the contributions of observed variation and covariation in vital rates to variation in population dynamics (Caswell 2000, 2001). Yet, despite their widespread utility for wildlife conservation (Doak, Kareiva, & Klepetka 1994; Seamans et al. 1999; Cooch, Rockwell, & Brault 2001; Fieberg & Ellner 2001; Johnson et al. 2010), very few population models have been developed for sea ducks, perhaps owing to the logistical difficulties associated with monitoring Arctic-breeding species throughout their entire life cycle. Of the models that have been developed (e.g. Gilliland et al. 2009), fewer still have evaluated the effects of environmental stochasticity on population dynamics (but see Schamber et al. 2009). Furthermore, no study has identified causal drivers of stochasticity in sea duck population dynamics. Consequently, a combination of long-term empirical study and rigorous population modeling efforts are needed to identify the demographic components most
strongly influencing population dynamics, and ultimately, the underlying variables that cause changes in these parameters.

The La Pérouse Bay common eider colony provides one of the longest datasets to empirically examine variation in and covariation between vital rates for North American sea ducks. In chapter 2 we showed that annual nest success declined across the 41 year study and varied considerably between years. In addition, annual nest success was influenced strongly by interactions with arctic foxes (Vulpes lagopus; an important terrestrial nest predator at LPB) and lesser snow geese (Chen caerulescens caerulescens; an abundance alternative prey source), and to a lesser extent by spring climate. Importantly, the strength and directions of the biotic effects were strongly modulated by the eventual exodus of the lesser snow goose colony from the eider colony, suggesting that local alternative prey abundance has important consequences for eider nest success. However, the relative effects of the observed variation in reproductive success (and the respective drivers of this variation) on eider population dynamics remain unclear, as do the consequences of covariation between highly variable vital rates at adjacent steps in the life cycle.

Here, we combine estimates of nest success with those for other vital rates from the La Pérouse Bay study population, and develop deterministic and stochastic matrix population models. We then use these models to evaluate the impacts of the variables responsible for long-term decline and variation in reproductive success on the population dynamics of the Hudson Bay eider (S.m. sedentaria). We employ a classic retrospective life table response experiment (LTRE) to decompose variation in the deterministic
growth rate into contributions from observed variation in vital rates across the years of the study. Next, we evaluate the relative effect of changes in both the mean and variance of vital rates on the stochastic growth rate using prospective stochastic perturbation analyses. We then examine the effect of a large-scale shift in local alternative prey abundance using a recently developed stochastic life table response experiment (SLTRE), and decompose differences in the stochastic growth rate before and after this shift into contributions from individual vital rates. Finally, to evaluate the effect of covariation between the two most variable vital rates (nest success and duckling survival) on population dynamics, we conduct all of our analyses under low, medium, and high covariation regimes.

Methods

Study Population

We collected demographic data for a breeding population of Hudson Bay common eider at La Pérouse Bay (LPB), approximately 30km east of Churchill, Manitoba, Canada. The breeding ecology of this population has been studied annually in 23 of the last 41 years (see chapter 2). At LPB, breeding adults migrate inland during spring (April – May) and breed colonially on the islands formed by the braided river deltas feeding into the bay. Following hatch, broods and attendant females follow the rivers to the coast where they remain until fledging (pers. obs.). *S. m. sedentaria* winter in Hudson Bay, feeding on marine benthic invertebrates under open leads in the sea ice, though the exact wintering locations of our study population are unknown.
Life Cycle and Matrix Model

Breeding in common eiders is delayed until at least age 2 and is often delayed until age 4 (Baillie & Milne 1982). Thus, following Gilliland et al. (2009), we approximated the annual life cycle of common eiders using a matrix model with four stage classes (first year, second year, third year, and fourth year and greater; Fig. 3.1). We constructed our matrix projection models for the limiting female portion of the population, and used a pre-breeding census and birth pulse parameterization. We generated life cycle graphs and transition matrices as functions of age-specific annual survival and fertility (Fig. 3.1). Specifically, we calculated the per capita fertility for females in stage class $s$ as:

$$ F_s = BP_s \times CS \times 0.5 \times NS \times HS \times DS \times JS, $$

where $BP$ is the breeding propensity of females (the proportion of females that attempt to breed in a year), $CS$ is full clutch size, 0.5 represents the ratio of eggs that are female (assumed to have 50:50 sex ratio at birth), $NS$ is nest success (the proportion of nests that hatch at least one egg), $HS$ is hatching success (the proportion of eggs in a successful clutch that hatch), $DS$ is duckling survival (the proportion of ducklings that survival to fledge), and $JS$ is juvenile survival (the proportion of fledglings that survive to the following year, and recruit into the first age class). Since the sex ratio and stage-specific breeding propensities are treated as constants in our analyses, we include them in our calculations of fertility but do not consider them in our results.
Vital Rates and Parameter Estimation

Where available, vital rate estimation was based on data for the LPB colony. Annual clutch size, hatching success, and nest success data are available for most years of study at LPB (Table 3.1). Annual estimates of vital rates for the LPB population were based on repeated visits to nests within the study area during the breeding season (for a detailed discussion of field methods see chapter 2). When no data were available for a vital rate from LPB (BP, DS, JS, and AS), rates were based on published studies of other populations. Where possible, we selected estimates from populations with similar conditions to those at LPB (see below). Since there are no published data that allow for robust estimates of process means and variances for breeding propensity, we assumed this vital rate to be fixed for each stage based on the results of Baillie and Milne (1982).

