5-2017

Effects of Variable and Changing Environments on Demography: Inferences from a Lesser Snow Goose Colony

David T. Iles
Utah State University

Recommended Citation

Iles, David T., "Effects of Variable and Changing Environments on Demography: Inferences from a Lesser Snow Goose Colony" (2017). *All Graduate Theses and Dissertations*. 5854.
https://digitalcommons.usu.edu/etd/5854

EFFECTS OF VARIABLE AND CHANGING ENVIRONMENTS ON DEMOGRAPHY: INFERENCES FROM A LESSER SNOW GOOSE COLONY

by

David T. Iles

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

David N. Koons, Ph.D. Major Professor	Christa P.H. Mulder, Ph.D. Committee Member
Karen Beard, Ph.D. Committee Member	Dan MacNulty, Ph.D. Committee Member
Joe Wheaton, Ph.D. Committee Member	Mark R. McLellan, Ph.D. Vice President for Research and Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2017

ABSTRACT

Effects of Variable and Changing Environments on Demography: Inferences from a Lesser Snow Goose Colony

by

David T. Iles, Doctor of Philosophy

Utah State University, 2017

Major Professor: Dr. David N. Koons
Department: Wildland Resources

Anthropogenic pressures have caused changes in both the mean and variance of environmental conditions, with associated effects on the demography of natural populations. The demographic effects of environmental change can manifest through direct (i.e., physiological) or indirect pathways (i.e., through shifts in species interactions). For many populations, environmental change will affect multiple life cycle stages simultaneously, thereby altering vital rate correlation structures with potentially important impacts on evolutionary fitness. The effects of environmental change will also often be habitat-specific, particularly when species interactions modify demographic sensitivity to climate. As a result, the effects of climate change are likely to vary across a species range, with important implications for range expansion and population viability.

In chapter 2, I examine the effects of joint vital rate responses to environmental drivers on the evolution of life histories in variable environments. I show that vital rate covariation, generated when multiple vital rates respond to a shared environmental driver, can fundamentally alter evolutionary selection pressures. Negative vital rate covariation promotes the evolution of demographic lability (stronger demographic responsiveness), while positive covariation promotes buffering (weaker demographic responsiveness), altering the range of life histories over which the evolution of buffered and labile vital rates are a predicted evolutionary outcome. By identifying the life histories for which selection pressures are most sensitive to environmentally-driven vital rate covariation, this study provides a richer understanding of both life history evolution and the capacity of species to cope with ongoing changes to contemporary environments.

In chapter 3, I use a long-term study of lesser snow geese to test the hypothesis that demographic and developmental responses to climate will be weakest in habitats where resource diversity is greatest. I find support for this hypothesis, and my results indicate that gosling demography is much more responsive to climate in recently colonized, freshwater habitats where landscape diversity and gosling diet diversity is low. These results underscore the potential importance of accounting for biotic interactions when predicting spatio-temporal responses to climate.

In chapter 4, I quantify the consequences of observed climate change for lesser snow goose population dynamics across habitats. I find that climate change increases population growth in all habitats, but that such increases are disproportionately large in novel inland freshwater habitats. These results suggest that in a warmer and more variable climate, the breeding range and population growth of lesser snow geese is likely to increase, counteracting current management efforts to reduce overabundant populations.

(159 pages)

PUBLIC ABSTRACT

Effects of Variable and Changing Environments on Demography: Inferences from a Lesser Snow Goose Colony

by

David T. Iles

The mean and variability of environmental conditions have changed as a result of human activity, and continued changes are predicted. The strongest effects on natural populations will often be channeled through species interactions, as shifts in species range limits and life cycle schedules will shift in relation to each other. These changes will often impact rates of survival, growth, and reproduction simultaneously, and these effects will likely differ across habitats.

In chapter 2, I used mathematical modeling and computer simulations to investigate the evolutionary significance of increasingly variable environments, and examine how evolutionary pressures change when multiple vital rates are affected simultaneously. I found that when multiple vital rates respond to a shared environmental driver, evolutionary selection pressures can be strengthened, weakened, or even reversed, adding an important dimension to existing life history theory.

In chapter 3, I examined whether snow goose sensitivity to climate differs between habitats, and whether these responses depended on the diversity of available plants. I found that geese were more sensitive to seasonal warmness in inland freshwater habitats where there are relatively few species of plants they consume, while they consistently produce relatively high numbers of offspring in coastal saltwater habitats.

In chapter 4, I constructed a population model to investigate the consequences of climate change for snow goose populations in coastal and inland habitats. I found that climate change will disproportionately improve population growth in inland areas, potentially offsetting management efforts to reduce currently overabundant populations.

ACKNOWLEDGMENTS

I am deeply grateful to my advisor, David Koons. I will forever appreciate his guidance and encouragement through the ups and downs of graduate school. I thank Robert Rockwell, Christa Mulder, Susan Felege, and Ken Abraham for countless interesting discussions that have shaped the way I think about science. I thank my committee members, Karen Beard, Dan MacNulty, and Joe Wheaton for valuable discussions and comments on my dissertation. Ryan Brook provided access to land cover maps that were invaluable for this work. I am extremely grateful to Marsha Bailey for her help (and patience) throughout my graduate studies at USU. I thank my fellow graduate students and friends, who, I am fortunate to say, are too many to name. I am deeply indebted to all the people whose hard work contributed to the legacy of research at La Pérouse Bay, and without whose contributions my project would not have been possible.

Financial support for this project was provided by the S.J. and Jessie E. Quinney Foundation Fellowship, Ducks Unlimited Canada, The National Geographic Society, California Waterfowl, Wapusk National Park, and The Hudson Bay Project.

I thank my mother for fostering my curiosity, for supporting me in pursuing my dreams, and for teaching me the value of working hard towards achieving them. Finally, I thank my father for instilling in me a sense of curiosity with nature, and for reminding me of the importance of occasionally slowing down to appreciate the journey.

David Iles

CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER 1

INTRODUCTION

Introduction

For many populations, the strongest effects of climate change are likely to be indirect, channeled through effects on species interactions (Tylianakis *et al.* 2008; Gilman *et al.* 2010; Wisz *et al.* 2013; Svenning *et al.* 2014). Thus, while it can have direct effects on the physiology of organisms, climate will often strongly interact with the biotic community to influence wildlife demography. This represents a considerable challenge for forecasting population dynamics under climate change because it suggests that demographic sensitivity to climate is likely to be dependent on the ecological community in which a population is immersed (Ehrlén & Morris 2015; Ehrlén *et al.* 2016).

Shifts in species phenology and ranges are among the most conspicuous effects of recent climate change (Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006). In general, there has been a strong average trend towards phenological advance and range expansion northward and/or to higher elevations for all taxonomic groups (Parmesan & Yohe 2003; Root *et al.* 2003). However, species responses are also highly individualistic and some species even exhibit delayed phenology and/or southward range expansion in response to climate change (Parmesan 2007; Thackeray *et al.* 2010).

Changes in either phenology or range dynamics can influence the ecological community with which a focal population interacts by affecting the spatial or temporal overlap of constituent species (Thackeray *et al.* 2010). These shifts are likely to therefore influence demographic climate sensitivity. Critically, this suggests that contemporary relationships between demographic rates and climate could fail to remain consistent if future climate reshuffles ecological assemblages (Alexander, Diez & Levine 2015; Alexander *et al.* 2016). Accounting for biotic interactions, and potential lability in these interactions under different climate regimes, is therefore recognized as a major challenge for applied ecology (Van der Putten, Macel & Visser 2010; Post 2013; Wisz *et al.* 2013).

In this introductory chapter, I briefly review the capacity for ontogenetic (i.e., developmental) and phenological shifts to alter species assemblages and interaction strengths. I then review the trophic mismatch concept as an important consequence of phenological and ontogenetic shifts for consumer-resource dynamics. I conclude this chapter by describing how my subsequent dissertation chapters attempt to address key knowledge gaps.

Ontogeny

Phenology is by definition a description of seasonal organism development. In birds, dates of migration, breeding, egg laying, hatching, and/or feather molting describe different developmental phases of both adult birds and their offspring. Similarly, dates of germination, shoot emergence, leaf-out, fruit development, and/or seed dispersal define the seasonal development of individual plants. Phenology can also encompass continuous variation in individual development, such as changes in body size, condition, or age.

Importantly, the behaviors, resource requirements, competitive abilities, and predator defenses of individuals often change over the course of individual development (Werner & Gilliam 1984; Yang & Rudolf 2010). For example, ontogenetic shifts in diet are especially prevalent in fish, where body size and gape-limitation strongly determine food web position (Scharf, Juanes & Rountree 2000). In plants, competitive ability is often associated with height (Schwinning & Weiner 1998), while plant nutritional quality for herbivores declines seasonally (Gadallah & Jefferies 1995). Plant-pollinator interactions and animal-facilitated seed dispersal depend upon synchrony of animal activity with sufficient flower or fruit development of plants (Howe & Smallwood 1982; Willson & Traveset 2000; Elzinga *et al.* 2007; Memmott *et al.* 2007). Phenological changes can therefore alter the relative developmental stages of co-occurring species and can strongly impact the strength and dynamics of species interactions, including whether species interact at all (Fig. 1.1; Werner & Gilliam 1984; Yang & Rudolf 2010). For this reason, the *relative* timing of phenological activity of interacting species is generally considered more relevant than absolute changes in species phenology (Durant *et al.* 2005; Visser & Both 2005).

Figure 1.1 illustrates the effect of ontogeny on species interactions. The length and horizontal position of each line represents the duration over which two species (blue and green) are present in the community. Furthermore, the seasonal phenology of species 1 is characterized by three discrete developmental stages (the solid, dashed, and dotted parts of its seasonal phenology line). As is common in ecological systems, the type and/or strength of interaction between species depends upon their relative developmental stages. Strong interactions occur when species 1 is in its “solid stage”, weak interactions occur during the “dashed stage”, and no interactions can occur during the “dotted stage,” representing a complete ontogenetic niche shift. Of note, changes in either the rate of development (i.e., duration of each stage class; Fig. 1.1a) or shifts in the entire phenology of development relative to other species (Fig. 1.1c) affects the duration and strength of species interactions (shading in Fig. 1.1).

Phenological Distributions

When individuals in a single population are asynchronous in their phenology, population-level development can be represented by a distribution (Forrest & Miller-Rushing 2010; Miller-Rushing *et al.* 2010; Musolin, Tougou & Fujisaki 2010). Furthermore, the distributions describing successive ontogenetic stages can differ, owing to stochastic environmental conditions and individual heterogeneity in response to environmental cues. For example, asynchronous migration phenology is common in birds (Sparks *et al.* 2005). At the onset of breeding, individuals gradually arrive at the breeding grounds up to some maximum seasonal abundance. Nevertheless, nesting, hatching, and fledging phenology during that season need not have similar temporal distributions. Of key importance in the context of climate change, the shape of a phenological distribution is labile if individuals in a population differ in their sensitivity to perturbations. For example, increasingly skewed arrival distributions have been observed in some bird species in response to climate change (Sparks *et al.* 2005), suggesting that only a subset of the population responds strongly to warming. Similarly, changes in the shape of flowering distributions have been observed in response to warming in numerous plant species (CaraDonna, Iler & Inouye 2014).

Figure 1.2 depicts a scenario in which changes in abundance throughout the season for two interacting species are driven by individual heterogeneity in arrival and departure phenology. In this example, population-level phenology of two interacting species is described by distributions rather than simply start and end dates. For simplicity, only a single ontogenetic stage for each species is represented. In this case, changes in either the shape of a species phenological distribution (Fig. 1.2b) or the position of a species distribution relative to an interacting species (Fig. 1.2c) can alter patterns in relative species abundance throughout the season. While the relative ontogeny of interacting species is constant in this scenario, the strength of interaction could change throughout the season if, for example, interactions are frequency-or density-dependent (Abrams & Ginzburg 2000).

By determining the temporal overlap and relative abundance of potentially interacting species, phenology affects diversity of species that co-occur at any point in time (Colwell & Lees 2000; CaraDonna, Iler & Inouye 2014). Changes in relative phenology can cause complete phenological mismatches between previously interacting species or novel phenological matches between previously non-interacting species. In a strict sense, this can result in the formation of so-called “no-analogue” communities (Williams & Jackson 2007) where changes in phenology fundamentally alter patterns of temporal species co-occurrence, in much the same way that shifts in range boundaries can influence spatial patterns of co-occurrence.

Figure 1.3 illustrates the effect of phenology on seasonal patterns of species richness. In Fig. 1.3a, four species occupy different brief phenological windows throughout the season. Maximum species richness during the season is two and is only attained briefly during periods of phenological overlap. In Fig. 1.3b, broader phenological windows for each species allow multiple species to overlap simultaneously, contributing to a peak richness of four in the middle of the season and consistently higher species richness throughout the season. Critically, this suggests that species diversity can be influenced by changes in phenology, and simultaneously, can influence the effect of phenological change on species demography.

Phenological changes that alter the richness, relative abundance, and/or species composition of ecological communities can have profound effects on population and community processes. The effects of species diversity on community stability are well-appreciated and have a long tradition of empirical and theoretical study (McCann 2000; Cottingham, Brown & Lennon 2001; Hooper *et al.* 2005; Haddad *et al.* 2011). Through averaging effects (Doak *et al.* 1998), insurance or portfolio effects (Yachi & Loreau 1999; Mulder, Uliassi & Doak 2001; Isbell *et al.* 2011), or negative covariance (Ives, Gross & Klug 1999; Yachi & Loreau 1999), increased diversity should generally lead to decreased temporal variance in the properties of a community within a single trophic level. For generalist consumers, increased resource stability should in turn lead to increased consumer stability by weakening pairwise interaction strengths and allowing consumers to flexibly switch between resources as they are available (MacArthur 1955; McCann 2000; Petchey 2000).

Trophic Mismatches and the Practical Difficulty of Defining a Yardstick

Trophic mismatch is defined as a temporal asynchrony between peak resource demand by consumers and peak resource availability (Miller-Rushing *et al.* 2010; Kerby, Wilmers & Post 2012) and therefore represents a vertically structured consequence (and narrow subset) of the larger phenomenon of phenological asynchrony (Post 2013). The concept was originally proposed as an explanation for inter-annual variability in cod productivity without reference to climate change (Cushing 1974; Cushing 1990; Leggett & Deblois 1994). Subsequently, with widespread recognition of climate-driven changes in phenology, the concept has been extended to investigations of temporal consumer-resource asynchronies in many systems. Examples include goose-plant (Dickey, Gauthier & Cadieux 2008; Aubry *et al.* 2013), polar bear-waterfowl (Rockwell & Gormezano 2009; Rockwell, Gormezano & Koons 2011), bird-insect (Visser *et al.* 1998; Charmantier *et al.* 2008; Strode 2015), raptor-passerine (Both *et al.* 2009), ungulate-plant (Post & Forchhammer 2008; Kerby & Post 2013), marine pelagic invertebrate (Edwards & Richardson 2004), intertidal invertebrate (Philippart *et al.* 2003), and seabird-fish-invertebrate communities (Frederiksen *et al.* 2006). Thus, trophic mismatches have been observed across a wide array of taxa, across multiple trophic levels (sometimes simultaneously in the same system), in terrestrial and aquatic systems, and across a range of latitudes.

Most documented examples of trophic mismatch have focused on specialized consumers that interact with a relatively small community of resources. For example, increasing mismatch between great tits and their caterpillar prey was inferred based on shifts in the mean date of bird laying (and thus hatching) relative to the date of peak caterpillar biomass (Visser *et al.* 1998). Trophic mismatch between ground-nesting geese and polar bears was assessed based on changes in polar bear onshore arrival phenology relative to the mean date of goose hatch (Rockwell, Gormezano & Koons 2011). In other situations, phenologically driven variation in resource quality may be more relevant than mismatches with resource abundance. For example, the effect of seasonal declines in plant quality on herbivore demography has been documented in a number of herbivores, including geese (Dickey, Gauthier & Cadieux 2008; Aubry *et al.* 2013; Doiron, Gauthier & Lévesque 2014; Doiron, Gauthier & Lévesque 2015) and caribou (Post & Klein 1999; Post & Forchhammer 2008).

In cases where the resource community is relatively depauperate, or when the phenological responses of different resources are highly correlated, defining a yardstick by which to measure phenological asynchrony is relatively straightforward (Visser & Both 2005); see examples discussed above. However, resource communities are often diverse and the constituent species have many different ontogenetic stages that can be utilized by consumers (e.g., leaf emergence, flowering, fruiting), each of which may respond differently to climate. In such cases, a single useful metric of mismatch may be difficult or impossible to derive.

For example, at La Pérouse Bay, lesser snow geese (*Chen caerulescens caerulescens*) are capable of consuming a wide array of plant species (see chapter 3; also see Gadallah & Jefferies 1995; Winiarski, McWilliams & Rockwell 2012). Leaf nutritional quality differs amongst plant species, changes over the course of seasonal development (Gadallah & Jefferies 1995; Doiron, Gauthier & Lévesque 2014), and many plant species produce conspicuous flowers and fruits that are also heavily consumed by developing goslings. Seasonal phenology also differs amongst plant species, and phenological responses to climate are idiosyncratic (Mulder, Iles & Rockwell 2016).

A Practical Solution

In many cases, it is unclear how a single metric of trophic mismatch could be usefully derived. In theory, a metric of mismatch could be derived for each plant species that is potentially consumed, although in practice phenological data are unlikely to be available for all species in diverse communities. Further, if multiple life cycle stages of a plant species are consumed by goslings and each potentially provides different nutritional benefits, then multiple mismatch metrics could be required for each plant species. Omnibus measures of plant community phenology, such as those derived using NDVI, may broadly describe green-up for dominant functional groups (Doiron *et al.* 2013), but it is unclear how reliable these metrics will be for less conspicuous species or different life cycle stages (e.g., flowering or fruit ripening) that may respond differently to climate than leaf development.

In diverse communities where climate effects are manifest through multiple indirect pathways, it may often be more useful to simply measure the demographic effects of climate variables that are known *a priori* to affect species interactions. In this approach, direct and indirect effects are implicitly included in measures of consumer climate sensitivity, rather than explicitly modelled using detailed estimates of phenology for many species. The influence of species interactions on climate sensitivity can then be inferred from differences in demographic responses across ecological communities or habitats. I use this approach in chapters 3 and 4 of this dissertation, given the diversity of plant species and life cycle stages consumed by geese and inadequate data to derive and ground-truth metrics of phenological mismatch.

Dissertation Outline

Chapter 2 – Fitness Consequences of Joint Vital Rate Responses to Environmental Variability across Life Histories

Increased environmental variability is a prevalent consequence of recent climate change (Tebaldi *et al.* 2006; IPCC 2012; Stocker *et al.* 2013) and can affect natural populations directly or indirectly (Boyce, Haridas & Lee 2006). Whether effects are channeled through direct or indirect pathways, environmental pressures will often influence multiple life cycle stages simultaneously, thereby altering demographic correlations. Within a population, vital rate correlations can fundamentally alter population growth, evolutionary fitness, and demographic sensitivity to environmental variation (Doak *et al.* 2005; Barraquand & Yoccoz 2013). Current theory to explain the evolution of life histories in variable environments encompasses the effects of non-linear demographic responses (i.e., reaction norms; Koons *et al.* 2009). Yet, current theory has not adequately examined the possibility for joint responses of vital rates to alter predicted evolutionary outcomes. In chapter 2, we evaluate the evolutionary significance of joint vital rate responses to environmental drivers across a diverse suite of simulated life histories. By identifying the life histories for which selection pressures are most sensitive to environmentally-driven vital rate covariation, we provide a richer understanding of both life history evolution and the capacity of species to cope with ongoing changes to contemporary environments.

Chapter 3 – Resource Diversity Reduces Demographic Sensitivity to Climate for a Keystone Herbivore

Although most studies of trophic mismatch focus on relatively specialized consumers exploiting a small resource community, ecological communities are often complex and even specialized consumers are often capable of consuming a wide diversity of species (Shipley, Forbey & Moore 2009). In diverse trophic networks, explicitly quantifying phenological asynchrony between consumers and resources is challenging (see discussion in preceding sections). Nevertheless, if climate effects are strongly channeled through indirect trophic pathways, ecological theory suggests that the demographic effects of climate (which implicitly account for trophic mismatches) are likely to differ across habitats, and additionally, that consumers inhabiting diverse resource communities should experience weaker demographic responses to climate. We test these hypotheses in chapter 3 by examining the demographic and developmental sensitivity of goslings to annual climate across a habitat and resource diversity gradient.

Chapter 4 – Climate Change Improves the Suitability of Novel Habitats for a Keystone Herbivore

Given that demographic responses to climate differ between habitats, in chapter 4 we broaden our investigation to quantify the consequences of observed climate change for lesser snow goose population dynamics. We use long-term demographic data from two habitats (traditional coastal salt marsh habitats and recently colonized inland freshwater marsh areas) to develop a spatially explicit stochastic population model, and quantify population growth under projected climate change. We find that climate change increases population growth in all habitats, but that such increases are disproportionately large in novel inland sedge meadow habitats. Our results suggest that in a warmer and more variable climate, the breeding range and population growth of lesser snow geese is likely to increase, counteracting current management efforts to reduce overabundant populations.

Chapter 5 – Conclusions

In chapter 5, I summarize the major conclusions from each chapter and suggest potentially fruitful areas of further research.

References

Abrams, P.A. & Ginzburg, L.R. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution,* **15,** 337-341.

Alexander, J.M., Diez, J.M., Hart, S.P. & Levine, J.M. (2016) When climate reshuffles competitors: a call for experimental macroecology. *Trends in Ecology & Evolution,* **31,** 831-841.

Alexander, J.M., Diez, J.M. & Levine, J.M. (2015) Novel competitors shape species/'responses to climate change. *Nature,* **525,** 515-518.

Aubry, L.M., Rockwell, R.F., Cooch, E.G., Brook, R.W., Mulder, C.P. & Koons, D.N. (2013) Climate change, phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. *Global Change Biology,* **19,** 149-160.

Barraquand, F. & Yoccoz, N.G. (2013) When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. *Theoretical Population Biology,* **89,** 1-11.

Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B. & Visser, M.E. (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology,* **78,** 73-83.

Boyce, M.S., Haridas, C.V. & Lee, C.T. (2006) Demography in an increasingly variable world. *Trends in Ecology & Evolution,* **21,** 141-148.

CaraDonna, P.J., Iler, A.M. & Inouye, D.W. (2014) Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences,* **111,** 4916-4921.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E. & Sheldon, B.C. (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science,* **320,** 800-803.

Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution,* **15,** 70-76.

Cottingham, K., Brown, B. & Lennon, J. (2001) Biodiversity may regulate the temporal variability of ecological systems. *Ecology Letters,* **4,** 72-85.

Cushing, D. (1974) The possible density-dependence of larval mortality and adult mortality in fishes. *The Early Life History of Fish*, pp. 103-111. Springer.

Cushing, D. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology,* **26,** 249-293.

Dickey, M.-H., Gauthier, G. & Cadieux, M.-C. (2008) Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology,* **14,** 1973-1985.

Doak, D.F., Bigger, D., Harding, E., Marvier, M., O'malley, R. & Thomson, D. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist,* **151,** 264-276.

Doak, D.F., Morris, W.F., Pfister, C., Kendall, B.E. & Bruna, E.M. (2005) Correctly estimating how environmental stochasticity influences fitness and population growth. *The American Naturalist,* **166,** E14-E21.

Doiron, M., Gauthier, G. & Lévesque, E. (2014) Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. *Journal of Ecology,* **102,** 508-517.

Doiron, M., Gauthier, G. & Lévesque, E. (2015) Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology,* **21,** 4364-4376.

Doiron, M., Legagneux, P., Gauthier, G. & Lévesque, E. (2013) Broad-scale satellite Normalized Difference Vegetation Index data predict plant biomass and peak date of nitrogen concentration in Arctic tundra vegetation. *Applied Vegetation Science,* **16,** 343-351.

Durant, J.M., Hjermann, D.Ø., Anker-Nilssen, T., Beaugrand, G., Mysterud, A., Pettorelli, N. & Stenseth, N.C. (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters,* **8,** 952-958.

Edwards, M. & Richardson, A.J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature,* **430,** 881-884.

Ehrlén, J. & Morris, W.F. (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters,* **18,** 303-314.

Ehrlén, J., Morris, W.F., Euler, T. & Dahlgren, J.P. (2016) Advancing environmentally explicit structured population models of plants. *Journal of Ecology,* **104,** 292-305.

Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E. & Bernasconi, G. (2007) Time after time: flowering phenology and biotic interactions. *Trends in Ecology & Evolution,* **22,** 432-439.

Forrest, J. & Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 3101-3112.

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C. & Wanless, S. (2006) From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology,* **75,** 1259-1268.

Gadallah, F. & Jefferies, R. (1995) Comparison of the nutrient contents of the principal forage plants utilized by lesser snow geese on summer breeding grounds. *Journal of Applied Ecology***,** 263-275.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution,* **25,** 325-331.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J. & Tilman, D. (2011) Plant diversity and the stability of foodwebs. *Ecology Letters,* **14,** 42-46.

Hooper, D., Chapin III, F., Ewel, J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J., Lodge, D., Loreau, M. & Naeem, S. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs,* **75,** 3-35.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics,* **13,** 201-228.

IPCC (2012) *Managing the risks of extreme events and disasters to advance climate change adaptation: special report of the intergovernmental panel on climate* *change*. Cambridge University Press, Cambridge, UK.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D. & van Ruijven, J. (2011) High plant diversity is needed to maintain ecosystem services. *Nature,* **477,** 199-202.

Ives, A., Gross, K. & Klug, J. (1999) Stability and variability in competitive communities. *Science,* **286,** 542-544.

Kerby, J. & Post, E. (2013) Capital and income breeding traits differentiate trophic match–mismatch dynamics in large herbivores. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **368**.

Kerby, J.T., Wilmers, C.C. & Post, E. (2012) Climate change, phenology, and the nature of consumer–resource interactions: advancing the match/mismatch hypothesis. *Trait-mediated indirect interactions: ecological and evolutionary perspectives*, pp. 508-525. Cambridge University Press Cambridge, UK.

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

Leggett, W. & Deblois, E. (1994) Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research,* **32,** 119-134.

MacArthur, R. (1955) Fluctuations of animal populations and a measure of community stability. *Ecology,* **36,** 533-536.

McCann, K.S. (2000) The diversity–stability debate. *Nature,* **405,** 228-233.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007) Global warming and the disruption of plant–pollinator interactions. *Ecology Letters,* **10,** 710-717.

Miller-Rushing, A.J., Høye, T.T., Inouye, D.W. & Post, E. (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 3177-3186.

Mulder, C., Uliassi, D. & Doak, D. (2001) Physical stress and diversity-productivity relationships: the role of positive interactions. *Proceedings of the National Academy of Sciences,* **98,** 6704-6708.

Mulder, C.P., Iles, D.T. & Rockwell, R.F. (2016) Increased variance in temperature and lag effects alter phenological responses to rapid warming in a subarctic plant community. *Global Change Biology,* **23,** 801–814.

Musolin, D.L., Tougou, D. & Fujisaki, K. (2010) Too hot to handle? Phenological and life-history responses to simulated climate change of the southern green stink bug Nezara viridula (Heteroptera: Pentatomidae). *Global Change Biology,* **16,** 73-87.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637-669.

Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology,* **13,** 1860-1872.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* **421,** 37-42.

Petchey, O.L. (2000) Prey diversity, prey composition, and predator population dynamics in experimental microcosms. *Journal of Animal Ecology,* **69,** 874-882.

Philippart, C.J., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadée, G.C. & Dekker, R. (2003) Climate-related changes in recruitment of the bivalve Macoma balthica.