Raw data were available to estimate average clutch size at LPB in all but three years of study, and precision in these estimates were available for all but two years (Table 3.1). To avoid bias in our estimates of clutch size by including incomplete clutches, nests were required to meet one of the following criteria for consideration in clutch size estimates: 1) egg candling indicated a non-zero incubation age on a visit in which eggs were counted, signaling the completion of egg-laying, 2) the same number of eggs were present in two successive visits, also signaling the completion of egg laying. If nests met either of these criteria on multiple visits, the maximum clutch size recorded on eligible visits was used. Without continuous monitoring of nests from the beginning of the laying period, it is impossible to determine if nests were partially depredated before eggs were
counted. However, we could not account for egg-dumping by other females, and we thus assumed that these opposing sources of potential bias were equivalent.

Hatching success, the proportion of eggs in a successful nest that survive to hatch, was estimated based on the number of ducklings observed at hatch rather than on the number of membranes present in successful nests. Although suitable for an indicator of nest success, egg membranes are easily washed or blown away from nests and sometimes eaten by predators as a source of calcium, potentially biasing estimates of hatching success low. Nests for which ducklings were observed and counted at hatch only represented a small subset of successful nests (and thus had high sampling variance), but restricting estimation to this sample removed bias.

We estimated nest survival by fitting generalized linear models of daily survival rate to encounter history data of nests at LPB (see chapter 2 for detailed field and analytical methods). Average annual estimates of nest success and precision in these estimates were obtained from the fully-saturated year effect model while accounting for visitor effects.

Difficulties associated with tracking broods at sea after leaving the nesting area prevented us from obtaining estimates of duckling survival at LPB. We therefore gathered published estimates of duckling survival from a similar breeding colony of *S. m. mollissima* in Scotland for use in our population models (Milne 1974). The most important predators of egg and ducklings in this system are gulls and corvids, representing a similar avian predator community to LPB. Of note, terrestrial egg and duckling predators were absent from Milne’s (1974) study area, yet contribute
significantly to nest failure at LPB (Schmutz, Robertson, & Cooke 1983; Robertson 1995). However, since eider ducklings are semi-precocial and follow the river delta into open water within 24 hours of hatch, terrestrial predators are probably responsible for relatively few duckling mortalities at LPB when compared to avian predators and other factors that affect ducklings once in open water. Consequently, the absence of terrestrial predators from Milne’s study population is unlikely to introduce major differences when compared to LPB.

For generating missing data in the deterministic LTRE and for stochastic analyses, we used a post-hoc variance decomposition procedure to separate process variation from sampling variation in CS, HS, NS, and DS while accounting for unequal sampling between years (Burnham et al. 1987). We then parameterized a gamma distribution for CS, and beta distributions for HS, NS, and DS with shape parameters corresponding to the estimated process means and variances.

There are no estimates of annual adult survival available for any population of S. m. sedentaria. We thus used published estimates of annual adult survival and associated process variance from a population of Pacific common eider (S. m. v-nigra), based on 11 years of mark-recapture efforts (Wilson et al. 2007). Although often considered the most morphologically and geographically distinct subspecies of common eider (Livezey 1995), this particular population of Pacific common eider has several important similarities to our study population. As with the LPB eider population, this Pacific eider population nests in a fairly dispersed colony compared to other breeding colonies of common eiders (Goudie et al. 2000); it is in close proximity to a large goose
colony; it has a similar suite of nest predators (arctic foxes, gulls, and jaegers); breeding adults are only short-distance migrants (Peterson & Flint 2002), and avian cholera outbreaks have not been observed in either population (Goudie et al. 2000). Accordingly, survival estimates of this population may be more representative of those of our study population than other populations of common eiders.

While several studies have examined the role of duckling body condition and/or the presence of avian cholera on juvenile survival (survival from fledging to 1 yr of age) and recruitment (e.g. Christensen 1999; Descamps et al. 2011), to the best of our knowledge there are no published estimates of common eider juvenile survival probabilities. Age-specific survival estimates based on known-fate studies of king eider (Somateria spectabilis) indicate that juvenile survival is approximately 0.71 of adult survival (Oppel & Powell 2010). King and common eider have a similar life history: both species have relatively high adult survival, delay breeding until at least age 2 (though often until age 3 or 4), and winter in polynyas on the sea ice (Goudie et al. 2000; Suydam 2000). Consequently, we estimated common eider juvenile survival based on the ratio of juvenile:adult survival for king eiders \( JS = 0.71 \times AS \); Oppel & Powell 2010). Also lacking a direct estimate of process variance for juvenile survival, we calculated an intermediate value for process variance between the two adjacent life stages, following life history predictions (Pfister 1998; Gaillard, Festa-Bianchet, & Yoccoz 1998). We calculated the percentage of the maximum coefficient of variation \( (CV_{\text{max}}; \text{Morris & Doak 2004}) \) of the beta distributions corresponding to the mean and variance of duckling and adult survival. We then generated a beta distribution for
juvenile survival with the specified mean (0.64) and variance corresponding to the average of the $CV_{\text{max}}$ of duckling and adult survival.

For long-lived organisms such as eiders, the predicted effect of changes in adult survival are higher when populations are declining (Stearns 1992). After preliminary results suggested that the modeled deterministic population growth rate was approximately 0.935, we adjusted the process means of vital rates not observed at LPB ($DS$, $JS$, and $AS$) to achieve a deterministic growth rate of 1.0 in the first 12 years of our study to avoid this bias. We then corrected the process variance to maintain the same $CV_{\text{max}}$ of the beta distributions as before the adjustment. Estimates of process mean and variance for vital rates used in our analyses are included in Table 3.2.

Rather than directly calculating the correlation among the three vital rates with the moderate sample sizes observed at LPB (i.e. $CS$, $HS$, and $NS$), we used a bootstrapping procedure to fill in years with missing data by sampling with replacement from the observed values. We then calculated the average correlation among vital rates after 5000 repetitions, and used this robust correlation structure as a baseline in our analyses. To examine the effect of covariance between nest success and duckling survival on population dynamics, we performed all matrix model analyses under three correlation scenarios: 0%, 25%, and 50% correlation between nest success and duckling survival, respectively. Each of these correlation scenarios also incorporated the observed correlation structure amongst $CS$, $NS$, and $HS$ at LPB. We also performed stochastic prospective perturbation analyses under a fourth scenario in which none of the vital rates were correlated, denoted as “control” to distinguish it from the 0% correlation scenario.
While not biologically plausible (and thus not used in retrospective analyses), the inclusion of a “control” correlation scenario provided a useful benchmark against which to compare the effects of the correlation structure observed at LPB on population dynamics.

For missing data in retrospective analyses and for simulated data in prospective analyses, random values of correlated vital rates were generated by using a Cholesky decomposition of the vital rate correlation matrix to correlate random standard normal deviates, which were then mapped onto the appropriate distributions for vital rates using the cumulative distribution function. The details of this method are described in Morris and Doak (2002, pp. 282 – 289).

Matrix Model Analyses

Following Miller et al. (2011) we focused our matrix analyses on the component vital rates ($v_k$) underlying matrix elements, rather than the matrix elements ($a_{ij}$) themselves. Thus, in our results we present adult survival as a lower-level vital rate, though because it appears directly in the projection matrix it may equally be considered a higher-level life cycle component as well.

To evaluate the contributions of variation in vital rates to variation in the deterministic growth rate ($\lambda$), we conducted a classic random design LTRE using the observed values of vital rates at LPB in each year of study. For years in which these vital rates were missing, and for vital rates that were not measured at LPB, we drew random values from each vital rate’s specified distribution, while conforming to the specified correlation structure. We estimated the deterministic growth rate ($\lambda_D$) from the mean
matrix ($\bar{A}$) based on average annual vital rates across all years of study. Deterministic sensitivities ($S_k$) and elasticities ($E_k$) for the vital rates comprising $\bar{A}$ were calculated analytically (Caswell 1978, 2001).

Contributions of each vital rate to variation in the deterministic growth rate, $V(\lambda_D)$, were calculated analytically using the approximations outlined by Caswell (1996, 2001). The results of the LTRE were averaged across 20000 repeated simulations under each correlation scenario to ensure that results were robust to random variation in simulated vital rates that were not observed at LPB (years missing $CS$ and/or $HS$, and all years for $DS$, $JS$, and $AS$).

We also constructed a stochastic population model to examine the effects of environmental variation on population dynamics. We calculated the stochastic growth rate ($\lambda_S$) using a Monte Carlo simulation by randomly drawing sets of vital rates from their specified distributions, while conforming to both the correlation structure observed at LPB (among $CS$, $HS$, and $NS$) and the correlation scenario between $NS$ and $DS$. The long-term stochastic growth rate was calculated as
\[
\log \lambda_S = \lim_{t \to \infty} (1/t) \log \left[ N(t) / N(0) \right],
\]
where $N(t)$ is the total abundance at time $t$ (Tuljapurkar, Horvitz, & Pascarella 2003). Preliminary results indicated that a projection over 100,000 time-steps was sufficient to reach asymptotic dynamics, and we thus used this time horizon for all stochastic projections. Following Haridas & Tuljapurkar (2005), we then calculated the elasticities of $\log \lambda_s$ to proportional changes in the mean and variance of lower-level vital rates, after discarding the first 2500 time steps to avoid transient dynamics.
The goal of our one-way design SLTRE was to examine how differences in either the mean or variability of vital rates between two alternative prey regimes contributed to observed differences in the stochastic growth rate. Historically, the LPB eider colony was bordered by a small colony of lesser snow geese, an alternative prey source for predators (such as arctic foxes and gulls) of eider eggs, ducklings, and adults. As a result of agricultural food subsidies along migration routes, the mid-continent population of snow geese increased exponentially over several decades, ultimately resulting in severe habitat degradation in Arctic and sub-Arctic staging, nesting, and brood rearing areas (Cooch et al. 1993, 2001; Abraham, Jefferies, & Alisauskas 2005). Our mechanistic nest success models (chapter 2) indicated that the eventual exodus of snow geese from the degraded epicenter of the colony strongly influenced common eider nest success, likely through indirect effects on the shared predator community. Thus, we recognized two “treatment” time periods in our response experiment (pre- and post-snow goose exodus), each representing a different alternative prey regime.