Limnology and Oceanography, **48,** 2171-2185.

Post, E. (2013) *Ecology of climate change: the importance of biotic interactions*. Princeton University Press.

Post, E. & Forchhammer, M.C. (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **363,** 2367-2373.

Post, E. & Klein, D.R. (1999) Caribou calf production and seasonal range quality during a population decline. *The Journal of Wildlife Management*, **63**, 335-345.

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

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

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature,* **421,** 57-60.

Scharf, F.S., Juanes, F. & Rountree, R.A. (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series,* **208,** 229-248.

Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia,* **113,** 447-455.

Shipley, L.A., Forbey, J.S. & Moore, B.D. (2009) Revisiting the dietary niche: when is a mammalian herbivore a specialist? *Integrative and Comparative Biology*, **49**, 274-290.

Sparks, T., Bairlein, F., Bojarinova, J., Hüppop, O., Lehikoinen, E., Rainio, K., Sokolov, L. & Walker, D. (2005) Examining the total arrival distribution of migratory birds. *Global Change Biology,* **11,** 22-30.

Stocker, T., Qin, D., Plattner, G., Tignor, M., Allen, S., Boschung, J., Nauels, A., Xia, Y., Bex, B. & Midgley, B. (2013) Climate Change 2013: The Physical Science Basis. Working Group I Contribution ot the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Strode, P.K. (2015) Phenological Asynchrony between Migrant Songbirds and Food Resources during Early Springs. Phenological Synchrony and Bird Migration: Changing Climate and Seasonal Resources in North America (eds Wood E M. & J.L. Kellermann), pp. 97–116. CRC Press.

Svenning, J.C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., Schiffers, K.H., Dullinger, S., Edwards, T.C. & Hickler, T. (2014) The influence of interspecific interactions on species range expansion rates. *Ecography,* **37,** 1198-1209.

Tebaldi, C., Hayhoe, K., Arblaster, J.M. & Meehl, G.A. (2006) Going to the extremes. *Climatic Change,* **79,** 185-211.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W. & Carvalho, L. (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology,* **16,** 3304-3313.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters,* **11,** 1351-1363.

Van der Putten, W.H., Macel, M. & Visser, M.E. (2010) Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 2025-2034.

Visser, M., Van Noordwijk, A., Tinbergen, J. & Lessells, C. (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences,* **265,** 1867-1870.

Visser, M.E. & Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences,* **272,** 2561-2569.

Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics,* **15,** 393-425.

Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment,* **5,** 475-482.

Willson, M.F. & Traveset, A. (2000) The ecology of seed dispersal. Seeds: the ecology of regeneration in plant communities (ed. M. Fenner), pp. 85-110. CABI Publishing, New York.

Winiarski, K.J., McWilliams, S.R. & Rockwell, R.F. (2012) Rapid environmental degradation in a subarctic ecosystem influences resource use of a keystone avian herbivore. *Journal of Animal Ecology,* **81,** 1132–1142.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A. & Guisan, A. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews,* **88,** 15-30.

Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences,* **96,** 1463-1468.

Yang, L.H. & Rudolf, V. (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters,* **13,** 1-10.

Figures

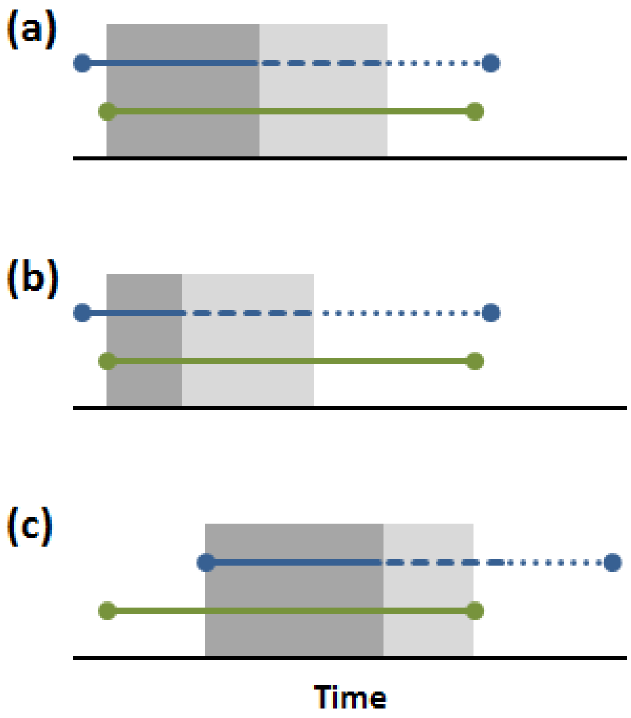

Fig. 1.1. The effect of changes in the rate and timing of ontogeny on interactions between two species (blue and green). (a) The strength of interactions between species (different shading) depends on the developmental stage (line type) of the blue species. (b) Developmental rate of the solid stage has increased while developmental rate of the dotted stage has slowed. (c) Developmental rates are the same as in A, but the timing of events relative to the green species has shifted.

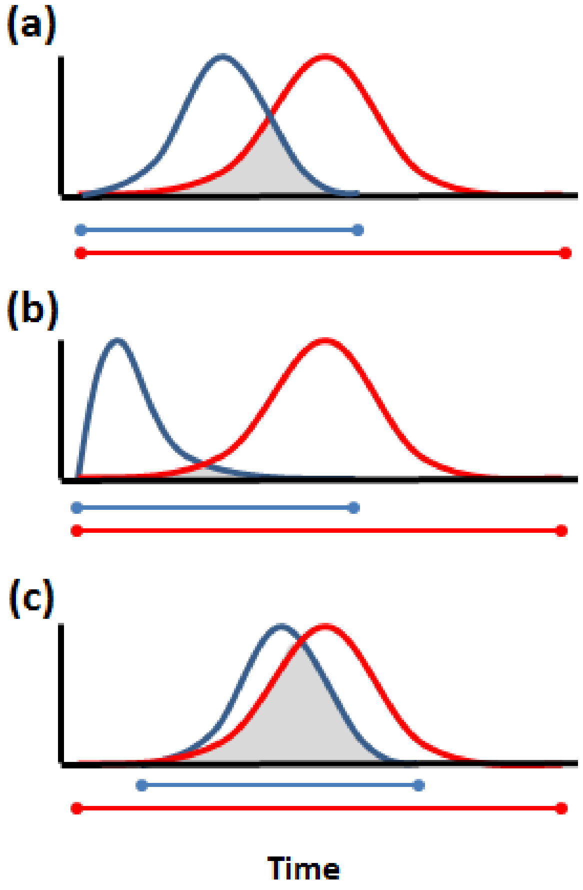

Fig. 1.2. The effect of changes in population-level phenological distributions on interactions between two species (blue and red). (a) Baseline interaction. (b) A change in the shape of the blue species temporal distribution affects degree of overlap. (c) A shift in the position of the entire distribution relative to other species affects the degree of overlap.

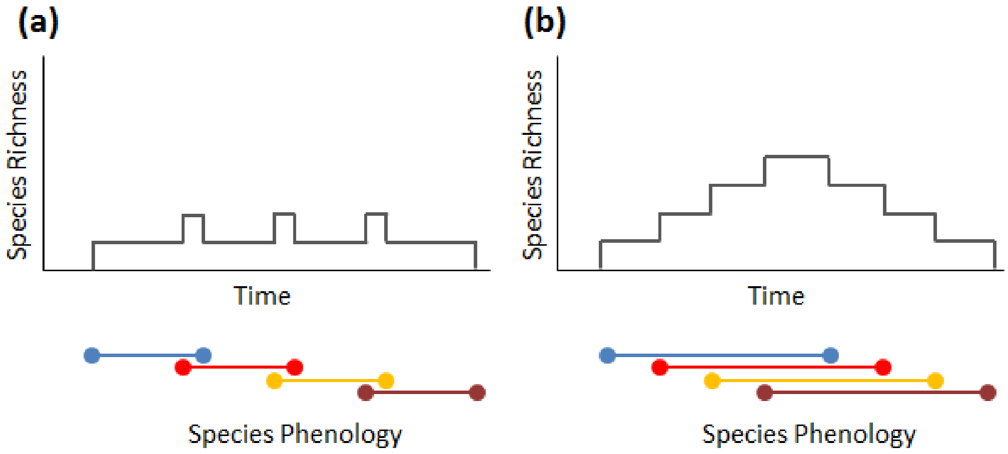

Fig. 1.3. Temporal patterns in species richness are influenced by changes in species phenology.

CHAPTER 2

FITNESS CONSEQUENCES OF JOINT VITAL RATE RESPONSES TO ENVIRONMENTAL VARIABILITY ACROSS LIFE HISTORIES

Introduction

Recent climate change has altered the frequency of extreme weather events and further changes to environmental variability are predicted (IPCC 2012; Karl et al. 1995; Stocker et al. 2013; Tebaldi et al. 2006). Increased environmental variability may affect species demography directly (e.g., extreme weather events affecting the birth and death rates of individuals; Dalgleish et al. 2010; Frederiksen et al. 2008) or indirectly (e.g., by affecting phenological associations between interacting species; Miller-Rushing et al. 2010). Predicting the demographic and evolutionary consequences of environmental variability represents an important challenge, and has a rich tradition of theoretical and empirical study (Boyce et al. 2006; Koons et al. 2008; Lewontin and Cohen 1969; Sæther and Engen 2015; Tuljapurkar 1990). Over the short-term, a careful consideration of the effect of environmental variability on population growth is necessary for guiding species conservation actions. At longer timescales, a clear understanding of the effects of environmental variability on population growth can illuminate the drivers of life history evolution (Tuljapurkar 1990).

In a time-varying environment, the effects of increased environmental variability on the stochastic population growth rate (λs; equivalent to mean fitness for a group of individuals sharing a particular allele, phenotype, or life history strategy; Benton and Grant 1996; Lewontin and Cohen 1969) ultimately depend on processes operating at two levels: 1) the relationships between the environment and vital rates, and 2) the relationships between vital rates and population growth rate (Boyce et al. 2006). In the following paragraphs, we discuss each in turn.

The shape of the relationship between the environment and a vital rate (henceforth the vital rate 'reaction norm') determines the effect of increased environmental variability on the vital rate distribution (fig. 2.1; also see Koons et al. 2009; Lawson et al. 2015). For example, if a vital rate is linearly related to an environmental driver, increased environmental variability only alters the vital rate variance. However, if the vital rate responds nonlinearly to an environmental driver, increased environmental variability can affect the mean, variance, and other statistical moments of the vital rate distribution simultaneously via Jensen's inequality (Koons et al. 2009; Ruel and Ayres 1999). If the vital rate reaction norm is concave (accelerating downwards), unfavorable environmental conditions tend to decrease a vital rate more than favorable conditions increase it and increased environmental variance will tend to reduce the mean of the vital rate distribution. A convex reaction (accelerating upwards) can induce an opposite response, and increased environmental variability can increase the mean of a vital rate distribution. In reality, reaction norms often contain concave and convex portions; common examples include sigmoid functions for survival or saturating reproduction responses (e.g., see examples in Barraquand et al. 2014; Barraquand and Yoccoz 2013; Jonzén et al. 2010; Van de Pol et al. 2010). In this case, the local curvature of the reaction norm about the mean environment determines the effect of increased environmental variance on the vital rate distribution (fig. 2.1; Koons et al. 2009).

Layered on top of this process, the stochastic population growth rate is a function of the distribution of vital rates as well as the correlation structure amongst them; together, the *joint* distribution of vital rates (Caswell 2001; Tuljapurkar 1990). If multiple vital rates respond to a common environmental driver, increased environmental variability impacts the marginal distributions of each affected vital rate as discussed above, as well as patterns of covariation among them (Boyce et al. 2006; Doak et al. 2005). Importantly, shifts in vital rate covariation impede the ability to "sum up" the independent fitness effects of shifts in the marginal vital rate distributions (Barraquand and Yoccoz 2013; Lawson et al. 2015). Yet, shared environmental drivers across life cycle stages are ubiquitous. For example, survival and reproduction in Eurasian oystercatchers are both nonlinear functions (in opposite directions) of winter temperature (Van de Pol et al. 2010), red kangaroo survival and reproduction are nonlinear functions of annual rainfall (Jonzén et al. 2010), and emperor penguin survival and reproduction are both related nonlinearly to Antarctic sea ice concentration (Jenouvrier et al. 2012). The role of the environment in establishing vital rate covariation is well studied in natural populations (e.g., Compagnoni et al. 2016; Coulson et al. 2005; Coulson et al. 2004; Davison et al. 2013; Doak et al. 1994; Ramula and Lehtilä 2005; Rotella et al. 2012), and ongoing, pervasive changes in vital rate covariation structures are therefore expected in variable and non-stationary environments (Boyce et al. 2006; Gotelli and Ellison 2006; Jenouvrier 2013).

Theory to explain the evolution of life histories in variable environments now encompasses the effects of nonlinear vital rate reaction norms. Demographic "buffering" is a predicted evolutionary outcome when selection favors a less responsive reaction norm in a variable environment, resulting in lower temporal variance in affected vital rates (Gillespie 1977; Koons et al. 2009; Pfister 1998). Conversely, selection that results in a more responsive reaction norm, and thus higher vital rate variance, has been termed demographic “lability”. Koons et al. (2009) identified the conditions under which environmental variation acting independently on vital rate reaction norms leads to selection for demographic lability or buffering. However, the effects of vital rate covariation on these selection pressures, generated when multiple vital rates share a common environmental driver, has not been thoroughly explored. Recently, Barraquand and Yoccoz (2013) demonstrated that vital rate covariance can reverse evolutionary predictions based on independent vital rate responses, but the generality of this result across life histories is unclear.

Here, we quantify the general importance of joint vital rate responses to environmental drivers across a diverse suite of simulated life histories. For each life history, we construct a series of stochastic population projections to determine the conditions under which selection favors demographic buffering (weaker vital rate responses to the environment; e.g., fig. 2.1A red line) or demographic lability (stronger vital rate responses to the environment; e.g., fig. 2.1B blue line), and the degree to which these pressures change when multiple vital rates share a common environmental driver. By identifying the life histories for which selection pressures are most sensitive to environmentally-driven vital rate covariation, we provide a richer understanding of both life history evolution and the capacity of species to cope with ongoing changes to contemporary environments.

Methods

Life History Simulations

We began by generating a diverse suite of life histories across which to explore the fitness impacts of joint vital-rate responses to variability in shared environmental drivers. Following Neubert and Caswell (2000), we used a flexible stage-structured matrix model that discriminates between non-reproductive juveniles and reproductive adults, and for which vital rates can vary through time:

$$\mathbf{A}(t) = \begin{bmatrix} S_J(t)(1-p) & F(t) \\ S_J(t)p & S_A(t) \end{bmatrix}, \tag{1}$$

where $S_J(t)$ denotes time-specific juvenile survival, $S_A(t)$ time-specific adult survival, $F(t)$ time-specific fertility (i.e., the contribution of adults to the juvenile stage class), and p represents maturation probability of juveniles (for simplicity, this parameter is time-invariant in our analyses). We allowed mean values of S_J and S_A (hereafter denoted by $\overline{S_J}$ and $\overline{S_A}$) to range from 0.1 to 0.9 while solving for $\bar{F}$ to yield replacement level fitness in a constant environment ($\lambda_1 = 1$). We considered both life histories with extremely delayed maturity ($p = 0.1$) and rapid maturity ($p = 1$). Our simulated life history landscape therefore accommodates a remarkably wide range of life histories, including those approaching semelparity ($\overline{S_A} \to 0$) and a high degree of iteroparity ($\overline{S_A} \to 1$), delayed and rapid maturity (see above), and ranging from those considered to have "slow" life histories (e.g., high $\overline{S_A}$, high $\overline{S_J}$, low $\bar{F}$, and low p) to those with extremely "fast" life histories (e.g., low $\overline{S_A}$, low $\overline{S_J}$, high $\bar{F}$, and high p).

Linking Vital Rates to Shared Environmental Drivers

Following Koons et al. (2009), we linked the vital rates S_A, S_J, and F to time-varying Gaussian environmental drivers, $x{\sim}Normal(0, 1)$, through nonlinear reaction norms using the logistic formula:

$$Y(t) = \frac{a}{1+be^{-\beta x(t)}}\,, \tag{2}$$

where $Y(t)$ is the value of the vital rate at time step t. Because survival probabilities are bounded by 0 and 1, the parameter a that controls the vital rate maximum was fixed at 1 for survival probabilities. For F, we conducted simulations where a = $1.5\bar{F}$, $2.5\bar{F}$, or $3.5\bar{F}$, representing situations in which F was close, intermediate, or far from its maximum value in average environmental conditions. The constant b was chosen such that $Y(t) = \bar{Y}$ when $x = 0$ (i.e., in average environmental conditions; calculated as $b = a/\bar{Y} - 1$). The parameter β describes the strength and direction of the relationship between the vital rate and the environmental driver. Environmental drivers are therefore linearly related to vital rates through a logit link function which produces nonlinear reaction norms on the real parameter scale.

Measuring Selection on Vital Rate Reaction Norms

Elasticities measure the change in logλ_S, and therefore the change in fitness, caused by a proportional change in a parameter of interest (Tuljapurkar et al. 2003). They have become popular tools for understanding the functional relationships between vital rates and population growth in both theoretical and applied contexts (Gaillard and Yoccoz 2003; Mills et al. 1999; Pfister 1998; Sæther and Bakke 2000; Silvertown et al. 1996).

Here, we quantify selection on vital rate reaction norms by measuring the change in logλ_S arising from a proportional change in the β parameter for each of the k vital rates that are linked to environmental drivers, which can be represented as:

$$E_{\beta_k} = \frac{\partial \log \lambda_S}{\partial \log \beta_k}. \tag{3}$$

Elasticities can be evaluated numerically by changing β_k by a small amount (denoted as $\Delta\beta_k$), and measuring the resulting change in long-term fitness (denoted as $\Delta\lambda_S$), using:

$$\frac{\partial\, log\, \lambda_S}{\partial\, log\, \beta_k} = \left(\frac{\Delta\lambda_S}{\lambda_S}\right)\left(\frac{\beta_k}{\Delta\beta_k}\right). \tag{4}$$

Positive values of E_{β_k} indicate that an increase in β_k increases fitness, while negative values indicate that an increase in β_k reduces fitness. Selection therefore favors a stronger vital rate response to an environmental driver if E_{β_k} and β_k are of the same sign. For example, if a vital rate responds positively to an environmental driver (β_k>0) and E_{β_k} is positive, this indicates that a stronger, more positive slope of the reaction norm will increase fitness. We calculated elasticities numerically using equation 4 by increasing β_k by 10% for each vital rate independently. We note that a smaller proportional perturbation of 5% produced similar results.

To explore the fitness consequences of environmental variation, we first linked the vital rates S_A, S_J, and F to independent Gaussian environmental drivers using equation 2 and quantified selection on vital rate reaction norms by measuring E_{β_k} for each vital rate. We then evaluated the degree to which selection pressures change when multiple vital rates share an environmental driver. As an initial investigation of these selection pressures, we focused our analysis on pairs of vital rates sharing an environmental driver (S_J and S_A, S_J and F, and S_A and F), but acknowledge that more complex multivariate responses are possible in nature. In each "joint response" scenario, the two vital rates were linked to the same Gaussian environmental driver through equation 2 while the third vital rate was linked to an independent Gaussian driver. A change in sign of E_{β_k} in shared *versus* unshared environmental scenarios indicates that vital rate covariation generated by shared environmental drivers can qualitatively alter demographic selection pressures and switch selection from buffering to lability or *vice versa*. To ensure our analysis captured the fitness effects of both positive and negative vital rate covariation, we conducted one set of simulations where vital rates responded to a common environmental driver in the same direction (e.g., $\beta_{S_J} = 1$ and $\beta_{S_A} = 1$) and a second set of simulations where vital rates responded in opposite directions (e.g., $\beta_{S_J} = 1$ and $\beta_{S_A} = -1$).

Results

We initially focus our presentation on results for simulations where fertility was far from its possible maximum (a=3.5) to facilitate comparison with results in Barraquand and Yoccoz (2013) and since recruitment is often well below its theoretical maximum in natural systems. We then compare these results to simulations where mean fertility is intermediate relative to its theoretical maximum (a = 2.5), or near its maximum (a = 1.5). We also focus on simulations where maturation probability is high (p=1) to facilitate comparison with models considered by Koons et al. (2009). However, we note that delayed maturity (p=0.1) influenced patterns in selective pressures across life histories, and we present these expanded results in Appendix A.

Selection on Vital Rate Reaction Norms

When vital rates responded to independent environmental drivers, selection tended to favor stronger, more labile vital rate responses to the environment when reaction norms were highly convex (i.e., far from their maximum; blue shading in fig. 2.2). Conversely, selection favored weaker, more buffered vital rate responses when reaction norms were highly concave (i.e., close to their maximum; red shading in fig. 2.2). Demographic selection pressures were weakest when vital rate reaction norms were weakly convex (darker shading in fig. 2.2). When mean fertility was far from its maximum (all life histories presented in fig. 2.2), selection favored more labile reaction norms for fertility for most life histories, except for those with extremely low adult survival. Selection on reaction norms was qualitatively similar for life histories with slow (p=0.1) and rapid maturity (p=1, pictured in fig. 2.2).

Vital rate covariation, driven by joint responses of vital rates to a shared environmental driver, was capable of reversing the direction of selection on vital rate reaction norms (solid and dotted white outlines in fig. 2.2). Negative covariation, generated when vital rates respond in opposite directions to a shared driver, favored selection for stronger vital rate responses to the environment and was capable of switching selection from buffering to lability (fig. 2.2, solid white outlines). Conversely, positive covariation favored selection for weaker vital rate responses and was capable of switching selection from lability to buffering (fig. 2.2, dotted white outlines).

Notably, vital rate covariation was only capable of fundamentally reversing selection pressures when baseline selection pressures in the absence of joint responses were weak (white boundaries tend to overlap life histories with relatively dark shading in fig. 2.2). As a result, the effects of covariation were most pronounced for life histories with weakly convex reaction norms. When reaction norms were highly nonlinear, thereby producing strong selection for either demographic buffering or lability, vital rate covariation was generally insufficient to overwhelm these selection pressures and reverse the direction of selection (white boundaries do not overlap bright hues in fig. 2.2). However, we note that covariation between F and other vital rates was capable of switching the direction of selection on the reaction norm for F across a wide range of life histories, even when the reaction norm for F was highly convex (fig. 2.2, rightmost column).

When mean fertility was intermediate relative to its maximum (a = 2.5), selection tended to favor weaker responses of fertility to the environment (red shading in bottom row of fig. 2.3). However, negative vital rate covariation was capable of reversing this selection pressure for a wide range of life histories (solid white outline). When mean fertility was close to its maximum (a = 1.5), the reaction norm for fertility was highly convex and weaker responses of fertility to the environment were strongly favored across all life histories (ubiquitous red shading in bottom row of fig. 2.4). Because these selection pressures were relatively strong, vital rate covariation did not alter the direction of evolutionary pressures on fertility reaction norms.

Discussion

Vital rate covariation, caused by the simultaneous responses of vital rates to a common environmental driver, can fundamentally alter overall population growth trajectories and amplify, dampen, or even reverse directions of demographic selection pressures (Doak et al. 2005; Tuljapurkar 1990). Recently, Barraquand and Yoccoz (2013) demonstrated that positive vital rate covariation generated by joint vital rate responses to a common environmental driver can reverse the positive effects of environmental variability. Here, we have explored the generality of this phenomenon across multiple pairwise vital rate linkages, when vital rates respond in either the same or opposite directions to environmental drivers, and across a wide spectrum of life histories, ranging from those with ‘slow’ to ‘fast’ life history tempos, semelparous to iteroparous reproductive schedules, and delayed to rapid maturity. Consistent with Barraquand and Yoccoz (2013), we found that positive vital rate covariation can counteract the positive fitness effects of environmental variation in a single vital rate. However, we also found that negative covariation generated when vital rates respond in the opposite direction to environmental drivers can reverse the negative effects of environmental variation for a wide range of life histories, particularly when channeled through reaction norms for fertility (fig. 2.2).

Our results reconfirm previous studies and theory that have shown convex reaction norms promote demographic lability, while concave reaction norms promote demographic buffering (Drake 2005; Koons et al. 2009; Morris et al. 2008). However, as an important step beyond previous investigations, we show that vital rate covariation adds an additional dimension to these selection pressures. Negative vital rate covariation promotes demographic lability, while positive covariation promotes buffering, altering the range of life histories over which the evolution of buffered and labile vital rates are a predicted evolutionary outcome. To emphasize the importance of vital rate covariation on selection, we only illustrated the most extreme cases where the direction of selection was reversed entirely (white outlines in figs. 2.2, 2.3, and 2.4).

Notably, we found that vital rate covariation could reverse selection pressures for a wide range of life histories, including those with low to high juvenile survival, adult survival, and fertility. However, for these life histories, vital rate covariation was generally only capable of overwhelming and reversing selection pressures when the marginal effect of selection on a vital rate reaction norm (i.e., in the absence of joint responses) was relatively weak. Yet, for a much wider range of life histories, joint vital rate responses and covariation will amplify or dampen selection pressures without completely reversing their direction, affecting rates of evolution and the overall sensitivity of populations to variable and changing environments.

Commonly, physical and physiological processes constrain vital rates to respond in the same direction to environmental stimuli. This should generate positive vital rate covariation that reduces overall fitness, selects for weaker vital rate responses to the environment, and promotes demographic buffering. Indeed, empirical evidence suggests that demographic buffering is a common evolutionary outcome (Morris and Doak 2004; Morris et al. 2008; Pfister 1998). Our results suggest that positive covariation between vital rates caused by joint responses to environmental drivers may help explain the apparent pervasiveness of demographic buffering in natural populations.

Opposite vital rate responses to environmental drivers have occasionally been documented in demographic studies (e.g., Van de Pol et al. 2010), and evolutionary trade-offs, by definition, will produce such patterns at the individual level (Van Noordwijk and de Jong 1986). Opposite responses to a shared environmental driver will generate negative vital rate covariation, which should promote demographic lability. The common eider (*Somateria mollissima*) is a long-lived sea duck with highly variable “boom-bust” reproduction that may provide an interesting example of demographic lability driven by opposing vital rate responses to environmental drivers. Population-wide nest failure is common, interrupted by occasional years of high nest success (Iles et al. 2013). However, early nest failure is predicted to save female eiders from severe declines in body condition over the course of incubation (Bottitta et al. 2003; Criscuolo et al. 2002) and reduce exposure to predators, with associated potential improvements in annual survival of failed nesters (Erikstad et al. 1998), but see Bottitta et al. (2003). The “boom-bust” pattern in eider recruitment may therefore be an adaptive life history strategy, driven by negative covariation between adult survival and nest success. A detailed test of this hypothesis would require experimental manipulation of nest success and timing of nest failure, as individual heterogeneity in female quality (i.e., a positive correlation between female body condition and reproductive performance at the population level; Yoccoz et al. 2002) may obscure environmentally-driven tradeoffs that emerge at the individual level and are responsible for the evolution of this strategy (Metcalf 2016; Van Noordwijk and de Jong 1986).

Because vital rate covariation may fundamentally alter the fitness consequences of increased environmental variation, our study illustrates the importance of explicitly linking vital rates to environmental drivers to accurately forecast shifts in joint vital rate distributions. Further, our study emphasizes that “environment-blind” approaches to forecasting are likely to be inadequate in many cases (see Jenouvrier 2013; Lawson et al.