In chapter 2 we considered the post-exodus time period to begin when permanent nest-density plots indicated that the snow goose exodus was complete in 1998. However, these plots only captured the tail-end of a gradual decline in local goose densities that was recognized as early as 1993 (Cooch et al. 1993), which likely affected eider reproductive success before the exodus was complete. Thus, for statistical balance we considered years prior to 1993 “pre-exodus,” and 1993 onwards “post-exodus,” resulting in 12 and 11 years of data in each treatment, respectively.
Using Davison et al.’s (2010) approach, we examined how the elasticities of matrix parameters combined with observed differences in vital rates between the pre- and post-exodus time periods contributed to differences in the stochastic growth rate. We calculated contributions of differences in the mean ($\mu_k$) and variability ($\sigma_k$) of vital rates to the difference in stochastic growth rate ($a = \log \lambda_s$) between the two time periods as:

$$a^{post} - a^{pre} \approx \sum_k [\log \mu_k^{(post)} - \log \mu_k^{(pre)}] E_k^\mu + \sum_k [\log \sigma_k^{(post)} - \log \sigma_k^{(pre)}] E_k^\sigma,$$

where $E_k^\mu$ and $E_k^\sigma$ are the stochastic elasticities evaluated at the mean matrix across the 23 years of study, with corresponding process variances. Thus, $\sum_k [\log \mu_k^{(post)} - \log \mu_k^{(pre)}] E_k^\mu$ quantifies the contribution of changes in the mean of vital rate $k$, while $\sum_k [\log \sigma_k^{(post)} - \log \sigma_k^{(pre)}] E_k^\sigma$ is the contribution of changes in the variance of vital rate $k$. Unlike deterministic LTREs, SLTREs account for fluctuations in age structure that coincide with stochasticity in the vital rates (Davison et al. 2010). Under each correlation scenario, we calculated the mean log-differences in vital rates between the two time periods across 25000 replications to ensure our results were robust to random variation in simulated vital rates.

**Results**

Consistent with life history predictions, adult survival was the least variable vital rate through time (approximately 23% of $CV_{max}$). In contrast, nest success and duckling survival were the most variable vital rates, both fluctuating at approximately 54% of their $CV_{max}$. 
The deterministic growth rate of the mean matrix across the 23 years of study was 0.967 (1.00 during the first 10 years). Deterministic elasticities indicated that \( \lambda_D \) is most strongly affected by proportional changes in adult survival \((E_{AS}^D \approx 0.94)\). Proportional changes in the vital rates constituting fertility have relatively minor impacts on \( \lambda_D \) \((E^D \approx 0.06)\).

The absolute contributions from vital rates in the deterministic random-design LTRE are summarized in Fig. 3.2, while the relative contributions from vital rates (rescaled to sum to 100%) are summarized in Fig. 3.3. Variation in \( \lambda_D \) (denoted as \( V(\lambda_D) \) henceforth) across the 23 years of study averaged 0.011, 0.012, and 0.014 for the three correlation scenarios (0%, 25% and 50% correlation between NS and DS), respectively. The variance of AS was responsible for 39 – 42% of \( V(\lambda_D) \). Similarly, (co)variances involving DS were responsible for 39 – 42% of \( V(\lambda_D) \), while NS was responsible for 12-17%. The combined contributions of CS, HS, and JS were responsible for less than 5% of \( V(\lambda_D) \) under all of the correlation scenarios. Increased correlation between NS and DS increased the relative contribution from CS, HS, and NS, while decreasing the relative contribution from DS, JS, and AS.

The long-term stochastic growth rates for the population under the three correlation scenarios were 0.962, 0.968, and 0.978, respectively, and 0.959 for the control scenario (no correlation between any vital rates). The elasticities of \( \lambda_s \) to the means and variances of matrix parameters are summarized in Fig 3.4. The stochastic elasticities for the means of vital rates are proportional to the deterministic elasticities (Haridas &
Tuljapurkar 2005), and indicate that increases in the mean of all vital rates will increase the stochastic growth rate of the population.