2015 and references therein for further discussion of this point). Vital rate elasticity analysis has become a popular tool for prospectively evaluating the fitness consequences of independent changes in the mean and/or variance of vital rates (Caswell 2001; Haridas and Tuljapurkar 2005). Importantly, vital rate elasticity analysis can be considered “environment-blind”, a point that is perhaps generally underappreciated. Joint nonlinear responses of vital rates to environmental drivers guarantee that vital rate means and (co)variances will shift simultaneously in response to environmental change, limiting the appeal of assessing independent changes in the mean or (co)variance of individual vital rates. Further, stochastic vital rate elasticities are strongly affected by vital rate covariation (Doak et al. 2005), which is likely to shift in response to changing environments. Often it will be more useful to evaluate the elasticity of population growth to changes in environmental drivers themselves, thereby implicitly accounting for nonlinear shifts in vital rate distributions and covariance structure (see examples in Gotelli and Ellison 2006; Jonzén et al. 2010).

Recent advances in data-driven statistics hold promise for accurately characterizing the strength and shape of joint vital rate responses to environmental drivers, a necessary task for accurately characterizing fitness in variable or nonstationary environments. Functional linear models, or splines, are a promising method for estimating the effects of covariates that occur over continuous domains, such as precipitation that can affect demography over a range of time horizons (Teller et al. 2016). Alternatively, the least absolute shrinkage and selection operator (LASSO) can handle a high number of covariates and ensures that covariates with little effect have regression coefficients close to zero (Tibshirani 1996). Both methods obviate the need to narrow the number of putative environmental drivers *a priori* (Teller et al. 2016). Alternatively, newly developed data-driven methods that help visualize the most important drivers of vital rates and population processes can greatly reduce the chances of failing to include important environmental covariates (Mesquita et al. 2015; Van de Pol et al. 2016). Such methods, when applied to multiple vital rates simultaneously, are likely to preserve and forecast emergent relationships in joint vital rate distributions more faithfully than other commonly applied techniques, such as model selection based on a small subset of candidate effects that may omit important drivers of vital rate (co)variation.

The modern world is characterized by increasingly variable environments (IPCC 2012; Karl et al. 1995; Stocker et al. 2013; Tebaldi et al. 2006), and complex joint responses of vital rates to environmental drivers are ubiquitous. Survival rates are inherently nonlinear, but additionally, environmental optima, saturating responses, interactions with other drivers, and density-dependent effects can produce nonlinear reaction norms. Even apparently linear responses measured over historical ranges of environmental variation may exhibit nonlinearity if environmental changes are sudden or drastic (Adler et al. 2013; Wolkovich et al. 2014). Pervasive and nonlinear shifts in vital rates and their covariation structures are therefore to be expected. Forecasting the responses of the world's biota in light of these changes represents a major challenge (Jenouvrier 2013; Lawson et al. 2015; Wolkovich et al. 2014). We have taken a step toward this goal by examining the consequences of joint nonlinear responses of vital rates to environmental variability across a diverse array of life histories. We have shown that covariation caused by joint vital rate responses can strongly impact the direction and rate of evolution, long-term population trends, and ultimately the ability of species to cope with changing environments. Joint vital rate responses therefore warrant careful consideration and incorporation into population viability analyses and analogues. Continued research that seeks to uncover generalities across species in their responses to environmental change, along with improved methods for linking environmental drivers to multiple demographic rates, will be of great importance for guiding conservation.

Literature Cited

Adler, P. B., K. M. Byrne, and J. Leiker. 2013. Can the past predict the future? Experimental tests of historically based population models. Global Change Biology 19:1793-1803.

Barraquand, F., T. T. Høye, J. A. Henden, N. G. Yoccoz, O. Gilg, N. M. Schmidt, B. Sittler et al. 2014. Demographic responses of a site-faithful and territorial predator to its fluctuating prey: long-tailed skuas and arctic lemmings. Journal of Animal Ecology 83:375-387.

Barraquand, F., and N. G. Yoccoz. 2013. When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. Theoretical Population Biology 89:1-11.

Benton, T., and A. Grant. 1996. How to keep fit in the real world: elasticity analyses and selection pressures on life histories in a variable environment. American Naturalist:115-139.

Bottitta, G. E., E. Nol, and H. G. Gilchrist. 2003. Effects of experimental manipulation of incubation length on behavior and body mass of common eiders in the Canadian

Arctic. Waterbirds 26:100-107.

Boyce, M. S., C. V. Haridas, and C. T. Lee. 2006. Demography in an increasingly variable world. Trends in Ecology & Evolution 21:141-148.

Caswell, H. 2001, Matrix population models: construction, analysis and interpretation. Sunderland, Massechusetts, Sinauer Associates Inc.

Compagnoni, A., A. J. Bibian, B. M. Ochocki, H. S. Rogers, E. L. Schultz, M. E. Sneck, B. D. Elderd et al. 2016. The effect of demographic correlations on the stochastic population dynamics of perennial plants. Ecological monographs.

Coulson, T., J.-M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology 74:789-801.

Coulson, T., F. Guinness, J. Pemberton, and T. Clutton-Brock. 2004. The demographic consequences of releasing a population of red deer from culling. Ecology 85:411-422.

Criscuolo, F., G. W. Gabrielsen, J. P. Gendner, and Y. Le Maho. 2002. Body mass regulation during incubation in female common eiders Somateria mollissima. Journal of Avian Biology 33:83-88.

Dalgleish, H. J., D. N. Koons, and P. B. Adler. 2010. Can life-history traits predict the response of forb populations to changes in climate variability? Journal of Ecology 98:209-217.

Davison, R., F. Nicolè, H. Jacquemyn, and S. Tuljapurkar. 2013. Contributions of covariance: Decomposing the components of stochastic population growth in *Cypripedium calceolus*. The American Naturalist 181.

Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. Ecological Applications 4:446-460.

Doak, D. F., W. F. Morris, C. Pfister, B. E. Kendall, and E. M. Bruna. 2005. Correctly estimating how environmental stochasticity influences fitness and population growth. The American Naturalist 166:E14-E21.

Drake, J. M. 2005. Population effects of increased climate variation. Proceedings of the Royal Society B: Biological Sciences 272:1823-1827.

Erikstad, K. E., P. Fauchald, T. Tveraa, and H. Steen. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology 79:1781-1788.

Frederiksen, M., F. Daunt, M. P. Harris, and S. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. Journal of Animal Ecology 77:1020-1029.

Gaillard, J.-M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84:3294-3306.

Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. The American Naturalist 111:1010-1014.

Gotelli, N. J., and A. M. Ellison. 2006. Forecasting extinction risk with nonstationary matrix models. Ecological Applications 16:51-61.

Haridas, C., and S. Tuljapurkar. 2005. Elasticities in variable environments: properties and implications. The American Naturalist 166:481-495.

Iles, D. T., R. F. Rockwell, P. Matulonis, G. J. Robertson, K. F. Abraham, J. C. Davies, and D. Koons. 2013. Predators, alternative prey and climate influence annual breeding success of a long-lived sea duck. Journal of Animal Ecology 82:683-693.

IPCC. 2012, Managing the risks of extreme events and disasters to advance climate change adaptation: special report of the intergovernmental panel on climate change. Cambridge, UK, Cambridge University Press.

Jenouvrier, S. 2013. Impacts of climate change on avian populations. Global Change Biology 19: 2036-2057.

Jenouvrier, S., M. Holland, J. Stroeve, C. Barbraud, H. Weimerskirch, M. Serreze, and H. Caswell. 2012. Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. Global Change Biology 18:2756-2770.

Jonzén, N., T. Pople, J. Knape, and M. Sköld. 2010. Stochastic demography and population dynamics in the red kangaroo Macropus rufus. Journal of Animal Ecology 79:109-116.

Karl, T. R., R. W. Knight, and N. Plummer. 1995. Trends in high-frequency climate variability in the twentieth century. Nature 377:217-220.

Koons, D. N., C. J. E. Metcalf, and S. Tuljapurkar. 2008. Evolution of delayed reproduction in uncertain environments: a life-history perspective. The American Naturalist 172:797-805.

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

Lawson, C. R., Y. Vindenes, L. Bailey, and M. Pol. 2015. Environmental variation and population responses to global change. Ecology Letters.

Lewontin, R. C., and D. Cohen. 1969. On population growth in a randomly varying environment. Proceedings of the National Academy of Sciences 62:1056-1060.

Mesquita, M. d. S., K. E. Erikstad, H. Sandvik, R. T. Barrett, T. K. Reiertsen, T. Anker-Nilssen, K. I. Hodges et al. 2015. There is more to climate than the North Atlantic Oscillation: a new perspective from climate dynamics to explain the variability in population growth rates of a long-lived seabird. Frontiers in Ecology and Evolution 3:43.

Metcalf, C. J. E. 2016. Invisible trade-offs: Van Noordwijk and de Jong and life-history evolution. The American Naturalist 187:iii-v.

Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3177-3186.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13:815-829.

Morris, W. F., and D. F. Doak. 2004. Buffering of life histories against environmental stochasticity: accounting for a spurious correlation between the variabilities of vital rates and their contributions to fitness. The American Naturalist 163:579-590.

Morris, W. F., C. A. Pfister, S. Tuljapurkar, C. V. Haridas, C. L. Boggs, M. S. Boyce, E. M. Bruna et al. 2008. Longevity can buffer plant and animal populations against changing climatic variability. Ecology 89:19-25.

Neubert, M. G., and H. Caswell. 2000. Density-dependent vital rates and their population dynamic consequences. Journal of Mathematical Biology 41:103-121.

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

Ramula, S., and K. Lehtilä. 2005. Importance of correlations among matrix entries in stochastic models in relation to number of transition matrices. Oikos 111:9-18.

Rotella, J. J., W. A. Link, T. Chambert, G. E. Stauffer, and R. A. Garrott. 2012. Evaluating the demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years of mark–recapture data. Journal of Animal Ecology 81:162-173.

Ruel, J. J., and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. Trends in Ecology & Evolution 14:361-366.

Sæther, B.-E., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642-653.

Sæther, B.-E., and S. Engen. 2015. The concept of fitness in fluctuating environments. Trends in Ecology & Evolution 30:273-281.

Silvertown, J., M. Franco, and E. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conservation Biology 10:591-597.

Stocker, T., D. Qin, G. Plattner, M. Tignor, S. Allen, J. Boschung, A. Nauels et al. 2013. Climate Change 2013: The Physical Science Basis. Working Group I Contribution ot the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK, Cambridge University Press.

Tebaldi, C., K. Hayhoe, J. M. Arblaster, and G. A. Meehl. 2006. Going to the extremes.

Climatic Change 79:185-211.

Teller, B. J., P. B. Adler, C. B. Edwards, G. Hooker, and S. P. Ellner. 2016. Linking demography with drivers: climate and competition. Methods in Ecology and Evolution 7:171-183.

Tibshirani, R. 1996. Regression shrinkage and selection via the lasso. Journal of the Royal Statistical Society. Series B (Methodological):267-288.

Tuljapurkar, S. 1990. Population dynamics in variable environments. New York, Springer.

Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. The American Naturalist 162:489-502.

Van de Pol, M., L. D. Bailey, N. McLean, L. Rijsdijk, C. R. Lawson, and L. Brouwer. 2016. Identifying the best climatic predictors in ecology and evolution. Methods in Ecology and Evolution.

Van de Pol, M., Y. Vindenes, B.-E. Sæther, S. Engen, B. J. Ens, K. Oosterbeek, and J. M. Tinbergen. 2010. Effects of climate change and variability on population dynamics in a long-lived shorebird. Ecology 91:1192-1204.

Van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist:137-142.

Wolkovich, E., B. Cook, K. McLauchlan, and T. Davies. 2014. Temporal ecology in the Anthropocene. Ecology Letters 17:1365-1379.

Yoccoz, N. G., K. E. Erikstad, J. O. Bustnes, S. A. Hanssen, and T. Tveraa. 2002. Costs of reproduction in common eiders (Somateria mollissima): an assessment of relationships between reproductive effort and future survival and reproduction based on observational and experimental studies. Journal of Applied Statistics 29:57-64.

Figures

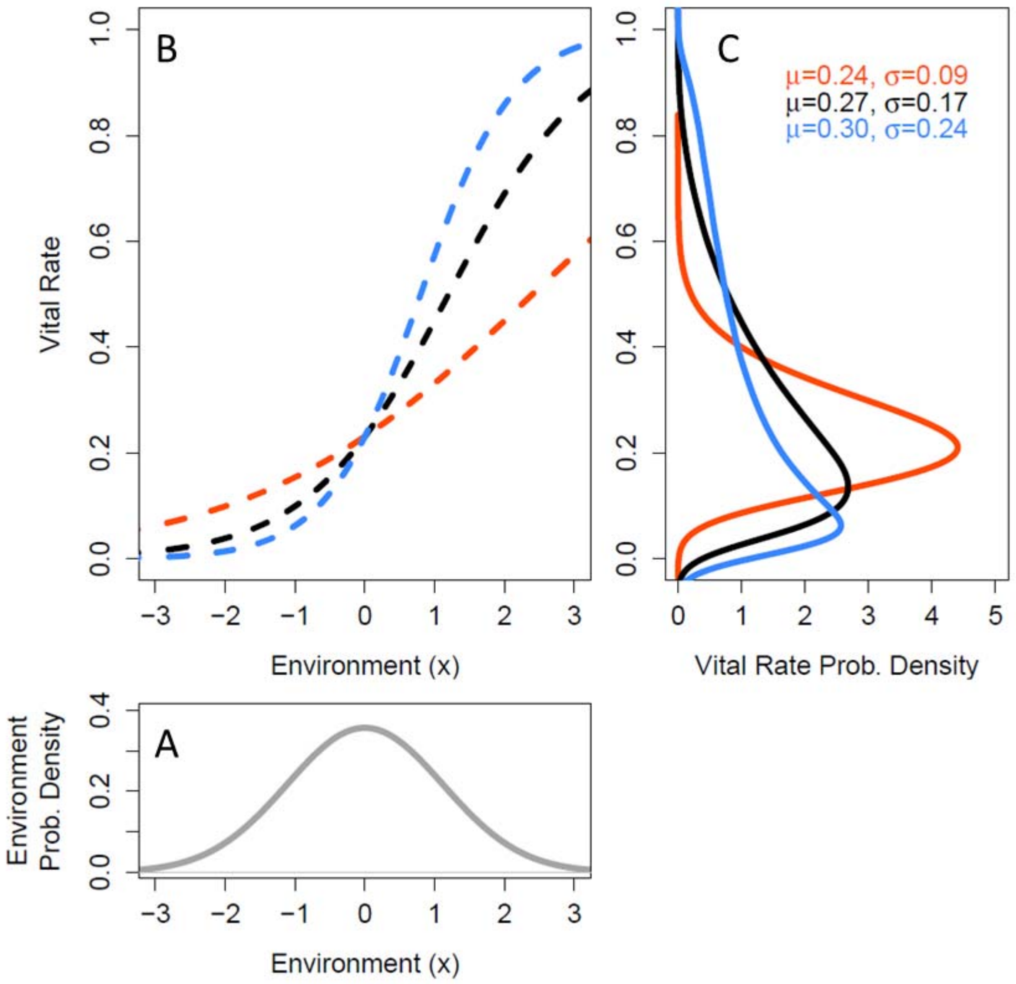

Figure 2.4: Effects of nonlinear vital rate reaction norms on vital rate distributions in variable environments. A variable environmental driver (panel A) is channeled through three nonlinear reaction norms (panel B) to produce three distinct vital rate distributions (panel C). Because the reaction norms are locally convex about the mean environment, a more labile reaction norm (blue) increases both the mean and variance of the vital rate distribution, while a more buffered reaction norm (red) decreases the relative mean and variance of the vital rate distribution.

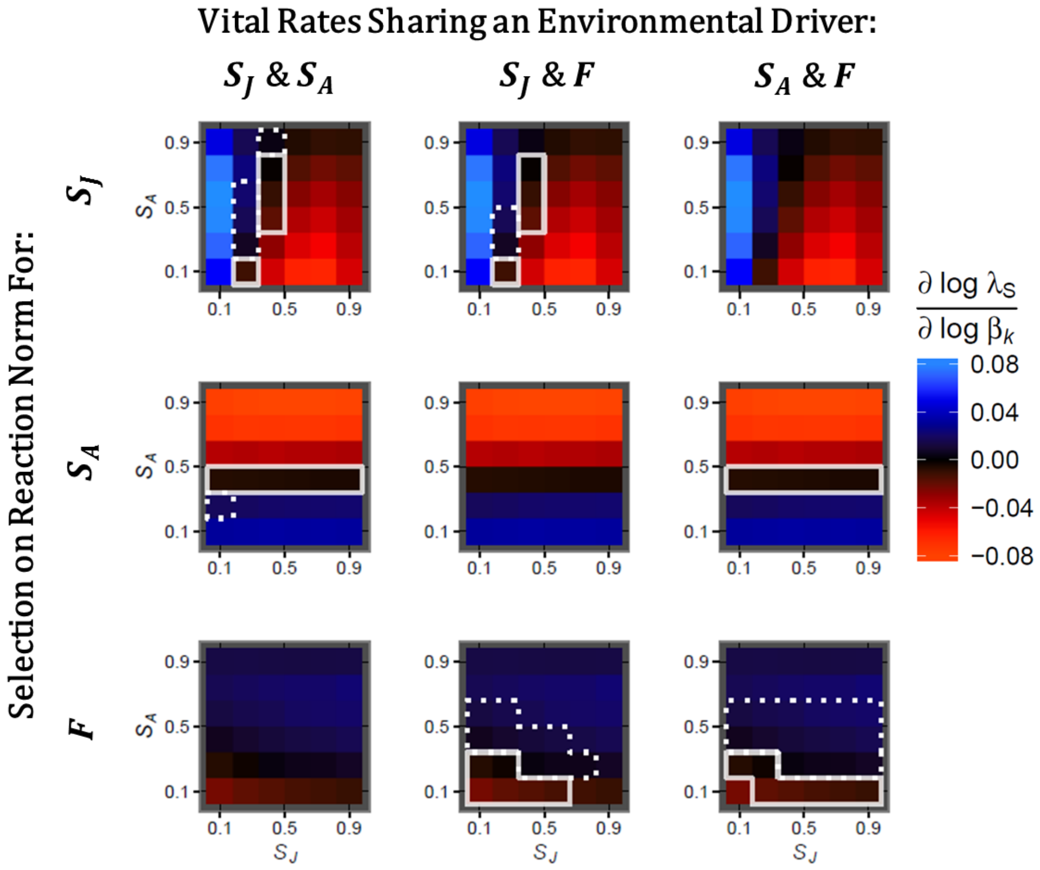

Figure 2.2: Fitness effect of an increase in slope of the reaction norm for juvenile survival (S_J), adult survival (S_A), and fertility (F) when vital rates are linked to time-varying environmental drivers. Red shading indicates selection for weaker vital rate responses (demographic buffering), blue shading indicates selection for stronger vital rate responses (demographic lability). White polygons indicate life histories where joint responses reverse the overall direction of selection on reaction norms. Solid line indicates effect of joint responses when vital rates respond in opposite direction to a shared environmental driver (negative covariation); dashed line indicates effects of joint responses when vital rates respond in the same direction to a shared environmental driver (positive covariation). In this figure, $p = 1$ and $a = 3.5$ (mean fertility is far from its maximum).

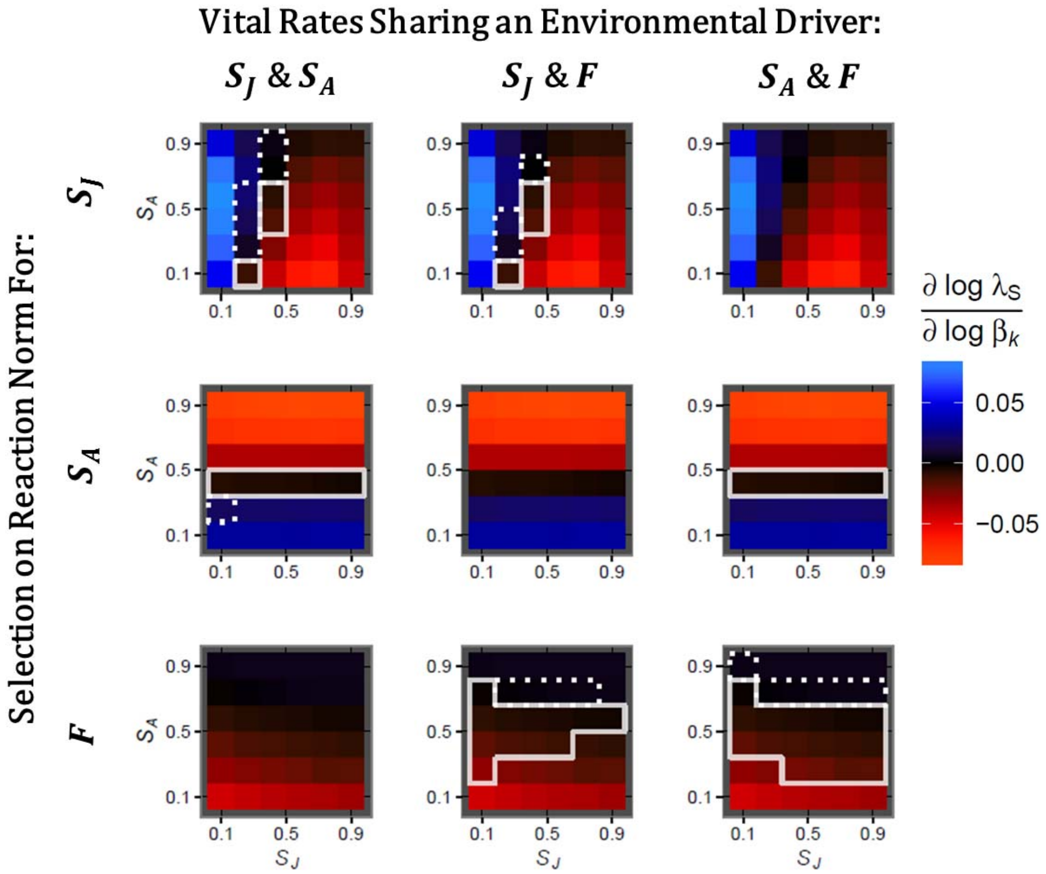

Figure 2.3: Fitness effect of increase in slope of reaction norm for juvenile survival (S_J), adult survival (S_A), and fertility (F) when vital rates are linked to time-varying environmental drivers. Figure is interpreted as in fig. 2.2. In this figure, $p = 1$ and $a = 2.5$ (mean fertility is intermediate relative to its maximum).

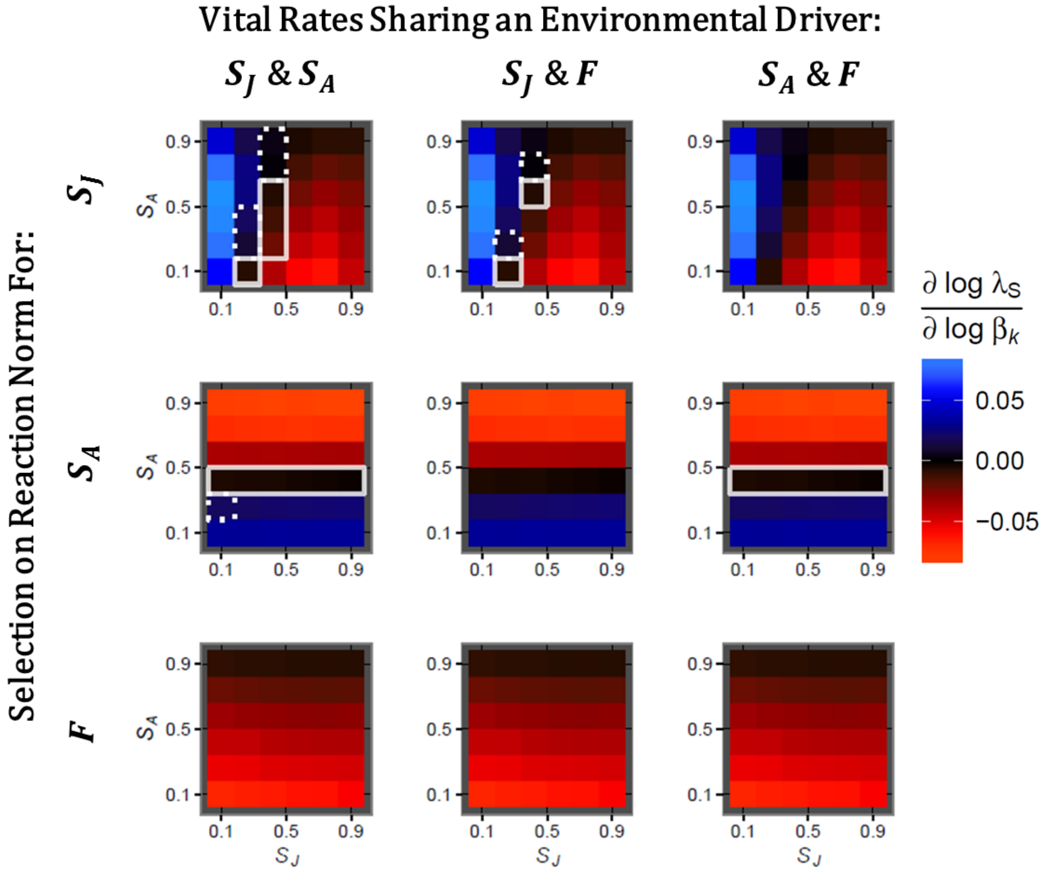

Figure 2.4: Fitness effect of increase in slope of reaction norm for juvenile survival (S_J), adult survival (S_A), and fertility (F) when vital rates are linked to time-varying environmental drivers. Figure is interpreted as in fig. 2.2. In this figure, $p = 1$ and $a = 1.5$ (mean fertility is close to its maximum).

CHAPTER 3

ENVIRONMENTAL SENSITIVITY OF SNOW GOOSE DEMOGRAPHY ACROSS A RESOURCE DIVERSITY GRADIENT

Introduction

Natural ecosystems are subjected to increasingly extreme anthropogenic pressures (IPCC 2012). As systems continue to be pushed outside the range of historic environmental variation, the maintenance of biodiversity ultimately depends on the dynamics of populations comprising ecological communities. A key agenda of modern ecological research is therefore to characterize the dynamics of natural populations through space and time, quantify relationships between demographic parameters and environmental factors, and make evidence-based projections under future change (Jenouvrier 2013; Ehrlén *et al.* 2016).

Despite promising recent efforts to relate demographic parameters to environmental drivers across space (reviewed in Ehrlén & Morris 2015), spatio-temporal population projections will often require detailed demographic data from multiple locations across a species' range (Schurr *et al.* 2012; Coutts *et al.* 2016). Relatively low-quality data (i.e., presence/absence data) are more often available across large spatial extents compared to detailed demographic datasets that tend to be limited in spatial scope (Schurr *et al.* 2012; Merow *et al.* 2014; Ehrlén *et al.* 2016). Thus, the possibility for assessing long-term demographic responses to environmental change, along with possible variation in these responses among populations, is limited to relatively few taxa (e.g., Doak & Morris 2010; Treurnicht *et al.* 2016).

There are nevertheless reasons to expect populations to differ in their sensitivity to environmental pressures, such that population responses to climate are idiosyncratic and habitat-specific (Tylianakis *et al.* 2008; Ettinger, Ford & HilleRisLambers 2011; Nicole *et al.* 2011). In particular, while climate can influence demographic parameters directly by affecting physiology, it can strongly impact demography indirectly by affecting species interactions (Tylianakis *et al.* 2008; Adler, Dalgleish & Ellner 2012; Alexander, Diez & Levine 2015; Alexander *et al.* 2016). For example, phenological asynchrony between consumers and resources, often driven by climate variation, is an indirect consequence of climate that has caused demographic change in many systems (reviewed in Miller-Rushing *et al.* 2010). Simultaneously, species interactions can feed back to modify the sensitivity of populations to climate (Ettinger, Ford & HilleRisLambers 2011; Adler, Dalgleish & Ellner 2012; Alexander, Diez & Levine 2015; Alexander *et al.* 2016). For example, the response of plant populations to climate warming depends strongly on the identity of competitors (Alexander, Diez & Levine 2015). Together, these effects will complicate attempts to extrapolate population dynamics across space and time. Accounting for species-climate feedbacks in ecological forecasting therefore remains a major challenge (Kissling *et al.* 2012; Ehrlén & Morris 2015; Alexander *et al.* 2016).

The lesser snow goose (*Chen caerulescens caerulescens;* hereafter “snow goose”) is a keystone herbivore that breeds in high latitude ecosystems, and a species for which the potential effects of phenological asynchrony with resources have recently been highlighted. Goslings are highly sensitive to resource quality on the breeding grounds, and reduced quality and availability of plant resources are associated with declines in gosling growth and survival (Cooch *et al.* 1991; Sedinger, Flint & Lindberg 1995; Dickey, Gauthier & Cadieux 2008; Aubry *et al.* 2013; Doiron, Gauthier & Lévesque 2015). The nutritional quality of leaves typically declines throughout the breeding season (Gadallah & Jefferies 1995) and warmer seasons cause these declines to occur more rapidly (Doiron, Gauthier & Lévesque 2014). Asynchrony between the date of gosling hatch and peak resource quality are therefore hypothesized to influence the early life demography of snow geese (Aubry *et al.* 2013; Doiron, Gauthier & Lévesque 2015). However, snow geese consume a variety of plant species from a range of habitat types (Winiarski, McWilliams & Rockwell 2012), and plant species differ in their nutritional quality, climate sensitivity, and phenology (Gadallah & Jefferies 1995; Mulder, Iles & Rockwell 2016). Thus, the consequences of environmental variability channeled through phenological mismatch with plants are likely habitat-specific.

In western Hudson Bay, expanding populations of snow geese have begun using novel inland habitats for nesting and brood rearing in addition to the coastal habitats that were traditionally used for breeding (Kerbes *et al.* 2006; Winiarski, McWilliams & Rockwell 2012). Along the Hudson Bay coast, the transition from coastal saltwater vegetation communities into vast inland freshwater meadows produces a strong gradient in vegetation communities and potentially influences resource availability (Riley 2003; Winiarski, McWilliams & Rockwell 2012). This system therefore provides an ideal opportunity to examine the degree to which habitat interacts with seasonal weather to influence consumer demography. For snow geese, this question is particularly of conservation relevance because management efforts have failed to curb population growth and attenuate the destructive potential of overabundant snow goose populations

(Alisauskas *et al.* 2011; Koons, Rockwell & Aubry 2014). Depending on the nature of demographic responses to climate across this habitat gradient, climate change could either mitigate or exacerbate conservation concerns.

To provide a deeper understanding of the factors that govern demographic responses to climate across habitats, we also test the prediction that resource diversity buffers consumers against the effects of environmental variation. Ecological theory predicts that greater resource diversity should stabilize consumer population dynamics, particularly for generalist consumers (McCann 2000; Jiang & Pu 2009; Haddad *et al.* 2011). This prediction follows from the insurance and averaging effects of diversity (Naeem & Li 1997; Doak *et al.* 1998; Yachi & Loreau 1999): diverse resource communities should provide more temporally consistent resources and habitat for consumers to exploit (Haddad *et al.* 2011). The positive effects of diversity on consumer population stability are amplified when most consumer-resource interactions are weak (McCann 2000; Wootton & Emmerson 2005), and when consumers can flexibly exploit resources that are most abundant and of high quality (Kondoh 2003). Given that species phenology often responds individualistically to environmental variation (Cleland *et al.* 2006; Parmesan 2007; Thackeray *et al.* 2010; Mulder, Iles & Rockwell 2016), a more diverse resource community will increase the probability that goslings are favorably synchronized with at least one resource across the range of environmental variation. Conversely, in a depauperate resource community, there are likely to be a range of environmental conditions that reliably result in mismatches between goslings and resources, which will manifest as strong effects of seasonal climate on gosling demography.

We first use a long-term dataset to investigate the effects of environmental variation on snow goose reproductive success and gosling body condition across a range of breeding habitats. We then test the prediction that demographic responses will be weakest in habitats with high resource diversity by quantifying the diversity of resources available to goslings at two scales: 1) at the landscape scale by measuring the diversity of land cover types available to goslings across the study area, and 2) at the level of individuals by measuring the diversity of resources identified in gut contents of goslings collected from across the range of habitats currently used for breeding. Finally, we assess whether spatial patterns in resource diversity corroborate patterns in demographic sensitivity to climate and determine if gosling responses to climate are indeed weakest in the habitats with greatest resource diversity.

Methods

Study Location and Data Collection

Annually since 1968, large flocks of adult snow geese and attendant goslings have been rounded up opportunistically at multiple locations across the Hudson Bay Lowlands in northern Manitoba, Canada as part of a long-term banding effort (Cooke, Rockwell & Lank 1995; Cooch, Rockwell & Brault 2001; Aubry *et al.* 2013), providing an unprecedented opportunity to study spatio-temporal drivers of herbivore demography. Historically, snow goose nesting and brood rearing areas were confined to a small area of coastal salt marsh at La Pérouse Bay. Salt marsh vegetation communities consist primarily of small graminoids including *Puccinellia phryganodes* and *Carex subspathacea*, along with a variety of perennial forbs (e.g., *Ranunculus cymbalaria*, *Argentina egedii*, and *Primula egalikensis*). Inland from the coastal salt marsh areas, the landscape transitions into expansive freshwater meadows dominated by large sedges (e.g., *Carex aquatilis* and *Scirpus cespitosus*). Following rapid population growth and concomitant degradation of salt marsh areas resulting from destructive foraging by overabundant adult snow geese (Abraham, Jefferies & Alisauskas 2005; Jefferies, Jano & Abraham 2005), the breeding colony expanded east and south into these inland freshwater landscapes (Aubry *et al.* 2013). Today, the nesting area is diffused over approximately 100 km of coastline and up to 10 km inland within Wapusk National Park (RF Rockwell unpublished data), and adults rear goslings across this range of landscapes (Mellor & Rockwell 2006; Winiarski, McWilliams & Rockwell 2012; Aubry *et al.* 2013).

Habitat Classification of Brood Rearing Areas

A primary goal of our study was to investigate demographic and developmental responses of goslings to climate across contemporary brood rearing habitats. To exploit long-term monitoring data, we assume that the landscape surrounding banding locations is representative of areas where goslings are reared. We make this assumption based on multiple consistent lines of evidence. First, gosling caecal parasite loads differ strongly between habitats, suggesting consistent and differentiated habitat use by individual goslings (Mellor & Rockwell 2006). Second, prior analysis of diet selectivity and stable isotope composition of gosling body tissue indicates that goslings are relatively consistent in habitat use during development(Winiarski, McWilliams & Rockwell 2012). Third, adults and goslings were occasionally captured multiple times within the same year. In these rare cases, the same individuals were recaptured in relatively consistent habitats on different dates (unpublished results), though we note sightings were often only separated by several days owing to short duration of banding operations in each year. Fourth, these lines of evidence corroborate personal observations (DT Iles) that individual flocks are found in consistent areas during brood rearing at our study site.

During banding operations, broods were often moved from their original location in order to amalgamate multiple small flocks for processing. In 2014 the mean distance between the original position of flocks and the location in which they were banded was 676 m (n = 37 small flocks, distance range: 49 to 1650 m). We therefore used a circular buffer with a radius of 2 km around banding locations to characterize brood rearing habitat, but we note that habitat classification based on a larger 5 km buffer was qualitatively similar and highly correlated (r = 0.82 between primary axes of land cover ordination based on 2 km and 5 km buffers).

Because of the dramatic change in coastal landscapes in the 1980s caused by destructive snow goose foraging, contemporary patterns in resource use by goslings may not reflect historical patterns prior to degradation (Jefferies, Jano & Abraham 2005; Winiarski, McWilliams & Rockwell 2012). To minimize this bias we only used data collected from 1990 onwards, after the majority of landscape degradation had occurred (see Appendix B for analysis of multi-temporal Landsat imagery confirming that landscape change was minimal from the 1990's onward). Importantly, the land cover map we use to classify brood rearing habitat was developed after the majority of degradation had occurred and therefore describes contemporary habitat composition. In total, geese were banded at 204 unique locations from 1990 to 2015 (4 to 14 locations per year).

We used Brook and Kenkel's (2002) land cover map for our study area to determine landscape composition surrounding each banding location. We extracted the percent composition of each land cover type within 2 km of each banding location and merged several similar land cover types into single categories (e.g., “sedge rich fen”, “sedge poor fen”, and “sedge larch fen” were collapsed into a single “sedge fen” category). We also removed any cells classified as water from the analysis because water is rarely used for foraging and the land cover map did not distinguish between fresh and salt water. In total, 8 distinct land cover types were encountered within 2 km of banding locations.

We used ordination (non-metric multidimensional scaling, MDS; metaMDS function in the *vegan* R package) to collapse land cover data at banding sites into primary axes of landscape variation (biplot of this ordination presented in Fig. B1 in Appendix B). The first MDS axis loaded positively on inland freshwater land cover classes (“spruce bog”, “peat plateau”, “heath upland”, and “sedge meadow”) and negatively on coastal saltwater land cover classes (“salt marsh”, “shoreline”, and “unvegetated ridge”). We therefore used measures along this axis (referred to as MDS1 hereafter) to describe the overall habitat at each banding location: highly negative values indicate highly coastal habitats, while highly positive values denote inland habitats (Fig. 3.1).

We extracted the proportion of area within 2 km of each banding location that was converted to bare ground since 1976 as a measure of local habitat degradation severity (details of the analysis are described in Appendix B). The severity of landscape degradation was highly correlated with landscape composition; degradation was concentrated primarily in coastal sites (Fig. B4 in Appendix B). Position along the landscape MDS1 axis therefore simultaneously describes landscape composition and severity of historical degradation at each banding location. However, because there was residual variation in this nonlinear relationship, we used smoothing within a generalized additive model (GAM) to regress MDS1 against local habitat degradation and extracted the residuals from this regression as a measure of residualized habitat degradation after controlling for landscape composition. This effect was then included as an explanatory covariate in competing models for reproductive success and gosling body condition (see below). GAMs were fit using the 'gam' function within the *mgcv* package in R.

Weather Data

Temperature and precipitation potentially affect gosling demography and development through direct (physiological) and indirect pathways (e.g., via effects on goose and plant phenology; Aubry *et al.* 2013; Doiron, Gauthier & Lévesque 2014; Doiron, Gauthier & Lévesque 2015; Mulder, Iles & Rockwell 2016). For each year of study, we calculated cumulative growing degree days at three ecologically relevant time periods: on calendar days 144, 174, and 204 (hereafter referred to as GDD_{144}, GDD_{174}, and GDD_{204}). Because the mean annual date of snow goose hatch across the study was day 174 (June 23), GDD_{174} describes overall seasonal warmness until mid-breeding season (i.e., until hatch in an average year). We considered GDD_{144} to be a metric of overall warmness leading up to average nest initiation, and considered GDD_{204} as a metric describing cumulative temperature throughout incubation, hatch, and pre-fledging period of goslings in an average year. All three warmness metrics were highly correlated ($r > 0.70$ for all pairwise comparisons), and we did not include multiple metrics of seasonal warmness as explanatory covariates in models for reproductive success or gosling development. Similarly, we calculated cumulative precipitation within the two weeks surrounding calendar days 144, 174, and 204 (denoted $precip_{144}$, $precip_{174}$, and $precip_{204}$). These covariates therefore describe early, mid, and late season wetness in each year of study and were not strongly correlated with each other ($r < 0.1$ for all pairwise comparisons) or with any of the metrics of cumulative seasonal warmness ($r < 0.15$ for all pairwise comparisons).

Seasonal warmness affects hatching phenology of snow geese at our site; goslings hatch later in cold seasons (Appendix B) likely because nesting is constrained by availability of snow-free nesting sites (Newton 1977). The time elapsed between goose hatching and banding operations could influence the proportion of goslings surviving until banding, as well as gosling size and condition at banding (Flint, Sedinger & Pollock 1995). To account for the potentially important effects of goose phenology (and thus time elapsed/gosling age at banding) beyond that which is explained by seasonal warmness, we extracted residuals from a GAM with spline smoothing that included seasonal warmness as a predictor of days elapsed since the mean hatch date of geese in each year of study. We included the effect of “residual age” as a potential covariate in models for reproductive success and gosling body condition.

Analysis of Snow Goose Reproductive Success

In some years of study, only highly coastal or inland sites were sampled. To avoid potential biases introduced by opportunistic sampling (e.g., more thoroughly sampling one habitat type in highly productive years), we only analyzed data from years in which at least 2 sites were sampled in both coastal ($MDS1 < 0$) and inland habitats ($MDS1 > 0$).

In total, 121 banding sites from 13 study years (5-13 banding sites per year) were included in our analysis of reproductive success. At each of these 121 locations, the numbers of adults and goslings in the banding flock were recorded, providing an index of reproductive success. Because banding operations take place 4-6 weeks after the mean hatching date of goslings, the proportion of goslings comprising each banding flock is a function of the number of eggs produced per female, the hatching success of eggs, and gosling survival until banding. Snow goose clutch size is relatively invariant and egg survival is extremely high owing to aggressive nest defense by both parent geese (Cooke, Rockwell & Lank 1995). Furthermore, non-breeders and adults that lose their entire clutch during the incubation period appear to emigrate from the study area prior to banding (RF Rockwell *pers. comm*). Thus, variation in the proportion of goslings comprising banding flocks is likely to primarily reflect variation in gosling survival following hatch.

We analyzed reproductive success data with generalized linear mixed models (GLMMs), treating success as a binomial response variable with number of goslings in each flock as “successes” and the total number of geese in each flock as the number of trials. We used a logit link to relate environmental covariates (i.e., habitat, warmness, precipitation, residualized gosling age, and residualized habitat degradation) to the response in a suite of competing models. We included landscape composition (MDS1 scores) as either a continuous covariate to describe the transition from coastal to inland habitats. We note, however, that habitat scores were highly bimodal, such that habitat composition at most sites was either highly coastal or higly inland (Fig. B2 in Appendix B). We included a random intercept in all models for year to account for multiple samples (i.e., banding locations) within each year and inter-annual variation not explained by the covariates.

To facilitate comparison of a reasonable number of models and avoid overfitting, we used a tiered approach for model selection and assessed relative support for competing models at each tier using Schwarz's information criterion (SIC; Schwarz 1978; also often called BIC). If covariates were not well supported individually (i.e., did not perform better than a model omitting those effects), we did not include them in more complex additive or interactive models with other covariates. We adopted this highly conservative tiered approach to model selection to avoid including spurious effects in final models.

First, we constructed a suite of models containing individual or combined additive effects of residualized degradation and gosling age covariates. Upon determining the best parameterization for these "control" covariates, we included them in all subsequent models. In the second and third tiers of model selection, we compared models containing linear effects of each of the three temperature covariates (GDD_{144}, GDD_{174}, and GDD_{204}) and precipitation covariates ($precip_{144}$, $precip_{174}$, and $precip_{204}$), respectively. Finally, upon determining the best temperature and precipitation covariates, we compared models containing interactions between habitat and the best weather covariates to explicitly test the hypothesis that environmental sensitivity depends on habitat. Support for habitat and environmental effects was assessed based on relative SIC and associated model weights, as well as effect sizes from the top model(s).

Analysis of Gosling Condition

To examine the responses of gosling size and body condition to seasonal weather across habitats, standard body morphometrics were recorded for a subset of female goslings at banding drives; females are philopatric to the study area and have been more intensively monitored because they have higher recapture rates than males. As with our analysis of reproductive success, we only included years in which goslings were measured in at least 2 banding drives from both coastal and inland areas. In total, our analysis included measurements for 1454 female goslings from 58 banding drives from 6 years between 1990 and 2015. We used the total length of the tarsus bone as a measure of gosling structural size (Dzubin & Cooch 1992; Cooke, Rockwell & Lank 1995; Cooch, Dzubin & Rockwell 1999). We calculated an index of gosling body condition by regressing body mass on tarsus length (i.e., body mass adjusted for structural size) using a GAMM to account for a nonlinear relationship while accounting for a random effect of year. We then extracted the residuals from this model as a measure of individual gosling body condition, likely representative of muscular condition rather than body fat reserves (Aubry *et al.* 2013).

We used GLMMs to relate habitat and weather covariates to gosling body condition (residual of mass-tarsus regression), using a Gaussian error structure and an identity link. We used the same tiered approach to model selection as for our analysis of reproductive success; we determined the best structure for covariates that control for effects of habitat degradation and residualized gosling age, then separately determined the best weather covariates, and finally fit additive and interactive effects for well-supported weather and habitat effects. As above, we assessed relative model support using SIC. We included random effects of banding location and study year in all models to account for repeated measurements and stochastic variation not explained by the covariates, respectively.

Analysis of Landscape Diversity

To assess the diversity of land cover types available to goslings across the study area, we calculated the proportion of the landscape comprised by different land cover types within a 2 km radius of each banding location. We then used the *renyi* function in the *vegan* package in R to calculate land cover diversity surrounding each banding location. At each banding site, we calculated two measures of land cover diversity (Hill 1973); 1) richness and 2) the exponent of Shannon diversity, denoted exp(H'), which also accounts for evenness of land cover types. Together, these measures describe the number and relative abundance of land cover types available to goslings within 2 km of each banding site. We regressed each of these measures against the landscape composition (MDS1), allowing us to evaluate how land cover diversity changes across the gradient from coastal to inland habitats.

Analysis of Gosling Diet Diversity

To examine spatial differences in gosling diet composition and associated seasonal patterns in gosling development, we collected goslings throughout the 2014 and 2015 seasons from representative coastal and inland brood rearing areas. Both years were exceptionally warm; in 2014 the value of GDD_{204} was in the 98th percentile of warmness across the study, while in 2015 GDD_{204} was in the 81st percentile. Goslings were humanely euthanized according to CWS permit 11-MB-SC001 (IACUC approval number

2208). Goslings were necropsied and gut contents removed. We first sorted gut contents to the level of family. Although we were unable to identify all graminoid leaves to the level of species, we sorted unknown grasses and *Carex* specimens into small (approx. 0 – 1 mm width), medium (approx. 1 – 3 mm width), and large (>3 mm width) specimens. Each size category likely encompasses multiple species or genera, and could thus be interpreted as a conservative estimate of species diversity or diversity of leaf traits consumed within plant genera (termed here as species diversity for simplicity). After sorting, we dried samples at room temperature and weighed them to the nearest milligram. We considered any items weighing less than 5 mg to be “trace” amounts of material potentially consumed incidentally and we therefore did not include these extremely rare items in subsequent analysis of diet diversity.

We extracted land cover data within 2 km of each gosling collection location and used loadings from the banding site land cover ordination to place goslings onto the same landscape MDS axes used in analyses of reproductive success and body condition. To compare the diet diversity of goslings collected in coastal and inland habitats, we categorized habitat scores according to their score on MDS1. Goslings collected in areas with MDS1 scores less than 0 were categorized as “coastal”, and goslings collected in areas with MDS1 greater than 0 were categorized as “inland” (note that the threshold of MDS1 score at 0 for classification successfully separated the highly bimodal scores across sites; Fig. B2 in Appendix B). Discretizing the continuous landscape scores allowed us to then use rarefaction to evaluate the relative diversity of diet items consumed by goslings collected in each habitat.

Rarefaction is a technique used to derive taxon sampling curves for different treatments (in this case habitats), providing standardized measures of biodiversity (Gotelli & Colwell 2001). By assessing the shape of rarefaction curves and the degree to which curves have saturated, we can also evaluate whether we would have been likely to discover additional plant species or families in gosling diets if we sampled more intensively. We constructed separate rarefaction curves for each habitat classification in 2014 and 2015. We also constructed separate rarefaction curves based on richness and the exponent of Shannon diversity, allowing us to evaluate how strongly our results were driven by rare diet items. Finally, we also constructed rarefaction curves for diet items identified to both the species and family levels. We used the iNEXT function supplied in the Supplement of Chao et al. (2014) to perform sample-based rarefaction and compute unconditional 84% confidence intervals (Gotelli & Colwell 2011). We concluded that diversity was significantly different if these confidence intervals did not overlap (where 84% confidence intervals produce a type I error rate of $P < 0.05$; Gotelli & Colwell 2011).

Results

Effects of Breeding Season Weather on Reproductive Success and Gosling Body Condition across Habitats

The top model for reproductive success contained an interaction between habitat and seasonal temperature (GDD_{204}). Thus, of the three seasonal temperature metrics we considered, cumulative growing degree days by calendar day 204 (GDD_{204}) was the best predictor of reproductive success. In the early stages of model selection, models containing only the individual effects of early, mid, or late season precipitation did not receive more support than a null model (ΔSIC was 1.7, 4.2, and 3.0 for early, mid, and late season precipitation, relative to a null model omitting these models), and we therefore did not include them in subsequent stages of model construction and selection. Habitat degradation (i.e., the residualized effect beyond that which was accounted for by habitat composition) and gosling age (beyond which was accounted for by breeding season temperature) were significant predictors of reproductive success, though the effect sizes of these predictors were much lower than habitat, temperature, and their interaction.

We found strong support for the hypothesis that seasonal temperature affected snow goose reproductive success differently across habitat types (ΔSIC = 75.3 for the best model omitting the interaction between habitat and temperature, and the model containing an interaction between habitat and temperature accounted for >99.9% of model weight; also see model selection results in Appendix B). Reproductive success responded more strongly to seasonal temperature in inland landscapes (Fig. 3.2; red lines) than in coastal landscapes (Fig. 3.2; blue lines). In general, flocks contained higher proportions of goslings in coastal habitats, but extremely warm years resulted in similar estimates of reproductive success across the landscape due to the strong positive response of reproductive success to seasonal warmness in inland areas (i.e., higher sensitivity to climate). We detected high residual inter-annual variability in reproductive success after accounting for habitat covariates, seasonal temperature, and residualized gosling age (thin lines in Fig. 3.2; std. dev of random year effect was 0.31 on the logit scale).

The top model for late-summer body condition only included random effects of site and year; models containing additional gosling age, habitat, or weather covariates were not well-supported predictors of body condition (Appendix B). Gosling body condition varied more among years than among sites (std. dev of random year and site effects were 49.2 and 38.7, respectively).

Land Cover Diversity across Habitats

Land cover diversity was strongly and non-linearly correlated with habitat (Fig. 3.3). Goslings inhabiting highly coastal sites (MDS1 < 0) had access to a greater diversity of land cover types than goslings in highly inland sites (MDS1 > 0). To directly evaluate the effect of land cover diversity on demographic sensitivity to temperature, we re-fit the top model for reproductive success after replacing the continuous habitat covariate (MDS1) with a covariate for landscape diversity (measured as exp(H') for land cover). A model including an interaction effect between land cover diversity and seasonal temperature greatly outperformed a model omitting this interaction (ΔSIC = 120.2). This model confirmed that reproductive success was significantly more sensitive to seasonal temperature in areas with lower land cover diversity.

Gosling Diet Diversity across Habitats

We identified plant specimens from gut contents of 99 goslings collected in 2014 and 2015, 85 of which contained at least 5 mg of material. We identified a total of 21 species in gosling gut contents (mean = 1.9 species per gosling, range = 1 to 5 species per gosling), comprising 12 plant families (mean = 1.8 plant families per gosling, range = 1 to 4 families per gosling). Total dry mass of contents in goslings ranged from 5 to 3281 mg. Small and medium grass and *Carex* leaves comprised the largest proportion of most gosling diets in both coastal and inland habitats, though coastal goslings consumed larger quantities of smaller species (Fig. 3.4). Inland goslings also consumed a variety of heavier graminoid species that were generally absent from the diets of coastal goslings (e.g, *Scirpus cespitosus* and *Equisetum variegatum*). Diets of several goslings collected from inland habitats contained a large number of *Andromeda polifolia* and *Dryas integrifolia* flowers. The leaves of these species are not likely to be highly digestible, but consumption of numerous flowers and fruit by several individuals indicates that certain phenological stages of these plant species may provide temporary resources pulses to goslings. Conversely, coastal gosling diets contained a variety of perennial forbs, including *Primula egalikensis*, *Ranunculus cymbalaria*, and *Argentina egedii*, though these were generally found in much smaller quantities than graminoid leaves.

Rarefaction indicated that diet diversity was greater for goslings in coastal habitats than inland habitats in both 2014 and 2015 (Fig. 3.5; left and right columns, respectively), whether plants were identified to the species or family levels (Fig. 3.5; top and bottom rows, respectively), and whether diversity was calculated as richness or exp(H'), the exponent of Shannon diversity (Fig. 3.5; solid and dashed lines, respectively). These differences were significant at the $P < 0.05$ level for plant species richness and exp(H') in 2014, plant species exp(H') in 2015, and plant family richness in 2015. In both coastal and inland areas, diet diversity (quantified at either the species or family level and measured using either richness or exp(H')) was greater in 2015 than 2014. These results therefore indicate that diet diversity was higher in habitats where demographic responses to temperature were weaker (i.e., coastal habitats).

Discussion

A detailed understanding of the relationships between demographic parameters and the environment is needed to produce reliable population forecasts in a changing world (Jenouvrier 2013). However, projecting range-wide responses based on relationships derived from a subset of the species range may be misleading if demographic sensitivity to climate is habitat-specific and influenced by resource availability (Sæther & Engen 2010; Jenouvrier 2013; Ehrlén & Morris 2015). We found that the relationship between demography and the environment depends on habitat, even over relatively small spatial scales (<10 km). Our study therefore adds to a growing body of literature that indicates demographic sensitivity to climate varies across space (e.g., Ettinger, Ford & HilleRisLambers 2011), further underscoring the challenge of projecting population responses to climate change in heterogeneous landscapes.

We found that while average reproductive success is currently lower in inland habitats than coastal habitats, warmer seasons disproportionately increase breeding success in novel inland landscapes. In western Hudson Bay, snow geese historically experienced strong effects of density dependence in their traditional coastal salt marsh breeding habitats, especially as these preferred habitats became heavily degraded (Cooch *et al.* 1991). However, the breeding population expanded into new habitats (Kerbes *et al.* 2006; Aubry *et al.* 2013), thereby relaxing density-dependent feedbacks and facilitating increased population growth (Koons, Rockwell & Aubry 2014). Inland habitats consisting of freshwater sedge meadows are approximately 150 times more abundant than coastal salt marsh habitats in the Hudson Bay Lowlands (Brook & Kenkel 2002), and given the strong positive responses of snow goose reproductive success to warming in inland habitats (Fig. 3.2), continued climate warming could substantially increase the proportion of the landscape that can support successful breeding. Lesser snow geese are officially listed as “overabundant” because of their detrimental effects to high-latitude coastal ecosystems (Leafloor, Moser & Batt 2012). Yet, management efforts to reduce their abundance have largely been unsuccessful (Alisauskas *et al.* 2011; Koons, Rockwell & Aubry 2014). As breeding season temperatures are becoming warmer and more variable at our study site (Mulder, Iles & Rockwell 2016), the increasing use of novel inland habitats could further impede management efforts to curb population growth.