The effect of proportional changes in variance of vital rates is complex, and depends upon the correlation scenario. Increases in the variance of JS and AS decreased \( \lambda_s \) for all correlation scenarios. Conversely, increases in the variance of CS and HS have slightly positive effects on \( \lambda_s \). In the 0% correlation scenario, increases in variance of both NS and DS decrease \( \lambda_s \). With 25% correlation between NS and DS, however, increases in the variance of NS have a positive impact on \( \lambda_s \), while there is almost no effect of changes in the variance of DS. Under the 50% correlation scenario, increases in the variation of both NS and DS have positive effects on \( \lambda_s \).

The results of the stochastic LTRE are summarized in Figs. 3.5 and 3.6. The stochastic growth rate of the population declined by 0.04, 0.05, and 0.06 in the post-exodus time period under the 0%, 25% and 50% correlation scenarios, respectively. Of the vital rates observed at LPB, mean nest success declined the most in the post-exodus time period, while mean hatching success only declined slightly. Conversely, the variance of nest success and hatching success both increased following the exodus of snow geese, by nearly the same ratio. Notably, mean clutch size did not change between the two time periods (the log difference was less than 0.005), yet the variance of clutch size declined more than any other vital rate following the goose exodus. As we increased the modeled correlation between DS and NS, both the mean and variance of DS declined in the post-exodus time period. Since juvenile and adult survival were not correlated to
any other vital rates in any of the scenarios, neither the mean nor variance of these vital rates changed between the two time periods.

**Discussion**

Life history theory predicts a trade-off between temporal variation in a vital rate and its proportional effect on the population growth rate, given that variation in the population growth rate is negatively related to fitness in stochastic environments (Tuljapurkar 1990a; Pfister 1998; Doak *et al.* 2005). As a consequence, selection is expected to buffer traits associated with adult survival against variation for long-lived organisms, resulting in a bet-hedging life history where the relatively high, stable survival of adults compensates for high temporal variation in fertility (Gaillard *et al.* 1998; Gaillard & Yoccoz 2003).

Our results support these predictions for common eiders; changes in adult survival have a disproportionate effect on both deterministic and stochastic population dynamics, when compared to other vital rates. However, despite the elasticity of mean adult survival being nearly 16 times higher than any other vital rate, variation in adult survival contributed less to actual variation in the deterministic population growth rate than the combined effects of nest success and duckling survival. Furthermore, covariation between NS and DS increased their relative contributions to variation in the growth rate across the study.

Using a recently developed stochastic extension to classic life table response experiments, we found that the stochastic growth rate of our study population declined following the snow goose exodus. Almost all of these differences were related to a
decline in mean nest success, and in turn, a decline in mean fertility. However, as we increased the modeled correlation between nest success and duckling survival, corresponding declines in duckling survival in the post-exodus time period nearly doubled this effect. Our chapter 2 results indicate that the exodus of snow geese (an abundant source of alternative prey to predators) from the areas surrounding the eider colony likely resulted in a high degree of prey-switching by local terrestrial and avian predators, thereby reducing eider nest success. However, there exists a high degree of overlap between predators of eggs and ducklings, and the processes responsible for changes in nest success likely affect duckling survival as well (Gabor et al. 2006). Our study demonstrates that the degree of overlap in the processes affecting these vital rates can have important implications for common eider population dynamics.

Early stochastic demographic theory predicted that increased variability in vital rates would negatively influence the population growth rate (Tuljapurkar 1990b; Pfister 1998). Contrary to these predictions, Doak et al. (2005) showed that neglecting correlations among life cycle components can yield misleading inference on the population-level effects of variation in vital rates. Specifically, they demonstrated that the negative consequences of increased variation in vital rates may be reduced or even reversed if vital rates are negatively correlated.

In our perturbation analyses, we explicitly included a scenario under which vital rates were uncorrelated, allowing us to examine the effects of both observed and hypothesized correlation among vital rates on common eider population dynamics. In accordance with traditional theory, all $E_k^\sigma$ were negative when no correlations among vital rates were
included. However, we found that even modest correlation between vital rates reversed these effects; increased variance of several vital rates had positive effects on the stochastic population growth rate. Furthermore, the correlation structure between vital rates in all modeled correlation scenarios improved λs compared to the control scenario. We emphasize that this occurred when “positive” correlations were included in the model (all correlations among vital rates observed at LPB were positive), which contradicts the examples presented in Doak et al. (2005). Consequently, these results demonstrate the importance of correctly accounting for correlation among vital rates when examining populations in stochastic environments.

Although the majority of differences in stochastic growth rate were attributable to changes in mean vital rates, understanding the consequences of changes in variation in vital rates is also important. While changes in the mean vital rates may have strong potential impacts on population growth, they may be much harder to achieve in reality (Tuljapurkar 2010). For example, under the three correlation scenarios, $E^{s\mu}$ for clutch size ranged from 57 to 78 times greater than $E^{s\sigma}$. However, since the mean clutch size did not change between the pre- and post-exodus time periods, the entire contribution of clutch size to differences in λs resulted from changes in its variance.