The early-life demographic responses of goslings to climate variation we detected are likely channeled through effects on the plant community (Aubry *et al.* 2013; Doiron, Gauthier & Lévesque 2015). Following hatch, goslings are highly sensitive to plant quality (Richman *et al.* 2015). Plant biomass and nutritional quality are both functions of plant phenology (Gadallah & Jefferies 1995; Doiron, Gauthier & Lévesque 2014), which is tied to seasonal warmness (Mulder, Iles & Rockwell 2016). But importantly, phenological responses of individual plant species are highly variable (Table S2 in Mulder, Iles & Rockwell 2016). Thus, the bottom-up effects of environmental variation are likely to depend on the identity and diversity of plant species within brood rearing habitats. Although previous studies have documented demographic and developmental effects of trophic mismatch on goslings (e.g. Dickey, Gauthier & Cadieux 2008; Aubry *et al.* 2013; Doiron, Gauthier & Lévesque 2015), our study offers new insights into these effects by examining responses of geese across a resource gradient.

All else being equal, theory suggests that specialist consumers should be more sensitive to trophic mismatch than generalists that can exploit multiple resource pulses throughout a season (McCann 2000; Miller-Rushing *et al.* 2010). Yet, even generalist consumers may experience strong effects of trophic mismatch if resource diversity is constrained by habitat. Spatial variation in resource communities could thus expose generalist sub-populations to very different levels of resource diversity across a landscape. Low resource diversity guarantees that most trophic interactions will be strong and that consumers cannot flexibly switch between a limited availability of resources. Together, these effects should lead to less stable consumer population dynamics in depauperate resource communities (McCann 2000; Kondoh 2003). If resource availability and quality for herbivores is strongly affected by climate, as in high-latitude ecosystems (Gadallah & Jefferies 1995; Doiron, Gauthier & Lévesque 2014), then these effects will manifest as stronger (i.e., more labile; Koons *et al.* 2009) demographic responses to climate when resource diversity is low. Our results are consistent with this hypothesis. Coastal landscapes contained more distinct land cover classes, and in greater relative evenness, than inland landscapes (Fig. 3.3). Demographic responses to seasonal temperature were weakest in coastal landscapes, and landscape diversity itself was a strong predictor of reproductive success and sensitivity to environmental variation. Furthermore, in both years we collected goslings, the diversity of plant species and families in gosling diets measured as either richness or Shannon diversity was greater in coastal than inland habitats (Fig. 3.5).

Diet contents of some goslings were relatively distinct; for example, different individual goslings had uniquely fed on large numbers of *Primula* and *Salix* fruits, *Ranunculus cymbalaria* leaves, flowers of *Andromeda polifolia* and *Dryas integrifolia*, and *Eleocharis palustris* culms. However, most gosling diets consisted of only a few graminoid groups. A higher frequency of distinct diets containing relatively rare species in coastal habitats (Fig. 3.4) is therefore likely responsible for the greater diet diversity we detected in these landscapes. Rare species can make significant contributions to ecosystem function (Lyons *et al.* 2005), and rare species often have relatively unique traits and low functional redundancy, thereby supporting important vulnerable ecosystem functions in variable environments (Isbell *et al.* 2011; Mouillot *et al.* 2013). Thus, while abundant and commonly consumed graminoids are likely necessary to support gosling growth and development, it is possible that other species may nevertheless provide important sources of nutrition in certain environmental contexts, especially in cold years where differences in reproductive success between coastal and inland areas are most pronounced.

Gosling diets in coastal landscapes tended to consume smaller graminoid leaves (e.g., *Puccinellia phryganodes*, *Carex subspathacea*, and *Festuca rubra*) than goslings in inland landscapes, where larger *Carex* and *Scirpus* leaves and relatively thick *Equisetum variegatum* stems were more commonly consumed. These findings are also consistent with Winiarski et al. (2012) who also sampled goslings across this habitat gradient at our study site. The smaller graminoids frequently consumed in coastal habitats typically have higher nutrient content and are more digestible than larger species more commonly consumed in inland landscapes (Gadallah & Jefferies 1995). The low nutrient content of common inland graminoids may amplify the direct effects of seasonal weather (e.g., by precluding goslings from recouping thermoregulatory costs in cold years; Beasley & Ankney 1988; Fortin, Gauthier & Larochelle 2000), contributing to the strong negative effects of cold seasons we detected.

The overall positive relationship we detected between goose reproductive success and seasonal warmness is qualitatively consistent with other studies of Arctic-nesting geese. For example, in a high-Arctic population of lesser snow geese, Alisauskas (2002) found a negative relationship between goose productivity and Arctic spring climate severity; thus, a positive relationship between productivity and seasonal warmness. Similarly, Morrissette *et al.* (2010) found a positive relationship between seasonal warmness and productivity in greater snow geese (though note curvilinear effect of Arctic Oscillation Index detected by Dickey, Gauthier & Cadieux 2008). A positive relationship between breeding season warmness and productivity has also been detected in pink-footed geese (Madsen *et al.* 2007; Jensen *et al.* 2014). Nevertheless, the relative strength of climate effects on gosling production across populations and species is unclear because studies use different metrics of performance (e.g., age ratios in pre-fledging flocks at breeding locations [our study; Morrisette et al. 2010], versus ratios in fall migration [Alisauskas 2002]) and because studies use different metrics of breeding season climate (e.g., measures of local seasonal warmness [our study], versus large-scale climate indices such as Arctic Oscillation index [Dickey, Gauthier & Cadieux 2008]).

We did not detect strong effects of habitat or seasonal weather on gosling body condition and in contrast to our findings, a separate analysis of spatio-temporal drivers of body condition at our site found that warmer breeding seasons resulted in lower gosling body condition near fledging (Aubry *et al.* 2013). Effects of seasonal weather and habitat on gosling development have also been detected in other populations (e.g., Sedinger, Flint & Lindberg 1995; Alisauskas 2002; Doiron, Gauthier & Lévesque 2015). Because we explicitly focused on comparisons between coastal and inland habitats from 1990 onwards, we restricted our analysis to a relatively small (but statistically balanced) subset of historical data and potentially reduced our ability to detect subtle environmental effects on gosling body condition. Yet, we note that models including the effects of breeding season temperature did reveal trends consistent with Aubry et al.'s (2013) findings; warmer seasons resulted in lower pre-fledging body condition. Subtle variation in gosling body condition can have important effects on subsequent survival (Hill *et al.* 2003; Aubry *et al.* 2013) and reproductive performance (Sedinger, Flint & Lindberg 1995). To better understand the consequences of environmental change for populations across habitats, models should therefore consider potential linkages between environmental drivers and multiple fitness components and account for the potential fitness consequences of vital rate covariation (Doak *et al.* 2005; Barraquand & Yoccoz 2013; Lawson *et al.* 2015). Thus, an important remaining question is whether differences in demographic sensitivity across habitats scale up to affect overall population dynamics, and how the effects of climate variation are either buffered or amplified by covariation generated between successive fitness components of the life cycle.

Characterizing population responses to environmental change is a considerable challenge, given that demographic sensitivity is habitat-specific and environmental factors may affect population dynamics through multiple pathways simultaneously. Here, we have shown that snow goose reproductive success responds differently to environmental variation across habitats and as a result, that continued climate warming will disproportionately increase reproductive performance in novel inland habitats. These differing responses may be driven by spatial patterns in landscape diversity, diet diversity, and diet quality. Further research that integrates habitat-specific effects of climate across the entire life cycle will provide deeper insights into the potential effects of climate change on the population dynamics of this overabundant keystone herbivore.

Such information will be crucial for forecasting population trends and spatial distributions, and for prioritizing management in variable and changing environments.

References

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

Adler, P.B., Dalgleish, H.J. & Ellner, S.P. (2012) Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology,* **100,** 478-487.

Alexander, J.M., Diez, J.M., Hart, S.P. & Levine, J.M. (2016) When climate reshuffles competitors: a call for experimental macroecology. *Trends in Ecology & Evolution,* **31**, 831-841.

Alexander, J.M., Diez, J.M. & Levine, J.M. (2015) Novel competitors shape species' responses to climate change. *Nature,* **525,** 515-518.

Alisauskas, R., Rockwell, R., Dufour, K., Cooch, E., Zimmerman, G., Drake, K., Leafloor, J., Moser, T. & Reed, E. (2011) Effect of population reduction efforts on harvest, survival and population growth of Midcontinent lesser snow geese. *Wildlife Monographs,* **179,** 1-42.

Alisauskas, R.T. (2002) Arctic climate, spring nutrition, and recruitment in midcontinent lesser snow geese. *The Journal of Wildlife Management*, **66**, 181-193.

Aubry, L.M., Rockwell, R.F., Cooch, E.G., Brook, R.W., Mulder, C.P. & Koons, D.N. (2013) Climate change, phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. *Global Change Biology,* **19,** 149-160.

Barraquand, F. & Yoccoz, N.G. (2013) When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. *Theoretical Population Biology,* **89,** 1-11.

Beasley, B.A. & Ankney, C.D. (1988) The effect of plumage color on the thermoregulatory abilities of lesser snow goose goslings. *Canadian Journal of Zoology,* **66,** 1352-1358.

Brook, R. & Kenkel, N. (2002) A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing,* **23,** 4761-4776.

Chao, A., Gotelli, N.J., Hsieh, T., Sander, E.L., Ma, K., Colwell, R.K. & Ellison, A.M. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs,* **84,** 45-67.

Cleland, E.E., Chiariello, N.R., Loarie, S.R., Mooney, H.A. & Field, C.B. (2006) Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences,* **103,** 13740-13744.

Cooch, E., Dzubin, A. & Rockwell, R. (1999) Using body size to estimate gosling age. *Journal of Field Ornithology*, **70**, 214-229.

Cooch, E., Lank, D., Rockwell, R. & Cooke, F. (1991) Long-term decline in body size in a snow goose population: evidence of environmental degradation? *Journal of Animal Ecology,* **60,** 483-496.

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

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

Coutts, S.R., Salguero-Gómez, R., Csergő, A.M. & Buckley, Y.M. (2016) Extrapolating demography with climate, proximity and phylogeny: approach with caution. *Ecology Letters,* **19,** 1429–1438.

Dickey, M.-H., Gauthier, G. & Cadieux, M.-C. (2008) Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology,* **14,** 1973-1985.

Doak, D.F., Bigger, D., Harding, E., Marvier, M., O'malley, R. & Thomson, D. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist,* **151,** 264-276.

Doak, D.F. & Morris, W.F. (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature,* **467,** 959-962.

Doak, D.F., Morris, W.F., Pfister, C., Kendall, B.E. & Bruna, E.M. (2005) Correctly estimating how environmental stochasticity influences fitness and population growth. *The American Naturalist,* **166,** E14-E21.

Doiron, M., Gauthier, G. & Lévesque, E. (2014) Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. *Journal of Ecology,* **102,** 508-517.

Doiron, M., Gauthier, G. & Lévesque, E. (2015) Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Global Change Biology,* **21,** 4364-4376.

Dzubin, A. & Cooch, E. (1992) *Measurements of geese: general field methods*. California Waterfowl Association.

Ehrlén, J. & Morris, W.F. (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters,* **18,** 303-314.

Ehrlén, J., Morris, W.F., Euler, T. & Dahlgren, J.P. (2016) Advancing environmentally explicit structured population models of plants. *Journal of Ecology,* **104,** 292-305.

Ettinger, A.K., Ford, K.R. & HilleRisLambers, J. (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology,* **92,** 1323-1331.

Flint, P.L., Sedinger, J.S. & Pollock, K.H. (1995) Survival of juvenile Black Brant during brood rearing. *The Journal of Wildlife Management*, **59**, 455-463.

Fortin, D., Gauthier, G. & Larochelle, J. (2000) Body temperature and resting behavior of greater snow goose goslings in the high Arctic. *The Condor,* **102,** 163-171.

Gadallah, F. & Jefferies, R. (1995) Comparison of the nutrient contents of the principal forage plants utilized by lesser snow geese on summer breeding grounds. *Journal of Applied Ecology*, **32**, 263-275.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters,* **4,** 379-391.

Gotelli, N.J. & Colwell, R.K. (2011) Estimating species richness. *Biological diversity: frontiers in measurement and assessment,* **12,** 39-54.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J. & Tilman, D. (2011) Plant diversity and the stability of foodwebs. *Ecology Letters,* **14,** 42-46.

Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology,* **54,** 427-432.

Hill, M.R., Alisauskas, R.T., Ankney, C.D. & Leafloor, J.O. (2003) Influence of body size and condition on harvest and survival of juvenile Canada geese. *The Journal of Wildlife Management*, **67** 530-541.

IPCC (2012) *Managing the risks of extreme events and disasters to advance climate change adaptation: special report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, UK.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D. & van Ruijven, J. (2011) High plant diversity is needed to maintain ecosystem services. *Nature,* **477,** 199-202.

Jefferies, R.L., Jano, A.P. & Abraham, K.F. (2005) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology,* **94,** 234-242.

Jenouvrier, S. (2013) Impacts of climate change on avian populations. *Global Change Biology,* **19,** 2036–2057.

Jensen, G.H., Madsen, J., Johnson, F.A. & Tamstorf, M.P. (2014) Snow conditions as an estimator of the breeding output in high-Arctic pink-footed geese Anser brachyrhynchus. *Polar Biology,* **37,** 1-14.

Jiang, L. & Pu, Z. (2009) Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *The American Naturalist,* **174,** 651-659.

Kerbes, R., Meeres, K., Alisauskas, R., Caswell, F. & Abraham, K. (2006) Inventory of nesting mid-continent lesser snow and Ross's geese in Eastern and Central Arctic Canada, 1997-98. *Canadian Wildlife Service Technical Report Series, Winnipeg, MB.*

Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McInerny, G.J., Montoya, J.M., Römermann, C., Schiffers, K. & Schurr, F.M. (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography,* **39,** 2163-2178.

Kondoh, M. (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science,* **299,** 1388-1391.

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

Koons, D.N., Rockwell, R.F. & Aubry, L.M. (2014) Effects of exploitation on an overabundant species: the lesser snow goose predicament. *Journal of Animal Ecology,* **83,** 365-374.

Lawson, C.R., Vindenes, Y., Bailey, L. & Pol, M. (2015) Environmental variation and population responses to global change. *Ecology Letters,* **18,** 724–736.

Leafloor, J., Moser, T. & Batt, B. (2012) Evaluation of special management measures for midcontinent lesser snow geese and Ross's geese. *Arctic Goose Joint Venture Special Publication. US Fish and Wildlife Service, Washington, DC and Canadian Wildlife Service, Ottawa, Ontario*.

Lyons, K.G., Brigham, C., Traut, B. & Schwartz, M.W. (2005) Rare species and ecosystem functioning. *Conservation Biology,* **19,** 1019-1024.

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

McCann, K.S. (2000) The diversity–stability debate. *Nature,* **405,** 228-233.

Mellor, A.A. & Rockwell, R.F. (2006) Habitat shifts and parasite loads of lesser snow geese (Chen caerulescens caerulescens). *Ecoscience,* **13,** 497-502.

Merow, C., Latimer, A.M., Wilson, A.M., McMahon, S.M., Rebelo, A.G. & Silander, J.A. (2014) On using integral projection models to generate demographically driven predictions of species' distributions: development and validation using sparse data. *Ecography,* **37,** 1167-1183.

Miller-Rushing, A.J., Høye, T.T., Inouye, D.W. & Post, E. (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 3177-3186.

Morrissette, M., Bêty, J., Gauthier, G., Reed, A. & Lefebvre, J. (2010) Climate, trophic interactions, density dependence and carry-over effects on the population productivity of a migratory Arctic herbivorous bird. *Oikos,* **119,** 1181-1191.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S. & Mouquet, N. (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology,* **11,** e1001569.

Mulder, C.P., Iles, D.T. & Rockwell, R.F. (2016) Increased variance in temperature and lag effects alter phenological responses to rapid warming in a subarctic plant community. *Global Change Biology,* **23,** 801–814.

Naeem, S. & Li, S. (1997) Biodiversity enhances ecosystem reliability. *Nature,* **390,** 507-509.

Newton, I. (1977) Timing and success of breeding in tundra-nesting geese. *Evolutionary Ecology*, pp. 113-126. Springer.

Nicole, F., Dahlgren, J.P., Vivat, A., Till-Bottraud, I. & Ehrlen, J. (2011) Interdependent effects of habitat quality and climate on population growth of an endangered plant. *Journal of Ecology,* **99,** 1211-1218.

Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology,* **13,** 1860-1872.

Richman, S.E., Leafloor, J.O., Karasov, W.H. & McWilliams, S.R. (2015) Ecological implications of reduced forage quality on growth and survival of sympatric geese. *Journal of Animal Ecology,* **84,** 284-298.

Riley, J. (2003) *Flora of the Hudson Bay Lowland and its postglacial origins*. NRC Research Press.

Sæther, B.-E. & Engen, S. (2010) Population consequences of climate change. Effects of climate change on birds (eds A. Møller, Fiedler W. & P. Berthold), pp. 191-212. Oxford University Press, New York.

Schurr, F.M., Pagel, J., Cabral, J.S., Groeneveld, J., Bykova, O., O'Hara, R.B., Hartig, F., Kissling, W.D., Linder, H.P. & Midgley, G.F. (2012) How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *Journal of Biogeography,* **39,** 2146-2162.

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

Sedinger, J.S., Flint, P.L. & Lindberg, M.S. (1995) Environmental influence on life-history traits: growth, survival, and fecundity in black brant (Branta bernicla). *Ecology,* **76,** 2404-2414.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W. & Carvalho, L. (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology,* **16,** 3304-3313.

Treurnicht, M., Pagel, J., Esler, K.J., Schutte-Vlok, A., Nottebrock, H., Kraaij, T., Rebelo, A.G. & Schurr, F.M. (2016) Environmental drivers of demographic variation across the global geographical range of 26 plant species. *Journal of Ecology,* **104,** 331-342.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters,* **11,** 1351-1363.

Winiarski, K.J., McWilliams, S.R. & Rockwell, R.F. (2012) Rapid environmental degradation in a subarctic ecosystem influences resource use of a keystone avian herbivore. *Journal of Animal Ecology,* **81,** 1132–1142.

Wootton, J.T. & Emmerson, M. (2005) Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 419-444.

Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences,* **96,** 1463-1468.

Figures

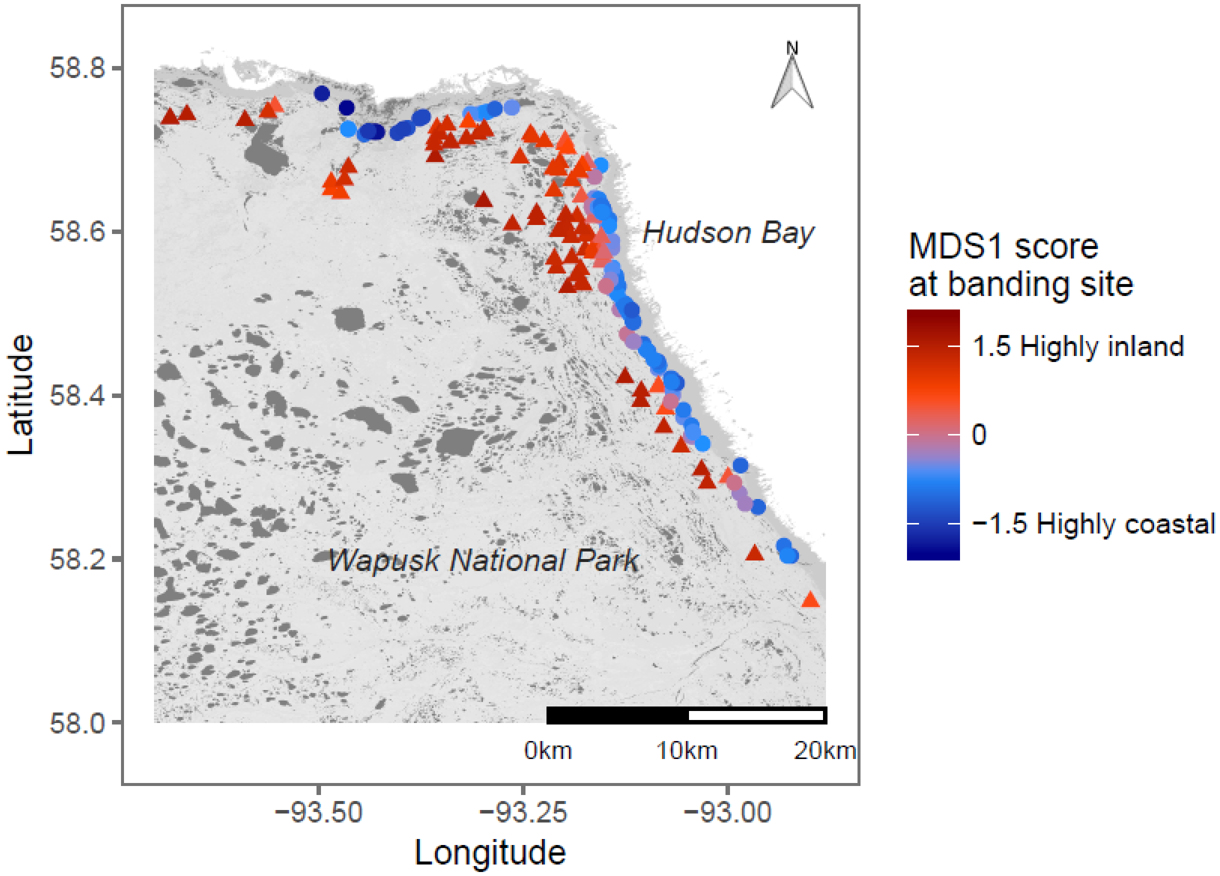

Fig. 3.1. Landscape composition within 2 km of banding locations. For presentation, only the northern part of the study area is pictured. Banding locations are colored according to their scores along the first axis of land cover ordination (nonmetric multidimensional scaling; MDS), which is based on Brook and Kenkel's (2002) land cover map for Wapusk National Park.

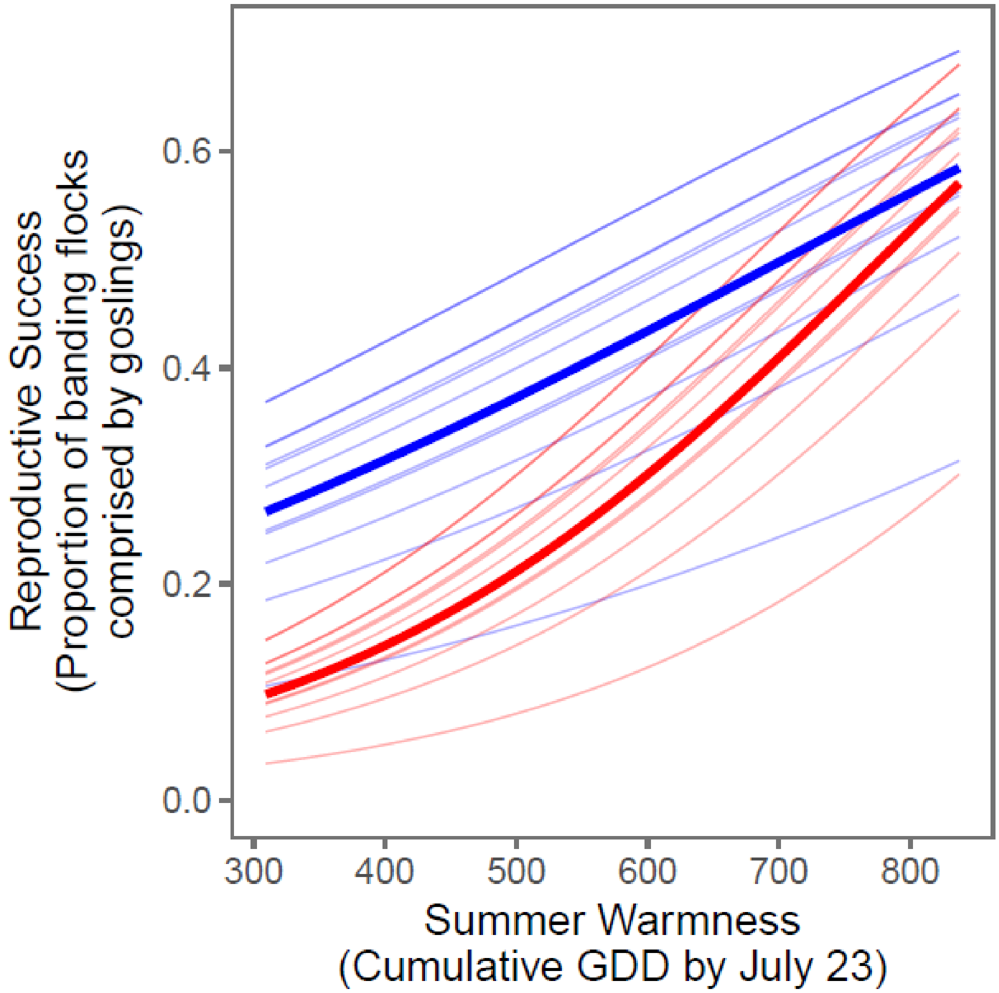

Fig. 3.2. Relationship between snow goose reproductive success and seasonal temperature (measured as cumulative growing degree days by calendar day 204) across habitats. Fitted curves show predicted responses in highly coastal habitats (5th percentile of MDS1 scores; blue curve) and highly inland habitats (95th percentile of MDS1 scores; red curve) controlling for residualized gosling age and habitat degradation. Thick lines show grand mean predictions from mixed effects model and thin lines depict random effects of study years.

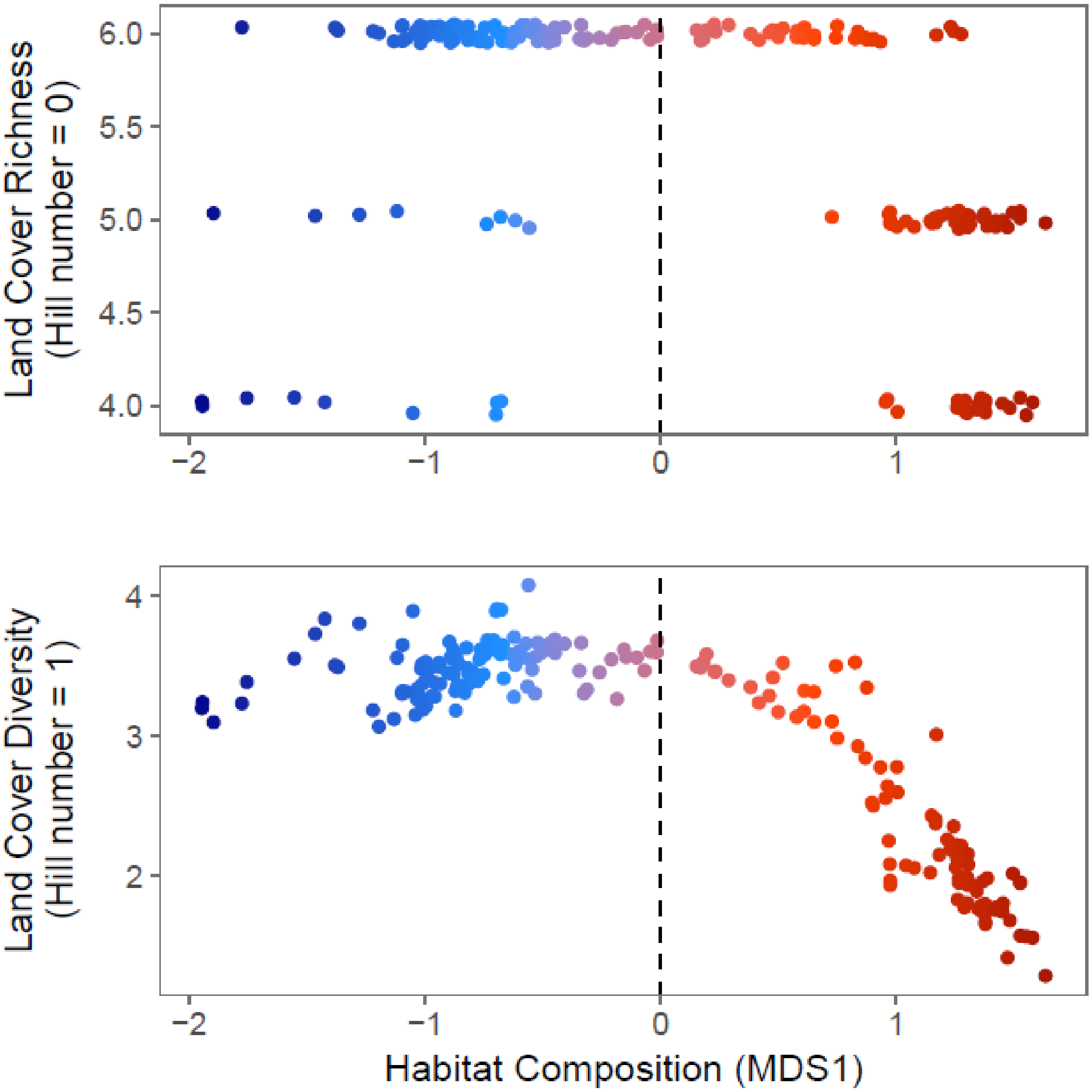

Fig. 3.3. Relationship between land cover diversity and habitat composition (MDS1 score, where more positive values indicate more inland sites). Land cover diversity was calculated using two standard measures: either as richness (Hill number = 0; top panel) or the exponent of Shannon diversity (Hill number = 1; top panel). Dashed line depicts threshold for discrete categorization of habitat (salt: MDS1 < 0, fresh: MDS1 > 0, where 0 is the mean of banding location MDS1 values).