In chapter 2, we also found that specific combinations of temperature and precipitation were associated with decreased nest success. Other studies have detected corresponding effects of climate on several parts of the common eider life cycle, including the timing of migration, reproductive success, and winter survival (Robertson & Gilchrist 1998; Lehikoinen, Kilpi, & Ost 2006; D’Alba, Monaghan, & Nager 2010;
Mehlum 2012). Climate models predict an increase in both the mean and variance of temperature and precipitation in high-latitude regions, with a constellation of potential impacts on arctic ecosystems (Houghton et al. 2001; Walther et al. 2002; Post et al. 2009). For example, with climate change, earlier thawing of the Arctic and Hudson Bay icepacks (Skinner et al. 1998; Vinnikov et al. 1999) has led to earlier onshore arrival of polar bears (Regehr et al. 2007). With earlier onshore arrival, there is increasing evidence that overlap with the nesting period of waterfowl is leading to higher nest and adult predation by polar bears, and increased potential for catastrophic nest failure in eider colonies (Drent & Prop 2008; Rockwell & Gormezano 2009; Rockwell, Gormezano, & Koons 2011; Iles et al. unpublished data).

In this study, we retrospectively examined the effect of changes in reproductive success across our study. However, research is needed that explicitly evaluates the potential for increased frequency of catastrophic nest failure in eider colonies, and prospectively examines the subsequent effects of reproductive “bust” years on population dynamics. Accordingly, studies that link the effects of temporal variation in the underlying environmental drivers of vital rates to population dynamics can reveal a much clearer, and potentially stronger effect of changes in variance on population growth (Jonzén et al. 2010; Tuljapurkar 2010).

This study underscores the importance of research that integrates long-term monitoring at multiple stages of the life cycle in order to fully understand the consequences of environmental variation on declining populations. Without long-term studies on many parts of the life cycle simultaneously and a robust understanding of the
correlation structure among vital rates, predictions of the potential effects of climate change on eider populations remain speculative. For example, we found that the growth rate of our study population was most sensitive to changes in adult survival. Yet, there were no long-term data available to estimate this vital rate for our study population and the drivers thereof, nor to estimate its correlation with other vital rates. Thus, future studies that link the environmental drivers of variation in vital rates to population processes will provide important insights into the effect of climate-driven perturbations to arctic systems on population dynamics, and ultimately, help guide the management of imperiled populations.

References


Ekroos, J., Fox, A.D., Christensen, T.K., Petersen, I.K., Kilpi, M., Jónsson, J.E., Green, M., Laursen, K., Cervencl, A., Boer, P.D., Nilsson, L., Meissner, W., Garthe, S. &


Table 3.1. Mean and standard error (in parentheses) of vital rates for common eiders breeding at La Pérouse Bay in each year of study. Vital rates measured at LPB were full clutch size ($CS$), nest success ($NS$), and hatching success ($HS$). -- denotes years in which data was not available for a particular vital rate.