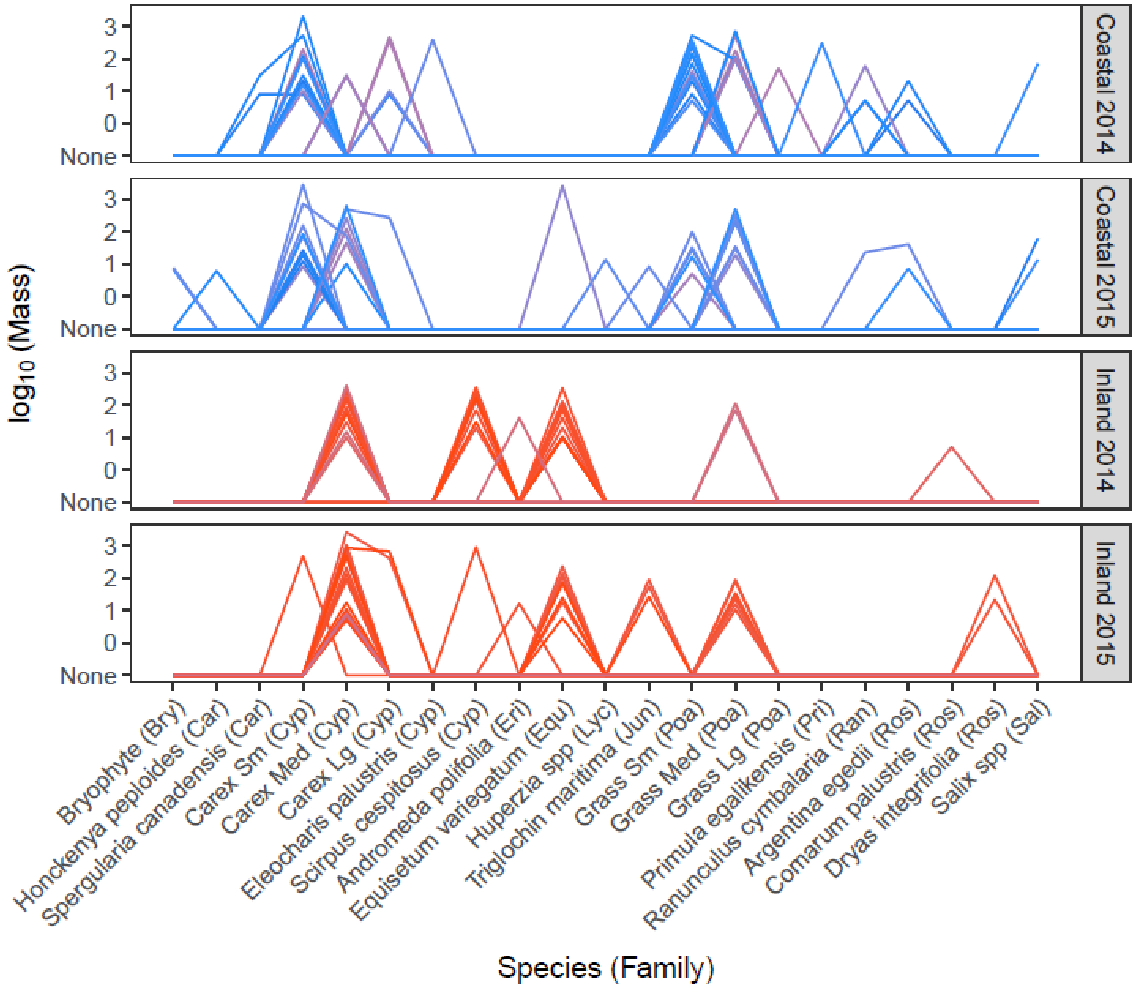

Fig. 3.4. Mass of diet items (in mg) identified from goslings collected in coastal and inland habitats in 2014 and 2015. Each line corresponds to a different gosling and is colored according to the habitat score (MDS1) in which that gosling was collected; shading uses same scale as Figs. 1, 2, and 3 (darker blue corresponds to more coastal habitats; darker red corresponds to more inland habitats). A line plot was used instead of boxplots to visualize potential correlations among diet items appearing within individual goslings. Note that y axis is a logarithmic scale to allow visualization of relatively rare items (i.e., $\log_{10}(\text{Mass}) < 1$).

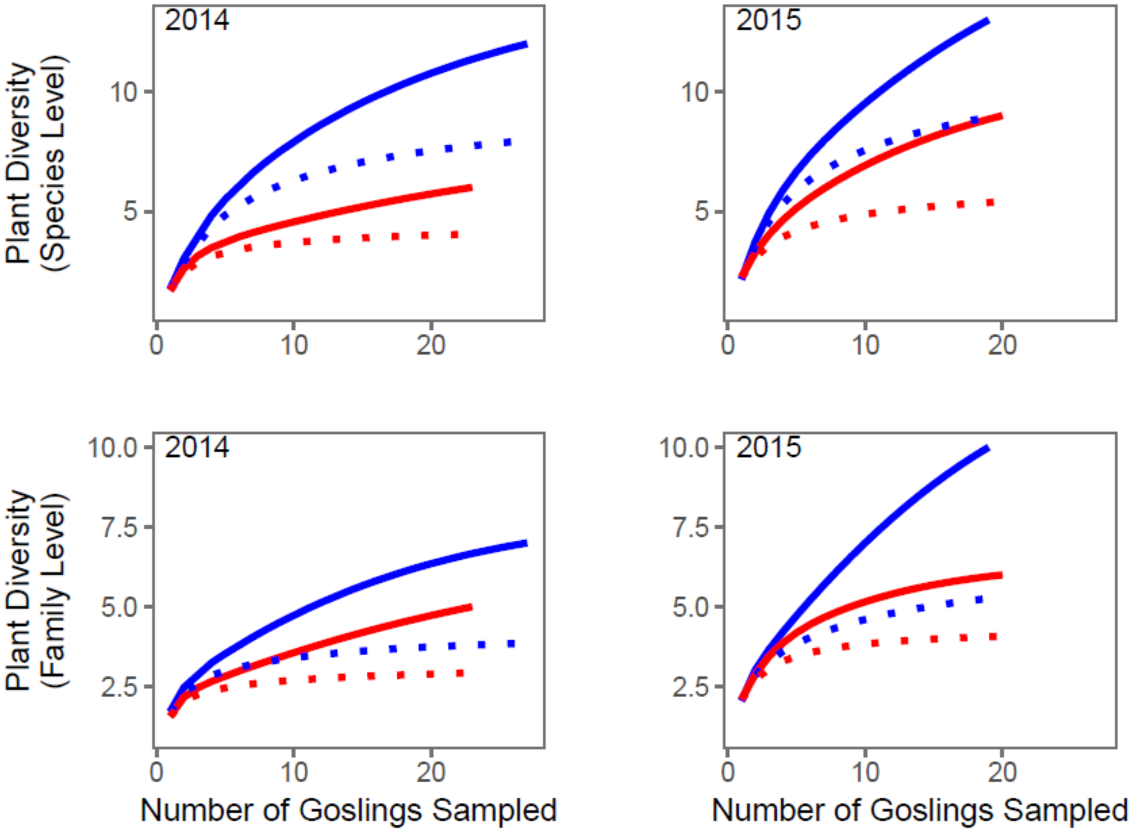

Fig. 3.5. Rarefaction curves for diets of goslings collected in coastal (blue lines) and inland habitats (red lines) when diet items were identified to species level (top row) or family level (bottom row). Rarefaction curves were calculated separately for 2014 (left column) and 2015 seasons (right column). Solid lines are rarefaction curves based on richness (Hill number 0), dashed lines are rarefaction curves based on the exponent of Shannon diversity (denoted exp(*H'*) in main text; Hill number 1). Confidence intervals are not shown for clarity of presentation but are discussed in Results section.

CHAPTER 4

CLIMATE CHANGE IMPROVES THE SUITABILITY OF NOVEL HABITATS FOR A KEYSTONE HERBIVORE

Introduction

Directional changes in multiple aspects of climate, coupled with increased variance (Tebaldi *et al.* 2006; Stocker *et al.* 2013) has already impacted species range limits and phenology (Parmesan 2006; Parmesan 2007), with concomitant impacts on the demography of affected populations (Boyce, Haridas & Lee 2006; Miller-Rushing *et al.* 2010; Jenouvrier 2013). Forecasting the future condition of populations remains a key goal of applied ecological research (Botkin *et al.* 2007; Bellard *et al.* 2012). A detailed understanding of the mechanisms by which the environment affects population dynamics is therefore necessary for guiding management in uncertain and changing climates (Jenouvrier 2013).

Accurately predicting the effects of environmental change on population dynamics is complicated by a variety of factors. Species interactions can modify demographic responses to climate (Ettinger, Ford & HilleRisLambers 2011; Wisz *et al.* 2013; Alexander, Diez & Levine 2015), and climate can feed-back to influence the suite of species with which a focal population interacts through shifts in phenology, range boundaries, or both (Williams & Jackson 2007; Tylianakis *et al.* 2008; Alexander *et al.* 2016). Variation in the biotic community can therefore cause differences in climate sensitivity between populations across a species range (Nicole *et al.* 2011; also see Chapter 3; Alexander, Diez & Levine 2015), potentially limiting the generality of demographic forecasts developed from data for a single population (Coutts *et al.* 2016).

Many natural populations of conservation concern also exhibit demographic stage structure, such that rates of birth, growth, and death depend on the size, age, or developmental stage of individuals in the population (Caswell 2001). In structured populations, multiple vital rates may respond simultaneously and in different ways to environmental factors, thereby preventing a linear mapping of environmental variation onto population growth (Koons *et al.* 2009; Lawson *et al.* 2015). Vital rate covariation can amplify or dampen environmental effects and can be generated when multiple vital rates respond jointly to environmental pressures (Doak *et al.* 2005; also see chapter 2 in this dissertation; Boyce, Haridas & Lee 2006). Demographic forecasts must therefore consider multiple pathways through which demography can be affected by environmental effects (Jenouvrier 2013).

Lesser snow geese (*Chen caerulescens caerulescens*) are Arctic-breeding, migratory herbivores for which the potential demographic effects of climate change have recently been highlighted (Rockwell, Gormezano & Koons 2011; Aubry *et al.* 2013; also see chapter 3). In the past several decades, breeding populations of lesser snow geese have expanded from traditional coastal saltmarsh habitats (Cooch *et al.* 1993), and now extensively use abundant inland freshwater meadows for brood rearing (Winiarski, McWilliams & Rockwell 2012; Aubry *et al.* 2013). In chapter 3, we found that the annual production of goslings responded more strongly to climate warming in inland freshwater meadows than in coastal saltmarsh habitats. Breeding season temperatures are increasing and becoming more variable in the Hudson Bay Lowlands (Mulder, Iles & Rockwell 2016). Climate change therefore has the potential to strongly and differentially alter the suitability of both traditional and novel breeding habitats. Novel inland sedge meadow habitats are over 120 times more abundant than traditional coastal saltmarsh (Brook & Kenkel 2002), and could therefore potentially provide a vast landscape for breeding populations of geese to exploit under future warming.

The possibility for climate change to improve the suitability of vast inland freshwater habitats for snow geese is particularly problematic from a management perspective. In the past several decades, expanding snow goose populations caused severe degradation of Arctic salt marsh habitats and changes to harvest regulations were subsequently implemented in an effort to reduce abundance (Abraham, Jefferies & Alisauskas 2005; Jefferies, Jano & Abraham 2005). However, while increased hunting pressure initially reduced adult survival, population growth has since continued unabated (Alisauskas *et al.* 2011; Koons, Rockwell & Aubry 2014). Warming temperatures may further attenuate management efforts by increasing annual snow goose reproductive success, especially if novel inland breeding habitats become suitable for positive population growth.

Nevertheless, it is unclear how warming and more variable temperatures will scale up to impact overall snow goose population dynamics in each habitat. Given that vital rate responses to environmental covariates are often nonlinear, changes in the mean and variance of climate can have different effects on population performance (Ruel & Ayres 1999; Lawson *et al.* 2015). Furthermore, vital rate covariation may be generated when multiple vital rates respond simultaneously to environmental pressures, which can buffer or amplify the effect of increased environmental variance (Doak *et al.* 2005; chapter 2 in this dissertation; Barraquand & Yoccoz 2013). If post-fledging survival of offspring responds in an opposite direction to reproductive success, increased productivity in warm seasons may be counterbalanced by decreased offspring survival, resulting in little overall effect on population dynamics (a phenomenon referred to as "demographic compensation"; Doak & Morris 2010). A population model that links demographic parameters to environmental drivers is therefore necessary to characterize the effects of climate change when channeled through multiple demographic rates simultaneously (Jenouvrier 2013; Ehrlén & Morris 2015).

Here, we develop a time-variant, stage-structured population model to investigate the consequences of habitat-specific demography and climate sensitivity on snow goose population dynamics. After developing our model, we first conduct an elasticity analysis that allows us to examine differences in the sensitivity of populations to climate perturbations across habitats. We then measure the rate of change in the mean and variance of seasonal warmness at our study site and use a series of population projections to estimate their combined effects on future habitat suitability.

We find that climate change increases population growth in all habitats, but that such increases are disproportionately large in novel inland sedge meadow habitats. Our results suggest that novel habitats will support stable populations of geese under continued climate change and allow for positive population growth in the short-term owing to stochastic fluctuations in climate. Our study therefore provides a lens through which to examine the effect of biotic and abiotic interactions on population and range dynamics, and offers an important example of the capacity for climate change to offset management efforts for a species of concern.

Methods

Study Area and Data Collection

Data were collected as part of a long-term study of lesser snow geese in the Cape Churchill region of the western Hudson Bay Lowlands. Annually, flocks of approximately 600 snow geese (range: 63 to 1982 individuals per flock) were opportunistically rounded up at multiple locations across the study area. Each individual is fitted with a uniquely numbered USGS leg band, and age and sex are recorded. Age ratios in late-summer banding drives provide an estimate of seasonal reproductive success (i.e., number of goslings produced per adult), and likely reflect gosling survival following hatch (chapter 3). Live recaptures of geese at our study site and hunter reports of leg-banded birds shot during the hunting season (dead recoveries) provide information to estimate annual survival. We restricted our survival analysis to females as this sex is philopatric to the breeding colony, and only used records for individuals captured and banded as goslings, and were therefore of known age.

Banding locations, which we assume are representative of local brood rearing areas, are distributed across approximately 100 kilometers of coastline in the Cape Churchill region and encompass both traditional coastal areas and novel inland habitats (see Fig. 3.1 in chapter 3 of this dissertation). We extracted the relative proportions of land cover classes within 2 km of each banding site, and used an ordination technique (nonmetric multidimensional scaling; NMDS) to collapse this multivariate land cover data into primary axes of landscape variation. The first axis of this ordination (MDS1) described the continuous transition from highly coastal habitats ($MDS1 < 0$) to highly inland habitats (MDS1 > 0). We used site-specific scores along this ordination axis as a measure of gosling habitat. We also used multi-temporal Landsat imagery to control for the possibly confounding effect of local habitat degradation (see chapter 3).

In chapter 3 we found that breeding season warmness, measured as the number of growing degree days that have accumulated by calendar day 204 (GDD_{204}), was a strong predictor of annual reproductive success at our study site. Previous research has also found that summer warmness is increasing and becoming more variable at our study site (Mulder, Iles & Rockwell 2016). We therefore used this metric of seasonal weather conditions in models for reproductive success and post-fledging survival of goslings as a basis for studying the potential consequences of climate change on snow goose population dynamics.

Model for Annual Reproductive Success

In chapter 3, we developed a model to relate annual habitat-specific reproductive success to environmental drivers. In this model, GDD_{204} was found to have non-linear effects on reproductive success, and this effect differed between coastal and inland habitats. The model accounts for effects of local habitat degradation and variation in hatching date between years, and includes random year effects to account for additional annual variation not explained by breeding season warmness. The model predicts the proportion of snow goose flocks that are comprised of goslings at the time of banding. To convert this response into an estimate of the number of goslings produced per female (and thus an estimate of seasonal reproductive success per female, F), we convert this proportional response to a ratio using $p/(1-p)$ where p is the proportion of banding flocks comprised by goslings.

Capture-Reencounter Model for Survival

We used a multistate model to quantify the effects of climate and habitat on post-fledging survival of females. The model consisted of two states (Fig. 4.1), alive (A) and dead (D) with the annual transition probability from state A to D (denoted as μ_i) representing mortality. Following Koons, Rockwell & Aubry (2014), we fixed the transition probability from state D to A to 0, thereby defining state D as an "absorbing state". Because mortality is described by μ_i (and therefore survival as 1- μ_i), we fixed remaining multistate survival probabilities for individuals in states A and D to 1 and 0, respectively.

We estimated μ_i conditionally on probabilities of observing individuals in state A (p_i^A; based on recapturing live individuals) and on recoveries of dead individuals in state D (p_i^D; based on individuals that were killed, retrieved, and reported by hunters). We fixed relevant detection probabilities to 0 in years where banding operations did not occur (1996, 1997, and 2009), and when certain age classes were not available for banding (e.g., no goslings were banded due to complete reproductive failure in 2002 and 2004).

Band recovery probability differs between hatch-year (HY) and after-hatch-year (AHY) snow geese (Cooch, Rockwell & Brault 2001). We therefore fit our multistate models with 2 age classes for probability of mortality ($\mu_{HY,i}$ and $\mu_{AHY,i}$) and dead recovery ($p_{HY,i}^D$ and $p_{AHY,i}^D$). Because snow geese do not breed until at least two years of age, and are thus not recaptured in their first year, we fixed recapture probability of 1 year olds to 0.

For probability of live recapture, we included a linear effect of age (up to 5 years old) to accommodate the fact that recapture increases up to 5 years of age as a function of breeding probability (Cooch, Rockwell & Brault 2001). Additionally, we included a cubic time trend for live recapture probability to allow this parameter to flexibly change over the course of our study, as this was the best supported temporal parameterization (Table C1 in Appendix C; discussed below). For the probability of dead recovery, we included an effect of published annual band-reporting rates in Alisauskas et al. (2011) with separate effects for each age class following Koons, Rockwell & Aubry (2014).

Our primary objective was to gain insight into the effects of breeding season temperature and habitat on population dynamics acting jointly through reproductive success and post-fledging (hereafter, 'hatch year') survival. Although we did not detect significant environmental effects on gosling body condition at the time of banding in chapter 3, our analysis may have lacked power to detect subtle responses given our highly conservation criteria for including data in our analysis. A separate analysis of this dataset using a longer time series of gosling morphometric measurements detected environmental effects on body condition, which scaled up to strongly affect first year survival (Aubry *et al.* 2013). Thus, effects of habitat and seasonal weather on post-fledge hatch-year survival of goslings are plausible.

We used a tiered model selection approach to determine the best structure for recapture and hatch-year survival probabilities. First, we fit a model that included interactive effects of seasonal warmness (GDD_{204}) and habitat composition (MDS1) on hatch-year survival of geese. As with our analysis of reproductive success, we corrected for spatial variation in severity of habitat degradation and temporal variation in hatch date by including “control” covariates in all models that describe the residual variation in these effects, after accounting for habitat composition and seasonal warmness (see chapter 3). This represented the most complex model structure for hatch-year survival that we considered. Using this parameterization for hatch-year survival, we fit four models that included different temporal trends in the probability of live recapture: no trend, a linear trend, a quadratic trend, and a cubic trend. Upon determining the best structure for live recapture (a cubic trend; Table C1 in Appendix C), we then fit a series of less complex models for hatch-year survival in addition to the model that included an interactive effect of habitat and warmness. These less complex models included: 1) no effects of habitat or warmness, 2) only an effect of warmness, 3) only an effect of habitat, 4) additive effects of habitat and warmness. We assessed relative support for competing models at each tier using Schwarz’s information criterion (SIC; Schwarz 1978; also often called BIC).

We did not fit annual effects of breeding season weather and habitat for survival of adult female geese. This choice was motivated by several factors. First, adult geese have extremely high annual survival with relatively low temporal process variation (Koons, Rockwell & Aubry 2014), suggesting that climate variation during the breeding season is unlikely to have strong effects on annual survival. Second, without knowledge of habitat use by individual adult geese in years when they were not observed, and use of agricultural habitats across the full annual life cycle (Abraham, Jefferies & Alisauskas 2005), we could not investigate habitat-specific effects of climate on adult survival.

Accounting for temporal variation in adult survival was nevertheless necessary to generate accurate conditional estimates of hatch-year survival. We used year-specific estimates of adult survival from Koons, Rockwell & Aubry (2014) to derive an informative rank-order covariate for $\mu_{AHY,i}$ in our models. For the years 2011-2015 in our study (which were not included in the previous study), we used the mean rank of adult survival for years 2006-2010 from Koons, Rockwell & Aubry (2014). We also included a separate effect for the year 2002 to account for extremely low adult survival in this year, which was not adequately described by our rank-order covariate. Estimates of annual adult survival from Koons, Rockwell & Aubry (2014) were highly correlated with estimates from our models and fell closely along a 1:1 line, indicating adult survival in our model closely aligned with estimates from their previous detailed analysis of adult survival.

Multistate models were fit using the ‘RMark’ package (Laake & Rexstad 2008) in R version 3.3.2, interfaced with Program MARK version 7.1 (White & Burnham 1999). Multistate models were also fit using the simulated annealing option to help achieve convergence.

Stochastic Population Model

We used our models for annual reproductive success (F) and hatch-year survival (S_{HY}) to construct a stage-structured time-varying population model, allowing us to investigate the overall effects of climate on snow goose population dynamics across habitats, as channeled through impacts on F and S_{HY}. We used a pre-breeding census parameterization and constructed annual projection matrices with five stage classes as:

$$\mathbf{A}[t] = \begin{bmatrix} 0 & BP_2 \cdot F[t] \cdot S_{HY}[t] & BP_3 \cdot F[t] \cdot S_{HY}[t] & BP_4 \cdot F[t] \cdot S_{HY}[t] & BP_{5+} \cdot F[t] \cdot S_{HY}[t] \\ S_{AHY} & 0 & 0 & 0 & 0 \\ 0 & S_{AHY} & 0 & 0 & 0 \\ 0 & 0 & S_{AHY} & 0 & 0 \\ 0 & 0 & 0 & S_{AHY} & S_{AHY} \end{bmatrix}, \quad (1)$$

where BP_i represents the probability that a female in stage class i attempts to breed. Annual breeding probability of each stage class was time-invariant our models, increased with age, and reached a maximum for females five years and older (BP_1 = 0; BP_2 = 0.35; BP_3 = 0.77; BP_4 = 0.83, BP_{5+} = 0.85 according to Cooch, Rockwell & Brault (2001). We allowed F and S_{HY} to vary through time according to estimated relationships with environmental drivers (as described above). We fixed S_{AHY} at its mean value, thereby omitting temporal variation in this parameter.

Annual, habitat-specific population growth rate was calculated as $\log(N_{t+1}/N_t)$. Assuming that adult geese and their offspring are consistent in their habitat use throughout life (i.e., perfect natal philopatry), the long-term stochastic growth rate of the population can be calculated separately for a particular habitat (i.e., based on a specific score of MDS1) as:

$$\log \lambda_{\mathrm{s,hab}} = \frac{1}{T}\sum_{t=0}^{T-1} \log\left(\frac{N_{t+1,hab}}{N_{t,hab}}\right), \quad (2)$$

where the time horizon T is a large number (set to 2 million in our analyses to minimize sampling variation across our simulations). In reality, although female geese are philopatric to natal brood rearing areas, there is likely some degree of flexibility in habitat use through time (Cooch *et al.* 1993). If annual habitat use of individual geese depends on climate or previous habitat use, a source-sink population model would be necessary to accurately characterize environmental effects while accounting for dispersal. We return to this point in the *Discussion*, where we discuss the interpretation of our measures of $\log\lambda_S$ under imperfect natal philopatry.

We used our stochastic population model to address two key questions. First, we performed an elasticity analysis to measure the relative effects of proportional changes in the mean and variance of seasonal warmness on $\log\lambda_S$ in each habitat, as channeled through effects on F and S_{HY} (but not other demographic parameters). Second, we quantified the effect of observed climate change on the relative suitability of coastal and inland habitats by examining the distribution of annual population growth rates, $\log(N_{t+1}/N_t)$, in each habitat and climate projection. Below, we discuss each of these approaches in more detail.

Elasticity Analysis for Changes in Climate

We performed an elasticity analysis to provide insights into the relative effects of proportional changes in the mean and variance of climate parameters on long-term population growth and to examine how these effects differ across habitats. We first calculated $\log\lambda_S$ in each habitat, assuming a stationary environmental distribution, using the mean and standard deviation of seasonal warmness between 1990 and 2015. We then increased the mean or standard deviation of seasonal warmness by 5% and calculated the resulting difference in $\log\lambda_S$ under each proportional change. Elasticities, defined as the proportional change in λ_S in each habitat arising from a proportional change in a climate parameter (x), were calculated numerically as:

$$\frac{\partial \log \lambda_{S,hab}}{\partial \log x} = \left(\frac{\Delta\lambda_{S,hab}}{\lambda_{S,hab}}\right)\left(\frac{x}{\Delta x}\right), \tag{3}$$

where $\Delta\lambda_{S,hab}$ is the absolute change in λ_s arising from an absolute change in the climate parameter (Δx).

Modeling Relative Habitat Suitability under Climate Change

Our final goal was to compare the relative suitability of coastal and inland habitats (traditional and novel habitats, respectively) under shifting climate regimes. To achieve this goal, we first estimated the rate of change in seasonal warmness at our study site. We fit four models to the entire time series of climate data: 1) a constant mean and variance, 2) a changing mean but constant variance, 3) a constant mean but changing variance, and 4) a changing mean and variance. Parameters describing the mean, variance, and temporal trends associated with each were estimated using maximum likelihood, assuming a normal distribution for seasonal warmness, following methods described in Bolker (2008; chapter 6), and using the 'bbmle' package in R (Bolker 2010). We assessed support for competing models using SIC.

Based on these rates of change, we calculated the projected mean and variance of seasonal warmness in each year between 1990 and 2100, assuming a constant rate of change in the future. We then conducted a series of long-term population projections for each year between 1990 and 2100, using the expected mean and variance of each climate variable that year as a basis for generating distributions of environmentally-determined vital rates. We used the resulting distributions of annual population growth (N_{t+1}/N_t) for each habitat in each year to gain insight into the capacity for climate change to alter habitat suitability. If future climate resulted in higher long-term growth rates (λ_s) in one or both habitats, we concluded that climate change will improve the long-term suitability of these areas. Further, the distribution of potential short-term (i.e., annual) values of N_{t+1}/N_t provides insight into the ability of climate change to affect short-term habitat suitability, which geese may exploit if there is sufficient flexibility in annual habitat choice. We discuss these points in further detail in the *Discussion.*

Results

Models for F and S_{HY}

Our model for annual habitat-specific reproductive success, F, is detailed in chapter 3 but we present results from this model in Fig. 4.2 for comparison with climate effects on post-fledging hatch year survival, S_{HY}. The model includes non-linear, highly convex effects of annual breeding season warmness (GDD_{204}) on the reproductive success of snow geese, and these effects depend on local habitat composition (MDS1). Because habitat composition is a continuous variable that describes the transition from coastal to inland habitats, we focus our presentation of results on either end of this continuum to provide a useful comparison of effect sizes in highly contrasting landscapes (where “highly coastal” and “highly inland” are defined as sites that have habitat composition MDS1 scores in the 5th and 95th percentiles, respectively). Warmer seasons resulted in greater production of goslings in both highly coastal and highly inland (Fig. 4.2). The strength of this effect differed between coastal and inland habitats; reproductive success responds much more strongly to climate in inland habitats than coastal habitats

(Fig. 4.2). As a result, reproductive success was lower in inland habitats than in coastal habitats under mean environmental conditions, but is similar to coastal habitats in warm seasons.

The best model for post-fledging survival, S_{HY}, included a weak but statistically significant effect of habitat (Table C2 and C3 in Appendix C). Goslings banded in highly inland sites had higher first-year survival than goslings banded in highly coastal sites. Based on this model, mean first-year survival for goslings banded in the most extreme coastal and inland habitats were 0.28 and 0.33, respectively. The top model did not include an effect of seasonal warmness on first-year survival. Adult survival, S_{AHY}, ranged from 0.79 to 0.90 over the course of our study, with a mean of 0.85.

Elasticity Analysis for Changes in Climate

Increases in both the mean and variance of seasonal warmness had positive effects on long-term population growth (λ_s) in both coastal and inland habitats (Fig. 4.3). However, the proportional effect of increases in mean seasonal warmness was approximately 1.49 times larger in highly inland habitats relative to highly coastal habitats. Similarly, the positive effect of increased inter-annual variability in seasonal warmness was 2.9 times larger in highly inland habitats than highly coastal habitats. Notably, the elasticity of λ_s to changes in the variance of GDD_{204} was larger than the elasticity to changes in the mean of GDD_{204} for highly inland habitats; proportional increases in the variance of GDD_{204} have a larger positive impact on λ_s than proportional increases in the mean of GDD_{204} and both of these effects are larger in highly inland habitats than highly coastal habitats. Population responses to warmer and more variable seasons are therefore much stronger in inland habitats than coastal habitats.

Population Growth under Climate Change

The mean and variance of annual breeding season warmness (GDD_{204}) have increased significantly since 1935 (Fig. 4.4; Table C4 in Appendix C). A statistical model for GDD_{204} that included a trend in both the mean and variance received slightly more support than a model that only included a trend in the mean ($\Delta SIC = 1.3$), and much more support than a model that included no trend in either the mean or variance ($\Delta SIC = 8.0$). We therefore conclude that there is strong evidence for a long-term warming trend and marginal support for increasing variance in seasonal warmness at our study site.

The long-term mean of $\log(N_{t+1}/N_t)$ in each habitat, $\log\lambda_s$, calculated in each year of study based on the projected mean and variance of seasonal temperature, describes long-term population trajectories if geese are perfectly philopatric to their natal habitats and thus do not switch habitats between years. Imperfect philopatry would result in source-sink dynamics, which would result a single population response somewhere between these two extremes. We nevertheless present these results as possible bounds between which populations will respond to observed rates of climate change.

Under the predicted climate distribution in 2015 (i.e., current climate), λ_s for populations inhabiting coastal habitats is greater than in inland habitats (Fig. 4.5). Long-term population growth rate increased progressed in both highly coastal habitats and highly inland habitats as climate change progressed and seasons became warmer and more variable. However, climate-driven increases in λ_s were greater in inland than coastal habitats; λ_s increased by approximately 5% between 1990 and 2100, while λ_s

increased by 9% in inland habitats over the same period. If climate trends continue until 2070, inland habitats will be as productive as coastal habitats are currently.

If geese are not perfectly philopatric to natal brood rearing habitats, the distribution of short-term (i.e., annual) population growth rates may be of greater relevance, as individuals may flexibly select breeding habitats on an annual basis based on cues for predicted habitat quality. Assuming no further degradation, currently occupied coastal habitats are consistently of relatively high quality and continue to improve with climate change (Fig. 4.5a, blue ribbon). Under current climate, inland habitats are much less suitable than coastal habitats and likely cannot support positive annual population growth in most years. However, the proportion of years resulting in positive population growth rapidly increased as climates become warmer and more variable.

Discussion

Demographic responses to climate can be strongly mediated by the biotic environment, resulting in differences in climate sensitivity across habitats and populations (Ettinger, Ford & HilleRisLambers 2011; Alexander, Diez & Levine 2015; Alexander *et al.* 2016). By affecting demography, the biotic and abiotic environment interact to determine the conditions under which positive population growth can be attained, thereby influence range limits (Sexton *et al.* 2009; Wiens 2011). Accounting for the interplay between the biotic and abiotic environment is therefore necessary for anticipating the capacity for populations to shift their ranges and maintain stable or growing populations in the face of changing climates (Tylianakis *et al.* 2008).

Here, we extended our investigation from chapter 3 and found that the differing responses of reproductive success across habitats scaled up to strongly affect population-level sensitivity to climate change. These differences disproportionately increase the short- and long-term suitability of novel habitats, relative to historical suitability (Figs. 4.3 & 4.5). If climate change continues at its current rate, inland habitats will support the same rate of population growth as coastal habitats do currently. Inland freshwater meadows represent novel brood rearing habitats for lesser snow geese in the Hudson Bay Lowlands (Winiarski, McWilliams & Rockwell 2012; Aubry *et al.* 2013). Because these landscapes are over 200 times more abundant than traditional coastal saltmarshes in the Hudson Bay Lowlands (Brook & Kenkel 2002), continued climate warming may also considerably augment the breeding range of this population of lesser snow geese.

Although inland habitats cannot support long-term population growth under current climates, highly stochastic environmental conditions allow for short-term (i.e., annual) population growth in approximately 25% of years (Fig. 4.5b, upper boundary on red ribbon intersects line depicting stable population growth), and the frequency of favorable years will increase under warming. Although snow geese are philopatric to natal breeding and brood rearing locations (Cooch *et al.* 1993; Cooke, Rockwell & Lank 1995), this behavior appears to have relaxed following severe degradation of traditional breeding areas, facilitating colony expansion into new habitats (Aubry *et al.* 2013). If geese are sufficiently flexible to exploit inland habitats only when conditions are favorable, such behavior could relax intraspecific competition and further improve overall population growth rates. In this way, even if inland habitats are not suitable for long-term population persistence, they may provide short-term refugia from effects of density dependence that strongly affect gosling growth and survival in coastal habitats (Cooch *et al.* 1991; Cooch *et al.* 1993; Aubry *et al.* 2013). Future studies that attempt to estimate snow goose site fidelity and dispersal as functions of habitat and climate will shed important light on the ability of these populations to cope with density dependence in variable environments.

Classical methods for modeling species distributions (often called "niche models") use species presence and possibly absence and relative abundance data to infer the set of conditions under which populations can persist (Araújo & Peterson 2012; Ehrlén & Morris 2015). However, populations may 'occupy' habitats that are unsuitable for long-term persistence for a variety of reasons, including an inability to disperse to suitable habitats or an imperfect ability to detect habitat quality, potentially resulting in ecological traps (Van Horne 1983; Kokko & Sutherland 2001). Our results underscore this point. Geese currently occupy inland habitats that appear unsuitable for long-term persistence given current climate, though such habitats may become suitable under future warming, a conclusion that is only apparent by examining long-term demographic responses to climate variation. There is therefore increasing interest using detailed demographic studies to generate future range estimates by determining the set of conditions that lead to positive population growth, either from low density or over the long-term (Holt 2009; Ehrlén & Morris 2015).

Fluctuating environmental conditions complicate the interpretation of an equilibrium range, particularly when movement between habitats of differing quality is possible (Holt 2009). In fluctuating environments, a particular patch may alternatively support positive or negative population growth over the short-term (Johnson 2004). When dispersal is possible, individual patches may function as “short-term sources” if individuals can accurately assess habitat quality and disperse accordingly (Schmidt 2004). Theory suggests that persistence is even possible in fluctuating environments when no patches support long-term persistence because individuals can “stitch together” a sequence of high quality habitats through dispersal (Gonzalez & Holt 2002; Holt 2009).

Overabundant populations of snow geese have severely degraded Arctic and sub-Arctic coastal ecosystems (Jefferies, Jano & Abraham 2005), triggering a trophic cascade that has impacted the abundance and richness of species at multiple trophic levels (Milakovic & Jefferies 2003; Abraham, Jefferies & Alisauskas 2005; Iles *et al.* 2013; Peterson 2013). Our models predict increasing suitability of vast freshwater landscapes, but assume that further degradation to habitats does not occur to alter demographic responses. This assumption is likely valid in the short-term, given that degradation to coastal habitats has largely attenuated (Appendix B) and because extreme degradation of inland habitats has rarely occurred at our study site. The mechanisms responsible for irreversible coastal degradation by destructive goose foraging, which include soil exposure and compaction, reduced infiltration, increased evaporation, and leaching of inorganic salts from marine clays, are less likely to occur in freshwater meadows where grubbing is less intense and the requisite abiotic feedbacks are not present (Abraham, Jefferies & Alisauskas 2005; Jefferies, Jano & Abraham 2005). However, other non-stationary environmental factors (e.g., temporal shifts in the predator community; Rockwell & Gormezano 2009; Rockwell, Gormezano & Koons 2011) could potentially alter the current relationships between snow goose demography, habitat, and seasonal weather. Anticipating the capacity for non-stationary processes to alter historical ecological relationships is extremely difficult (Adler, Byrne & Leiker 2013), but will become increasingly important in a non-stationary era and is critical area of ongoing research (Milly *et al.* 2007).

Our study adds to a growing body of literature that indicates demography varies markedly across space (Doak & Morris 2010; Coutts *et al.* 2016) and responses to climate vary across habitats (Ettinger, Ford & HilleRisLambers 2011; Alexander, Diez & Levine 2015). Such idiosyncrasies will complicate efforts to extrapolate observed climate responses to new habitats and ecological communities, diminish the ability to forecast range shifts under novel climate regimes, and hamper efforts to anticipate future management concerns (Tylianakis *et al.* 2008; Alexander, Diez & Levine 2015). For example, the increasing utilization of freshwater landscapes by snow geese was unanticipated prior to degradation of traditional coastal habitats. Nevertheless, demographic approaches for forecasting abundance and distributions remain promising, as they account for non-equilibrium dynamics and non-linear responses to climate (Ehrlén & Morris 2015). Such approaches will be necessary to guide management in rapidly shifting and highly uncertain environmental regimes.

References

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

Adler, P.B., Byrne, K.M. & Leiker, J. (2013) Can the past predict the future? Experimental tests of historically based population models. *Global Change*

Biology, **19,** 1793-1803.

Alexander, J.M., Diez, J.M., Hart, S.P. & Levine, J.M. (2016) When climate reshuffles competitors: a call for experimental macroecology. *Trends in Ecology & Evolution,* **31,** 831-841.

Alexander, J.M., Diez, J.M. & Levine, J.M. (2015) Novel competitors shape species' responses to climate change. *Nature,* **525,** 515-518.

Alisauskas, R., Rockwell, R., Dufour, K., Cooch, E., Zimmerman, G., Drake, K., Leafloor, J., Moser, T. & Reed, E. (2011) Effect of population reduction efforts on harvest, survival and population growth of Midcontinent lesser snow geese. *Wildlife Monographs,* **179,** 1-42.

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology,* **93,** 1527-1539.

Aubry, L.M., Rockwell, R.F., Cooch, E.G., Brook, R.W., Mulder, C.P. & Koons, D.N. (2013) Climate change, phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. *Global Change Biology,* **19,** 149-160.

Barraquand, F. & Yoccoz, N.G. (2013) When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. *Theoretical Population Biology,* **89,** 1-11.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters,* **15,** 365-377.

Bolker, B. (2010) bbmle: Tools for general maximum likelihood estimation. R package version 0.9.

Bolker, B.M. (2008) *Ecological models and data in R*. Princeton University Press.

Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R. & Faith, D.P. (2007) Forecasting the effects of global warming on biodiversity. *Bioscience,* **57,** 227-236.

Boyce, M.S., Haridas, C.V. & Lee, C.T. (2006) Demography in an increasingly variable world. *Trends in Ecology & Evolution,* **21,** 141-148.

Brook, R. & Kenkel, N. (2002) A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing,* **23,** 4761-4776.

Caswell, H. (2001) *Matrix population models: construction, analysis and interpretation,* 2 edn. Sinauer Associates Inc., Sunderland, Massechusetts.

Cooch, E., Jefferies, R., Rockwell, R. & Cooke, F. (1993) Environmental change and the cost of philopatry: an example in the lesser snow goose. *Oecologia,* **93,** 128-138.

Cooch, E., Lank, D., Rockwell, R. & Cooke, F. (1991) Long-term decline in body size in a snow goose population: evidence of environmental degradation? *Journal of Animal Ecology***, 60**, 483-496.

Cooch, E., Rockwell, R.F. & Brault, S. (2001) Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. *Ecological Monographs,* **71,** 377-400.Cooke, F., Rockwell, R.F. & Lank, D.B. (1995) *The Snow Geese of La Pérouse Bay: Natural Selection in the Wild*. Oxford University Press Oxford.

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

Coutts, S.R., Salguero-Gómez, R., Csergő, A.M. & Buckley, Y.M. (2016) Extrapolating demography with climate, proximity and phylogeny: approach with caution. *Ecology Letters*, **19**, 1429–1438.

Doak, D.F. & Morris, W.F. (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature,* **467,** 959-962.

Doak, D.F., Morris, W.F., Pfister, C., Kendall, B.E. & Bruna, E.M. (2005) Correctly estimating how environmental stochasticity influences fitness and population growth. *The American Naturalist,* **166,** E14-E21.

Ehrlén, J. & Morris, W.F. (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecology Letters,* **18,** 303-314.

Ettinger, A.K., Ford, K.R. & HilleRisLambers, J. (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology,* **92,** 1323-1331.

Gonzalez, A. & Holt, R.D. (2002) The inflationary effects of environmental fluctuations in source–sink systems. *Proceedings of the National Academy of Sciences,* **99,** 14872-14877.

Holt, R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences,* **106,** 19659-19665.

Iles, D.T., Rockwell, R.F., Matulonis, P., Robertson, G.J., Abraham, K.F., Davies, J.C. & Koons, D. (2013) Predators, alternative prey and climate influence annual breeding success of a long-lived sea duck. *Journal of Animal Ecology,* **82,** 683-693.

Jefferies, R.L., Jano, A.P. & Abraham, K.F. (2005) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology,* **94,** 234-242.

Jenouvrier, S. (2013) Impacts of climate change on avian populations. *Global Change Biology*, **19**, 2036–2057.

Johnson, D.M. (2004) Source–sink dynamics in a temporally heterogeneous environment. *Ecology,* **85,** 2037-2045.

Kokko, H. & Sutherland, W.J. (2001) Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research,* **3,** 603-610.

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

Koons, D.N., Rockwell, R.F. & Aubry, L.M. (2014) Effects of exploitation on an overabundant species: the lesser snow goose predicament. *Journal of Animal Ecology,* **83,** 365-374.

Laake, J. & Rexstad, E. (2008) RMark–an alternative approach to building linear models in MARK. *Program MARK: a gentle introduction***,** C1-C113.

Lawson, C.R., Vindenes, Y., Bailey, L. & Pol, M. (2015) Environmental variation and population responses to global change. *Ecology Letters*, **18**, 724–736.

Milakovic, B. & Jefferies, R. (2003) The effects of goose herbivory and loss of vegetation on ground beetle and spider assemblages in an Arctic supratidal marsh. *Ecoscience,* **10,** 57-65.

Miller-Rushing, A.J., Høye, T.T., Inouye, D.W. & Post, E. (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 3177-3186.

Milly, P., Julio, B., Malin, F., Robert, M., Zbigniew, W., Dennis, P. & Ronald, J. (2007) Stationarity is dead. *Ground Water News and Views,* **4,** 6-8.

Mulder, C.P., Iles, D.T. & Rockwell, R.F. (2016) Increased variance in temperature and lag effects alter phenological responses to rapid warming in a subarctic plant community. *Global Change Biology*, **23**, 801–814.

Nicole, F., Dahlgren, J.P., Vivat, A., Till-Bottraud, I. & Ehrlen, J. (2011) Interdependent effects of habitat quality and climate on population growth of an endangered plant. *Journal of Ecology,* **99,** 1211-1218.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637-669.

Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology,* **13,** 1860-1872.

Peterson, S.L. (2013) Legacy Effects of Habitat Degradation by Lesser Snow Geese on Ground-Nesting Savannah Sparrows along the Hudson Bay Lowlands. MS, Utah State University.

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

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

Ruel, J.J. & Ayres, M.P. (1999) Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution,* **14,** 361-366.

Schmidt, K.A. (2004) Site fidelity in temporally correlated environments enhances population persistence. *Ecology Letters,* **7,** 176-184.

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

Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415-436.

Stocker, T., Qin, D., Plattner, G., Tignor, M., Allen, S., Boschung, J., Nauels, A., Xia, Y., Bex, B. & Midgley, B. (2013) Climate Change 2013: The Physical Science Basis. Working Group I Contribution ot the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Tebaldi, C., Hayhoe, K., Arblaster, J.M. & Meehl, G.A. (2006) Going to the extremes. *Climatic Change,* **79,** 185-211.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters,* **11,** 1351-1363.

Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*, **47**, 893-901.

White, G.C. & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study,* **46,** S120-S139.

Wiens, J.J. (2011) The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* **366,** 2336-2350.

Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment,* **5,** 475-482.

Winiarski, K.J., McWilliams, S.R. & Rockwell, R.F. (2012) Rapid environmental degradation in a subarctic ecosystem influences resource use of a keystone avian herbivore. *Journal of Animal Ecology,* **81,** 1132–1142.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A. & Guisan, A. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews,* **88,** 15-30.

Figures

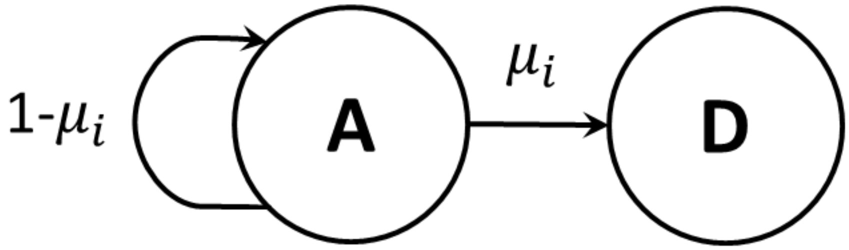

Figure 4.5. Schematic of multistate model used to analyze joint live/dead recovery data for lesser snow geese breeding in the Cape Churchill region of western Hudson Bay. Probability of mortality, μ_i, is defined as the probability of transitioning from a live (A) to dead (D) state, and is estimated conditionally on the probability of recapturing live individuals during banding drives and recovering dead individuals from hunter harvest across North America, the latter of which allows for the estimation of true rather than apparent survival.

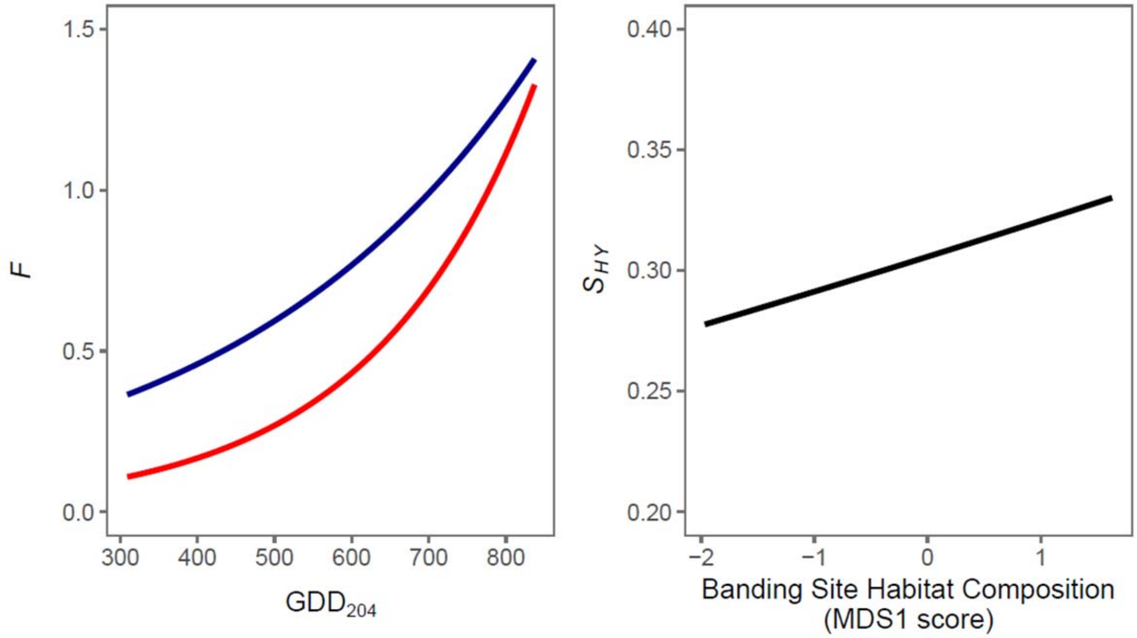

Figure 4.2. Demographic responses of snow geese to environmental drivers. Left panel: Seasonal warmness (GDD$_{204}$) affects reproductive success (*F*) differently across habitats. Blue lines correspond to responses for geese in highly coastal habitats (5th percentile of habitat MDS1 scores); red lines depict responses for geese occupying highly inland habitats (95th percentile of habitat MDS1 scores). Right panel: post-fledging first year survival of goslings (S_{HY}) is affected by banding site land cover composition (measured as site score along a primary land cover ordination axis, where positive values of MDS1 indicate more inland sites). Seasonal warmness did not significantly affect first year survival.

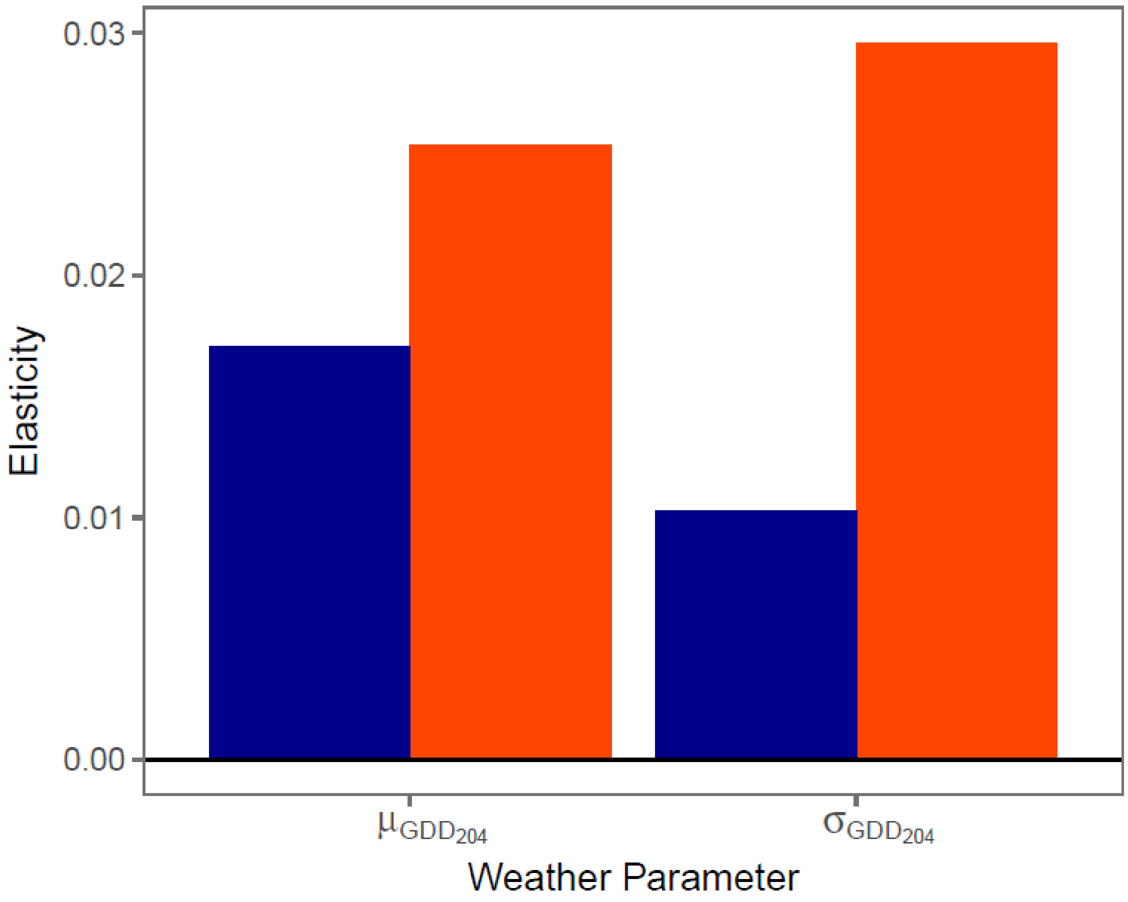

Figure 4.6. Elasticity of λ_s to increases in the mean (μ) and standard deviation (σ) of seasonal warmness, calculated based on conditions across the duration of our study (1990-2015). Blue bars depict effect size in highly coastal habitats (5th percentile of habitat MDS1 scores); red bars depict effect size in highly inland habitats (95th percentile of habitat MDS1 scores).