<table>
<thead>
<tr>
<th>Year</th>
<th>$CS$</th>
<th>$NS$</th>
<th>$HS$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1972</td>
<td>4.3 (--)</td>
<td>0.617 (0.046)</td>
<td>--</td>
</tr>
<tr>
<td>1973</td>
<td>4.4 (--)</td>
<td>0.455 (0.054)</td>
<td>--</td>
</tr>
<tr>
<td>1976</td>
<td>4.8 (0.08)</td>
<td>0.961 (0.019)</td>
<td>0.880 (0.025)</td>
</tr>
<tr>
<td>1977</td>
<td>4.7 (0.07)</td>
<td>0.795 (0.041)</td>
<td>0.915 (0.017)</td>
</tr>
<tr>
<td>1978</td>
<td>--</td>
<td>0.289 (0.022)</td>
<td>--</td>
</tr>
<tr>
<td>1979</td>
<td>--</td>
<td>0.560 (0.024)</td>
<td>--</td>
</tr>
<tr>
<td>1980</td>
<td>--</td>
<td>0.565 (0.025)</td>
<td>--</td>
</tr>
<tr>
<td>1984</td>
<td>3.9 (0.07)</td>
<td>0.332 (0.028)</td>
<td>--</td>
</tr>
<tr>
<td>1985</td>
<td>4.3 (0.05)</td>
<td>0.712 (0.042)</td>
<td>--</td>
</tr>
<tr>
<td>1986</td>
<td>4.5 (0.05)</td>
<td>0.694 (0.055)</td>
<td>--</td>
</tr>
<tr>
<td>1991</td>
<td>4.3 (0.14)</td>
<td>0.529 (0.036)</td>
<td>0.882 (0.029)</td>
</tr>
<tr>
<td>1992</td>
<td>3.7 (0.16)</td>
<td>0.075 (0.019)</td>
<td>0.621 (0.075)</td>
</tr>
<tr>
<td>1993</td>
<td>4.4 (0.12)</td>
<td>0.169 (0.026)</td>
<td>0.867 (0.067)</td>
</tr>
<tr>
<td>1994</td>
<td>4.6 (0.14)</td>
<td>0.386 (0.032)</td>
<td>0.492 (0.062)</td>
</tr>
<tr>
<td>1995</td>
<td>4.4 (0.12)</td>
<td>0.395 (0.037)</td>
<td>0.783 (0.117)</td>
</tr>
<tr>
<td>1996</td>
<td>4.0 (0.09)</td>
<td>0.643 (0.038)</td>
<td>0.881 (0.058)</td>
</tr>
<tr>
<td>1997</td>
<td>4.3 (0.09)</td>
<td>0.658 (0.055)</td>
<td>--</td>
</tr>
<tr>
<td>2000</td>
<td>4.6 (0.08)</td>
<td>0.100 (0.028)</td>
<td>--</td>
</tr>
<tr>
<td>2002</td>
<td>4.4 (0.06)</td>
<td>0.656 (0.031)</td>
<td>0.792 (0.068)</td>
</tr>
<tr>
<td>2003</td>
<td>4.3 (0.05)</td>
<td>0.110 (0.011)</td>
<td>--</td>
</tr>
<tr>
<td>2009</td>
<td>3.8 (0.14)</td>
<td>0.033 (0.019)</td>
<td>--</td>
</tr>
<tr>
<td>2010</td>
<td>4.2 (0.05)</td>
<td>0.366 (0.025)</td>
<td>0.744 (0.102)</td>
</tr>
<tr>
<td>2011</td>
<td>4.1 (0.09)</td>
<td>0.002 (0.001)</td>
<td>--</td>
</tr>
</tbody>
</table>
Table 3.2. Age-specific mean vital rates and temporal process variance (in parentheses) used in matrix projection models for common eider. Vital rates are breeding propensity (BP), full clutch size (CS), nest success (NS), hatching success (HS), duckling survival (DS), juvenile survival (JS), and adult survival (AS). “n” represents the number of years in which data were available to estimate the vital rates, or the number of years on which estimates were based if published data from other populations were used. * denotes vital rates specific to this study population. Ŧ denotes vital rates that were adjusted to achieve λ=1 in the first half of the study. “-” denotes vital rates for which there were no years of data, and were thus simulated.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Vital rate</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4+</th>
<th>n</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>BP</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>0.26</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td>CS*</td>
<td>4.30 (0.075)</td>
<td>4.30</td>
<td>4.30</td>
<td>4.30</td>
<td>20</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>NS*</td>
<td>0.44 (0.071)</td>
<td>0.44</td>
<td>0.44</td>
<td>0.44</td>
<td>23</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>HS*</td>
<td>0.79 (0.015)</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>10</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>DS Ŧ</td>
<td>0.17 (0.041)</td>
<td>0.17</td>
<td>0.17</td>
<td>0.17</td>
<td>10</td>
<td>Milne (1974)</td>
</tr>
<tr>
<td></td>
<td>JS Ŧ</td>
<td>0.65 (0.034)</td>
<td>0.65</td>
<td>0.65</td>
<td>0.65</td>
<td>-</td>
<td>Oppel &amp; Powell (2010)</td>
</tr>
<tr>
<td></td>
<td>AS Ŧ</td>
<td>0.9 (0.005)</td>
<td>0.9</td>
<td>0.9</td>
<td>0.9</td>
<td>11</td>
<td>Wilson et al. (2007)</td>
</tr>
</tbody>
</table>
Fig. 3.1. Life cycle diagram and transition matrix used for modeling the population dynamics of *S.m. sedentaria*. Stage classes represented in this model are: first year, second year, third year, and fourth year and greater adult females. $S_A$ = adult survival, $F$ = fertility.
Fig. 3.2. Absolute contributions (C) of variances and covariances of vital rates to variation in the deterministic growth rate ($V(\lambda_D)$), measured using a deterministic random design LTRE under three correlation scenarios. Vital rates examined were clutch size (CS), nest success (NS), hatching success (HS), duckling survival (DS), juvenile survival (JS), and adult survival (AS). % corr denotes the correlation between NS and DS.
Fig. 3.3. Rescaled contributions (% C) of variances and covariances of vital rates to variation in the deterministic growth rate ($V(\lambda_D)$), measured using a deterministic random design LTRE under three correlation scenarios. Vital rates examined were clutch size ($CS$), nest success ($NS$), hatching success ($HS$), duckling survival ($DS$), juvenile survival ($JS$), and adult survival ($AS$). % corr denotes the correlation between $NS$ and $DS$. Contributions sum to 100% under each correlation scenario.
Fig. 3.4. Elasticities ($E^\mu$) of $\lambda_s$ to changes in the means ($\mu$) and variances ($\sigma$) of vital rates under three correlation scenarios and a “control” correlation scenario. Vital rates examined were clutch size ($CS$), nest success ($NS$), hatching success ($HS$), duckling survival ($DS$), juvenile survival ($JS$), and adult survival ($AS$). % corr denotes the correlation between $NS$ and $DS$. control denotes a scenario with no correlation between any vital rates (i.e. observed correlation between $CS$, $NS$, and $HS$ at LPB removed). Note the differences in scale between the two plots.
Fig. 3.5. Log-differences in the means (μ) and variances (σ) of vital rates between the post- and pre-exodus snow goose time periods under three correlation scenarios. Vital rates examined were clutch size (CS), nest success (NS), hatching success (HS), duckling survival (DS), juvenile survival (JS), and adult survival (AS). % corr denotes the correlation between NS and DS.
Fig. 3.6. Contributions of log-differences in the mean ($C^\mu$) and variance ($C^\sigma$) of vital rates to differences in log-$\lambda_s$ between the post- and pre-exodus snow goose time periods under three correlation scenarios. Vital rates examined were clutch size ($CS$), nest success ($NS$), hatching success ($HS$), duckling survival ($DS$), juvenile survival ($JS$), and adult survival ($AS$). % corr denotes the correlation between $NS$ and $DS$. Note the differences in scale between the two plots.
CHAPTER 4
CONCLUSIONS

Anthropogenic changes have disproportionately affected both the biotic and abiotic environments in Arctic ecosystems (Vinnikov et al. 1999; Houghton et al. 2001; Post et al. 2009). However, accurately predicting the consequences of perturbations to natural populations requires an understanding of both the processes that drive variation in demographic parameters, and how variation in vital rates affects population dynamics (Caswell 2000; Doak et al. 2005; Haridas & Tuljapurkar 2005). The seemingly ubiquitous life-history trade-off between variation in a vital rate and its proportional effect on a population (Pfister 1998; Gaillard, Festa-Bianchet, & Yoccoz 1998; Morris & Doak 2004; but see Koons et al. 2009) necessitates both a prospective examination of the functional relationships between vital rates and population processes, and a retrospective evaluation of the actual contributions of variation in vital rates to population dynamics (Caswell 2000). Furthermore, rigorous consideration of the correlations amongst vital rates is imperative for correctly estimating the consequences of perturbations to the factors governing population processes (Doak et al. 2005; Morris et al. 2008).

The common eider (Somateria mollissima), along with many other sea duck species, has experienced long-term declines across much of its range (Robertson & Gilchrist 1998; Gilliland et al. 2009). Yet, despite the extensive research attention given to common eiders, the demographic causes of these declines are poorly understood (Goudie, Robertson, & Reed 2000; Ekroos et al. 2012). Previous studies indicate that, consistent with life history predictions, common eider adult survival is relative high and
stable through time, while annual reproductive success is highly variable (Coulson 1984; Goudie et al. 2000). However, very few population models have been developed for sea ducks. Thus, the drivers of variation in reproductive success, the relative effects of the observed variation on eider population dynamics, and the consequence of covariation between highly variable vital rates remains unclear.

In Chapter 2, we examined variation in annual nest success across a 41 year study for a population of Hudson Bay common eiders (S. m. sedentaria). Specifically, we evaluated the effects of variation in arctic fox abundance (Vulpes lagopus; an important terrestrial predator), the availability and spatial distribution of lesser snow geese (Chen caerulescens caerulescens; a highly abundant alternative prey species), and breeding season climate on annual common eider nest success.

We found that nest success declined over the course of the study, but was also highly variable across years. Additionally, variation in nest success was largely driven by a complex interaction between predators and alternative prey, as well as breeding season climate. The increased abundance of local alternative prey buffered annual fluctuations in arctic fox abundance, yet was also responsible for the long-term decline in eider nest success, suggesting apparent competition with snow geese via other predator species (e.g. gulls). Additionally, the sudden exodus of snow geese from the eider colony had a dramatic negative impact on common eider nest success. The effect of breeding season climate was subtle compared to the influence of biotic factors, and indicated that the effect of climate depended on the stage of the breeding season. Cold, wet conditions
in early spring were associated with decreased nest success, while warm, wet conditions in late spring were associated with improved eider nest success.

In Chapter 3, we developed a population model to examine, both prospectively and retrospectively, the contributions of environmental stochasticity on common eider population dynamics. We then used a recently developed stochastic life table response experiment to determine the impact of long-term changes in the abundance of alternative prey on eider population dynamics, through corresponding effects on the statistical properties of the underlying vital rates. Additionally, since the processes responsible for changes in nest success potentially affect other vital rates simultaneously, we also modeled several levels of covariation amongst vital rates.

We found that, consistent with life history predictions, proportional changes in adult survival have the largest impact on population dynamics. However, since adult survival is also highly stable through time, the vital rates comprising fertility contributed more to actual variation in population growth. The eventual exodus of alternative prey from the eider colony reduced the long-term stochastic growth rate of the population, primarily through negative impacts on mean nest success. Furthermore, the inclusion of correlation between nest success and duckling survival exacerbated this effect. We also found that correlations amongst vital rates can dramatically alter the effect of changes in the variability of vital rates on population dynamics, and in some cases, even reverse the predictions made in the absence of correlations.

These studies highlight the importance of long-term ecological research at multiple trophic levels and across multiple stages of the life cycle. Such research allows
a simultaneous examination of the drivers of variation in population parameters, as well as the relationships among multiple vital rates. Long-term studies that attempt to link the environmental drivers of variation in vital rates to population processes provide important insights into the effect of perturbations to arctic systems on population dynamics, and are needed to properly inform the conservation of populations amidst changing environmental conditions.

References