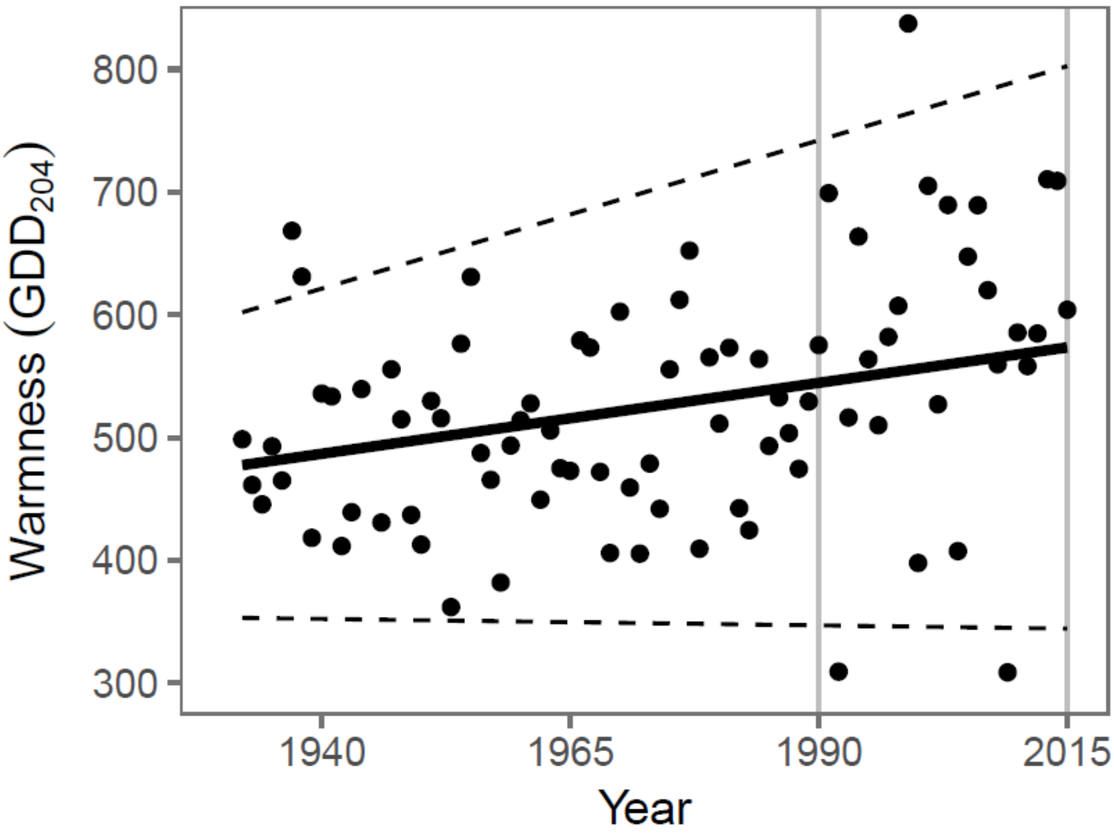

Figure 4.4. Estimated rate of change in the mean (solid black lines) and variability (dashed black lines depict ±2 standard deviations from the mean) of breeding season warmness.

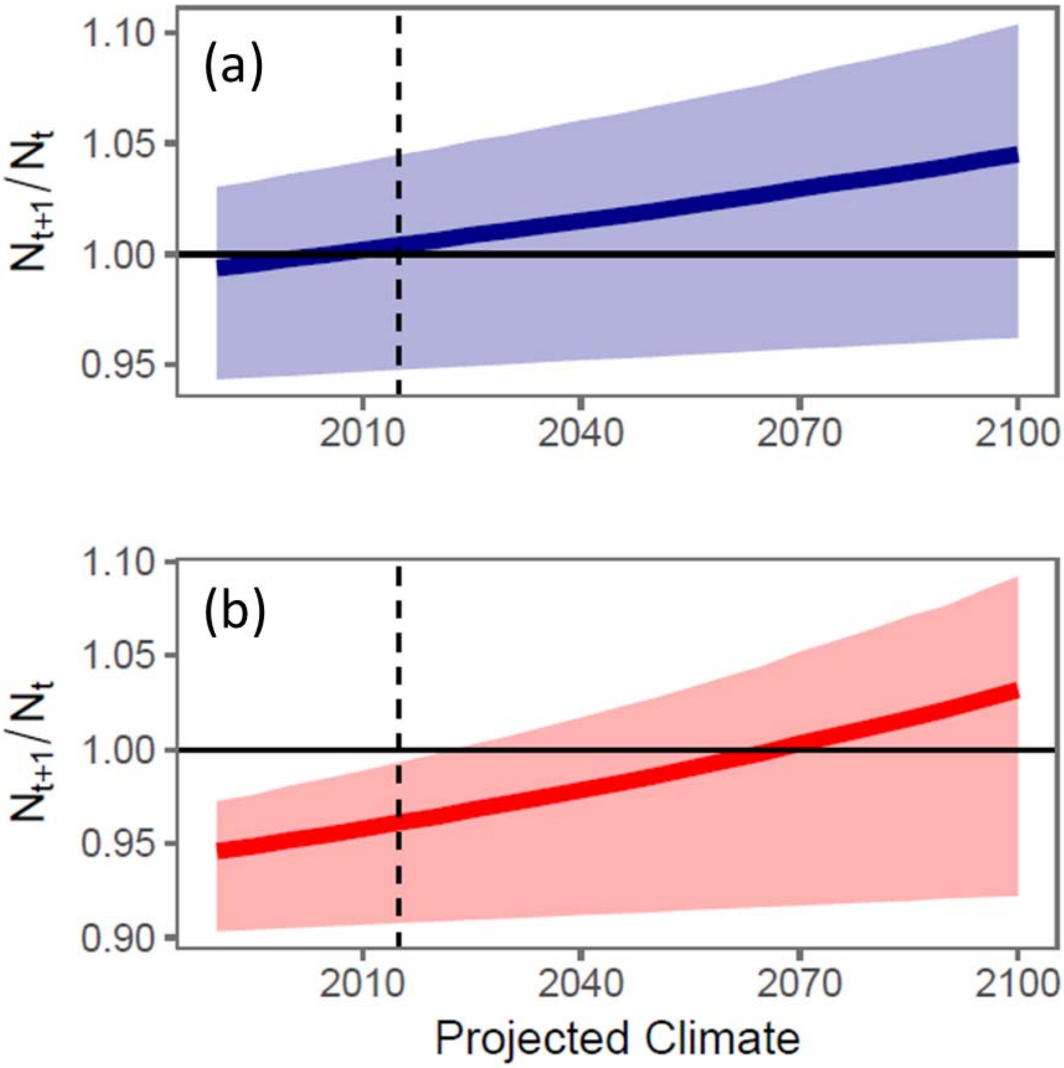

Figure 4.7. Distributions of population growth rates under projected climate distributions in traditional coastal habitats (blue) and novel inland habitats (red). Solid colored lines indicate long-term population growth rate in a variable environment, $\log\lambda_S$, in each habitat under projected climate in each year of study. Shaded ribbons indicate 25 and 75 percentiles for annual growth rates under projected climate. A higher proportion of shading above the x-axis (solid black line) indicates a higher frequency of years in which conditions are favorable for positive annual population growth.

CHAPTER 5

CONCLUSIONS

Changes in both the mean and variance of climate (Tebaldi *et al.* 2006; IPCC 2012; Stocker *et al.* 2013) have already impacted species range limits and phenology (Parmesan 2006; Parmesan 2007), affecting the demography of natural populations (Boyce, Haridas & Lee 2006; Miller-Rushing *et al.* 2010; Jenouvrier 2013). Thus, while climate can influence natural populations directly through effects on physiology, the strongest effects of climate change are likely to occur through its effects on species interactions (Tylianakis *et al.* 2008). Often, these effects will influence multiple vital rates simultaneously, altering vital rate correlation structures with potentially important consequences for population dynamics (Boyce, Haridas & Lee 2006).

In chapter 2, we found that vital rate correlations, generated when vital rates respond jointly to a shared environmental driver, can fundamentally alter demographic selection pressures in variable environments. The effects of vital rate correlations were especially capable of reversing selection pressures when the marginal effect of selection on a vital rate reaction norm (i.e., in the absence of joint responses) was relatively weak. Our study therefore adds an important layer to existing theory for life history evolution: for many life histories, both the shape of vital rate reaction norms (Koons *et al.* 2009) and joint responses of vital rates (chapter 2; also see Barraquand & Yoccoz 2013) are needed to predict fitness in a time-varying environment. Our results also underscore the importance of explicitly linking multiple vital rates to environmental drivers in order to accurately characterize shifts in joint vital rate distributions.

If the effects of climate primarily manifest through indirect pathways, climate sensitivity will be strongly habitat-specific, and indeed this prediction has empirical support (Tylianakis *et al.* 2008; Wisz *et al.* 2013; Svenning *et al.* 2014; Alexander, Diez & Levine 2015; Alexander *et al.* 2016). Ecological theory also predicts that if climate variation affects the strength of consumer-resource interactions (e.g., through the well-documented phenomenon of trophic mismatch; Cushing 1990; Miller-Rushing *et al.* 2010), consumers will have weaker responses when exposed to higher resource diversity, owing to the multiple mechanisms underlying diversity-stability relationships (McCann 2000). We tested these hypotheses in chapter 3 using a long-term study of lesser snow geese (*Chen caerulescens caerulescens*), finding that gosling production and development in relatively species-poor inland areas was much more sensitive to climate variation than in species-rich coastal habitats. Our results therefore indicate that projections of future species ranges and population trajectories will often be misleading if demographic relationships are only estimated based on data from a subset of potential habitats or ecological communities (Coutts *et al.* 2016). Future research should seek to determine whether globally consistent response curves can be estimated by leveraging data from multiple populations across a species range or through experiments (Adler, Byrne & Leiker 2013). Alternatively, if species interactions strongly modify demographic responses such that no globally consistent response curve exists, then attempts to produce spatio-temporal population forecasts in changing climates may be significantly undermined.

In chapter 4, we examined the population dynamic consequences of climate change for lesser snow geese in traditional (i.e., coastal) and novel (i.e., inland) habitats.

Inland sedge meadow habitats are over 120 times more abundant than traditional coastal saltmarsh (Brook & Kenkel 2002), and if suitable for positive population growth under future warming, could significantly offset ongoing management efforts to curb overabundant snow goose populations. Expanding our analysis from chapter 3, we found that multiple demographic rates respond differently to climate variation across habitats. This finding is consistent with other studies that have shown substantial demographic variation across space (Doak & Morris 2010; Coutts et al. 2016), likely influenced by species interactions (Tylianakis et al. 2008; Alexander, Diez & Levine 2015). Under future warming, our population model suggests that short- and long-term habitat suitability will increase in inland areas. If geese can exploit inland habitats only when conditions are favorable, highly stochastic climate fluctuations could relax intraspecific competition and further improve overall population growth rates. Thus, the potential for short-term dispersal suggests that measures of long-term habitat suitability often used in species distribution models could be insufficient to describe future range boundaries (Holt 2009).

The degree to which species interactions interact with climate to affect consumer demography will likely depend on a variety of ecological factors, including life history. Recent comparative analyses have suggested that demography varies strongly among populations within a single species, potentially limiting the ability to extrapolate across space (Coutts *et al.* 2016). Further research is needed to determine the degree to which demographic responses to climate vary across populations, whether the responses of specific vital rates can be more reliably extrapolated than others, and how the effectiveness of such extrapolations depend on life history. Often, demographic data is expensive to collect, requiring large sample sizes and long time series to estimate demographic relationships. As a consequence, demographic datasets are often poorly replicated across space, and spatio-temporal projections must therefore assume that small-scale dynamics faithfully represent dynamics at larger scales. Continued research is needed to determine the practical limits of this assumption; such insights will be critical for forecasting population performance under ongoing climate change.

References

Adler, P.B., Byrne, K.M. & Leiker, J. (2013) Can the past predict the future? Experimental tests of historically based population models. *Global Change Biology,* **19,** 1793-1803.

Alexander, J.M., Diez, J.M., Hart, S.P. & Levine, J.M. (2016) When Climate Reshuffles Competitors: A Call for Experimental Macroecology. *Trends in Ecology & Evolution*.

Alexander, J.M., Diez, J.M. & Levine, J.M. (2015) Novel competitors shape species/'responses to climate change. *Nature,* **525,** 515-518.

Barraquand, F. & Yoccoz, N.G. (2013) When can environmental variability benefit population growth? Counterintuitive effects of nonlinearities in vital rates. *Theoretical population biology,* **89,** 1-11.

Boyce, M.S., Haridas, C.V. & Lee, C.T. (2006) Demography in an increasingly variable world. *Trends in Ecology & Evolution,* **21,** 141-148.

Brook, R. & Kenkel, N. (2002) A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing,* **23,** 4761-4776.

Coutts, S.R., Salguero-Gómez, R., Csergő, A.M. & Buckley, Y.M. (2016) Extrapolating demography with climate, proximity and phylogeny: approach with caution. *Ecology Letters*.

Cushing, D. (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in marine biology,* **26,** 249-293.

Doak, D.F. & Morris, W.F. (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature,* **467,** 959-962.

Holt, R.D. (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences,* **106,** 19659-19665.

IPCC (2012) *Managing the risks of extreme events and disasters to advance climate change adaptation: special report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, UK.

Jenouvrier, S. (2013) Impacts of climate change on avian populations. *Global Change Biology*.

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

McCann, K.S. (2000) The diversity–stability debate. *Nature,* **405,** 228-233.

Miller-Rushing, A.J., Høye, T.T., Inouye, D.W. & Post, E. (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **365,** 3177-3186.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics***,** 637-669.

Parmesan, C. (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology,* **13,** 1860-1872.

Stocker, T., Qin, D., Plattner, G., Tignor, M., Allen, S., Boschung, J., Nauels, A., Xia, Y., Bex, B. & Midgley, B. (2013) Climate Change 2013: The Physical Science Basis. Working Group I Contribution ot the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Svenning, J.C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., Schiffers, K.H., Dullinger, S., Edwards, T.C. & Hickler, T. (2014) The influence of interspecific interactions on species range expansion rates. *Ecography,* **37,** 1198-1209.

Tebaldi, C., Hayhoe, K., Arblaster, J.M. & Meehl, G.A. (2006) Going to the extremes. *Climatic change,* **79,** 185-211.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters,* **11,** 1351-1363.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A. & Guisan, A. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews,* **88,** 15-30.

APPENDICES

Appendix A – Supplementary Information for Chapter 2

In the main text of chapter 2, we presented results when maturation probability was high (*p*=1). Here, we present the results of demographic simulations when maturity is delayed (p=0.1).

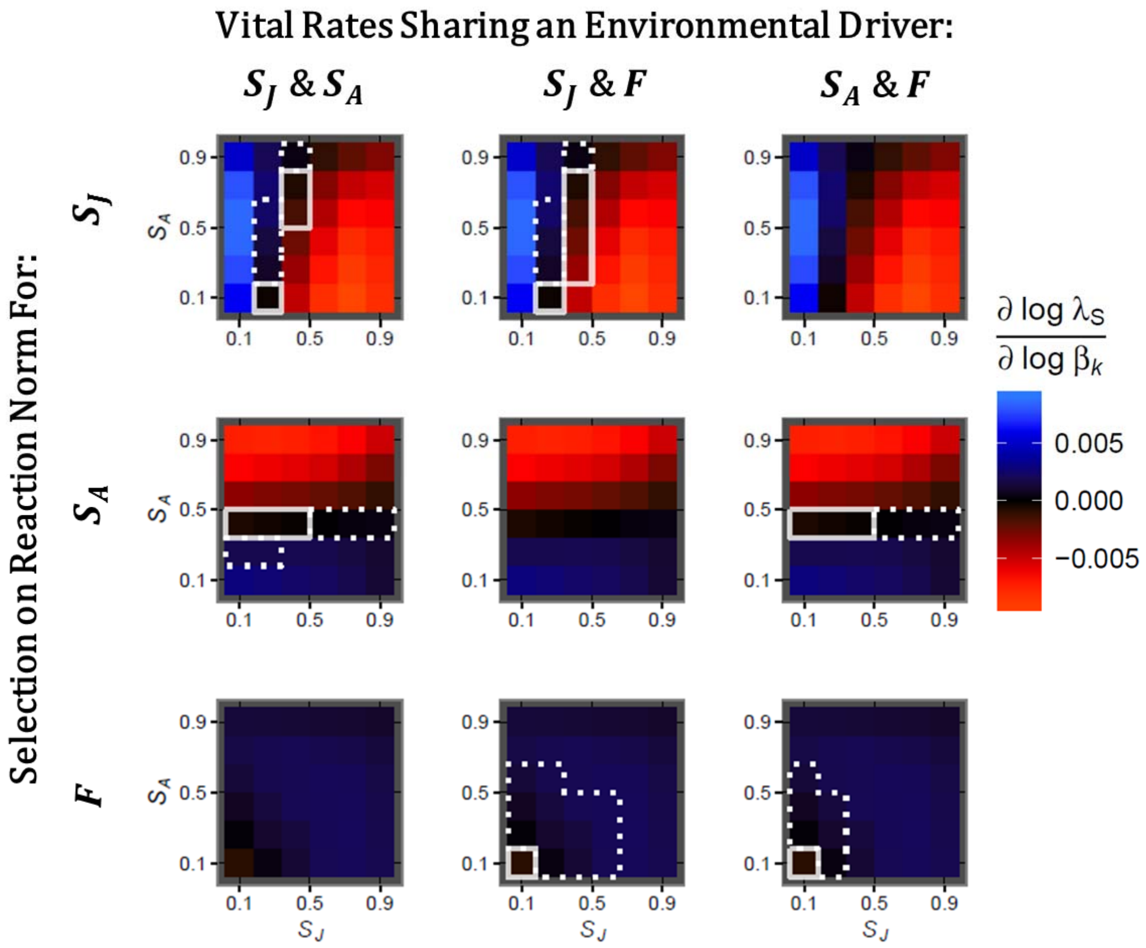

Figure A1: Fitness effect of an increase in slope of the reaction norm for juvenile survival (S_J), adult survival (S_A), and fertility (F) when vital rates are linked to time-varying environmental drivers. Red shading indicates selection for weaker vital rate responses (demographic buffering), blue shading indicates selection for stronger vital rate responses (demographic lability). White polygons indicate life histories where joint responses reverse the overall direction of selection on reaction norms. Solid line indicates effect of joint responses when vital rates respond in opposite direction to a shared environmental driver (negative covariation); dashed line indicates effects of joint responses when vital rates respond in the same direction to a shared environmental driver (positive covariation). In this figure, $p = 0.1$ (delayed maturity) and $a = 3.5$ (mean fertility is far from its maximum).

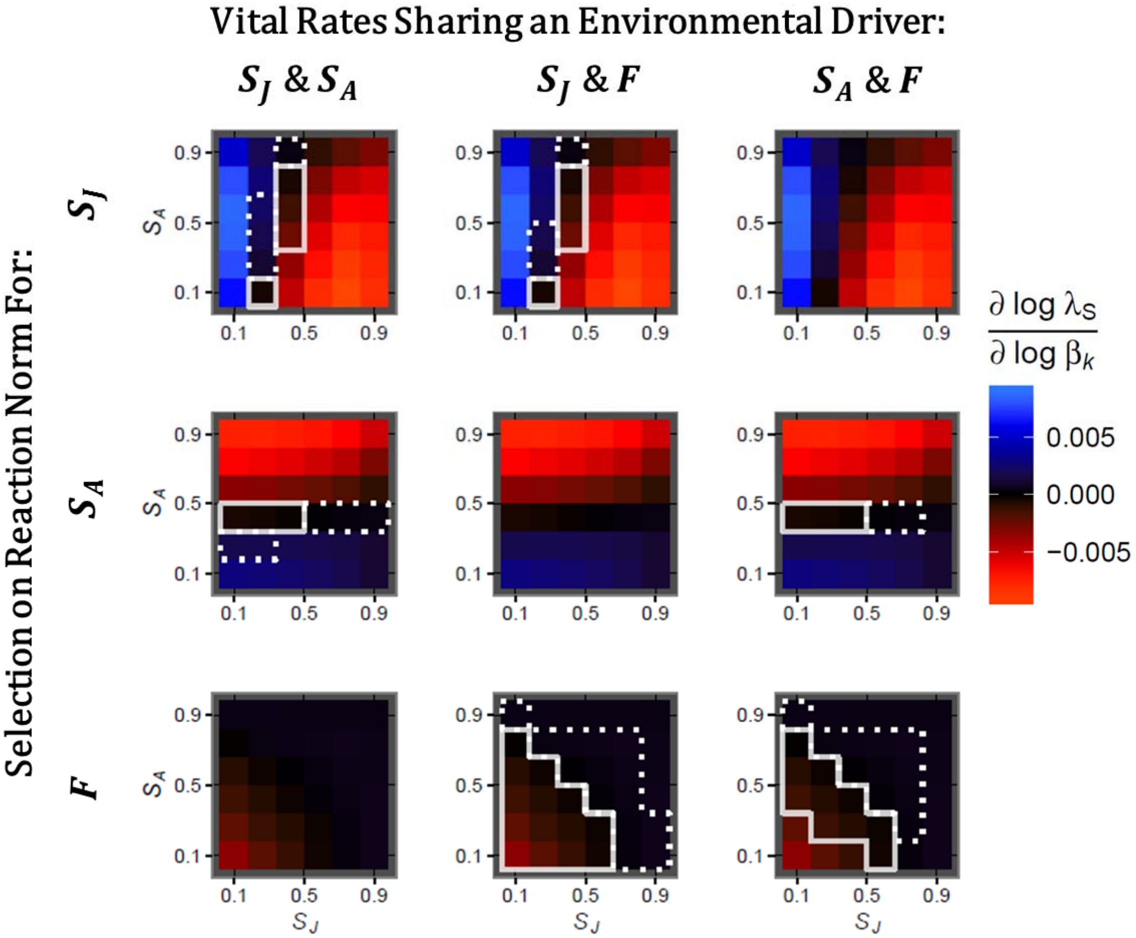

Figure A2: Fitness effect of increase in slope of reaction norm for juvenile survival (S_J), adult survival (S_A), and fertility (F) when vital rates are linked to time-varying environmental drivers. Figure is interpreted as in fig. A1. In this figure, $p = 0.1$ (delayed maturity) and $a = 2.5$ (mean fertility is intermediate relative to its maximum).

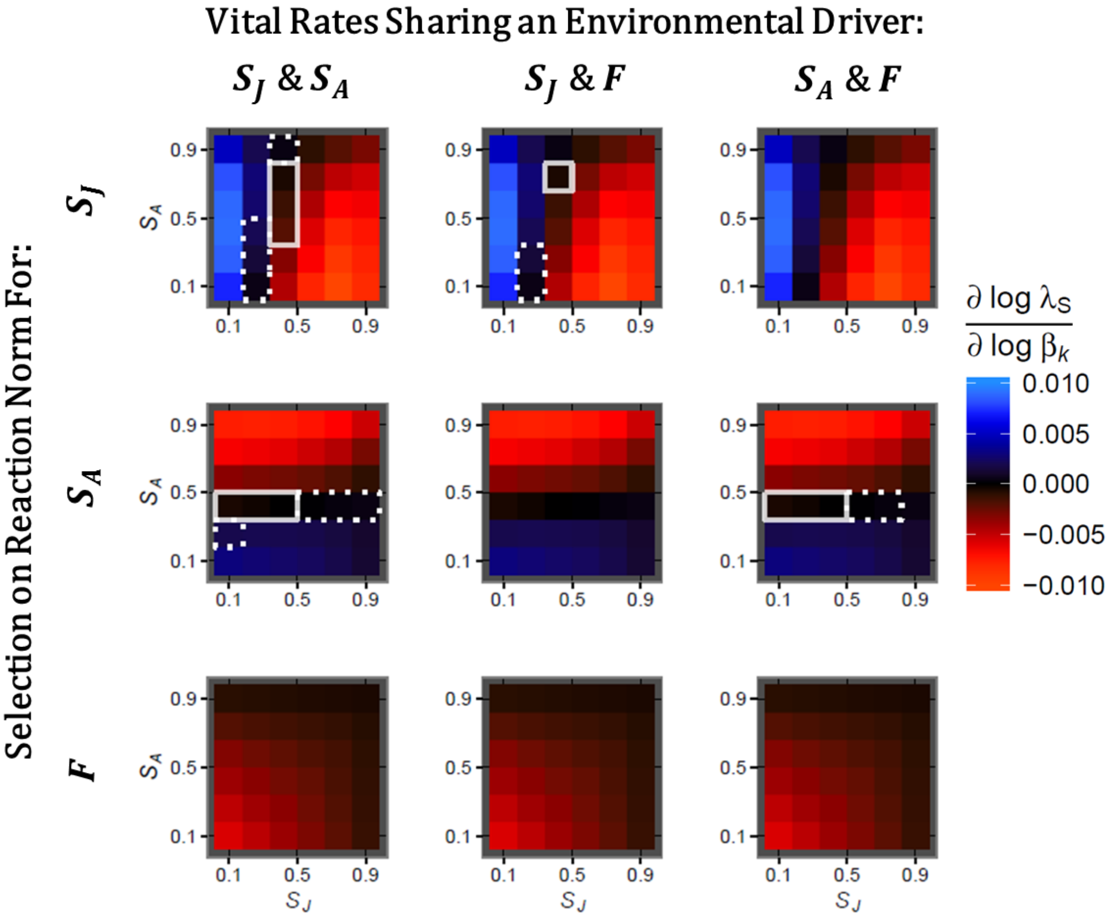

Figure A3. Fitness effect of increase in slope of reaction norm for juvenile survival (S_J), adult survival (S_A), and fertility (F) when vital rates are linked to time-varying environmental drivers. Figure is interpreted as in fig. A1. In this figure, $p = 0.1$ (delayed maturity) and $a = 1.5$ (mean fertility is close to its maximum).

Appendix B – Supplementary Information for Chapter 3

We used ordination (non-metric multidimensional scaling, MDS; metaMDS function in the *vegan* R package) to collapse land cover data at banding sites into primary axes of landscape variation. A biplot for this ordination is presented in Fig. B1. Scores along the first axis describe a banding location's position along a gradient from highly coastal areas (negative scores) to highly inland areas (positive scores).

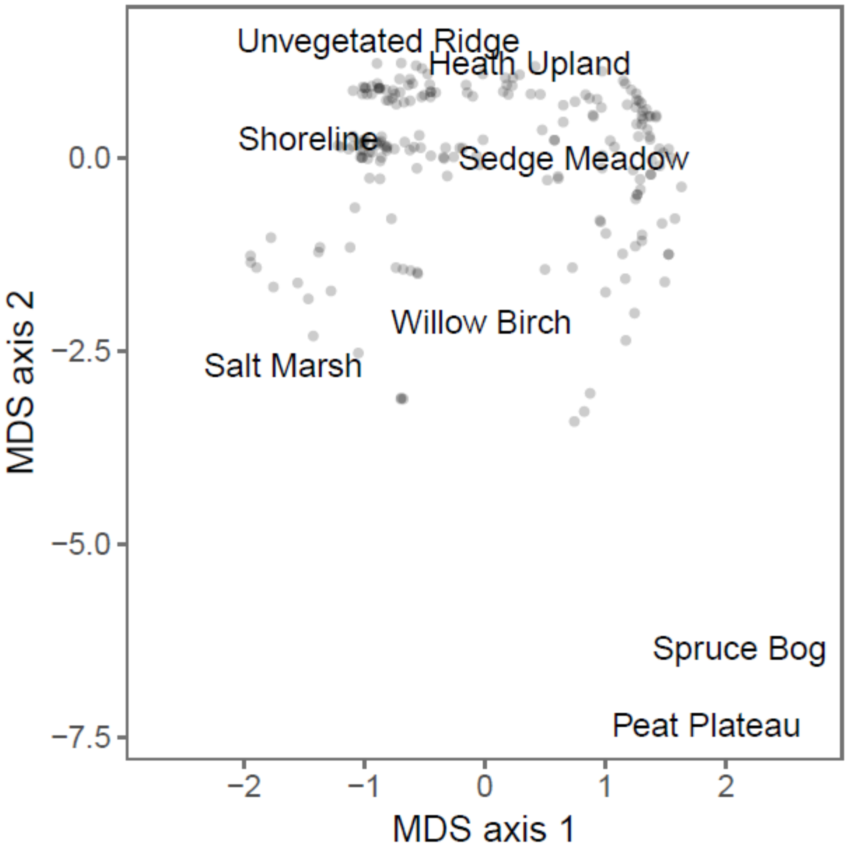

Fig. B1. Biplot of ordination for land cover classes.

Landscape composition surrounding banding locations was highly bimodal (Fig. B2); sites tended to either be highly coastal (negative values of MDS1) or highly inland (positive values of MDS1). We therefore developed a categorical measure of landscape by classifying any sites with scores lower than zero as “coastal” and sites with scores higher than zero as “inland”.

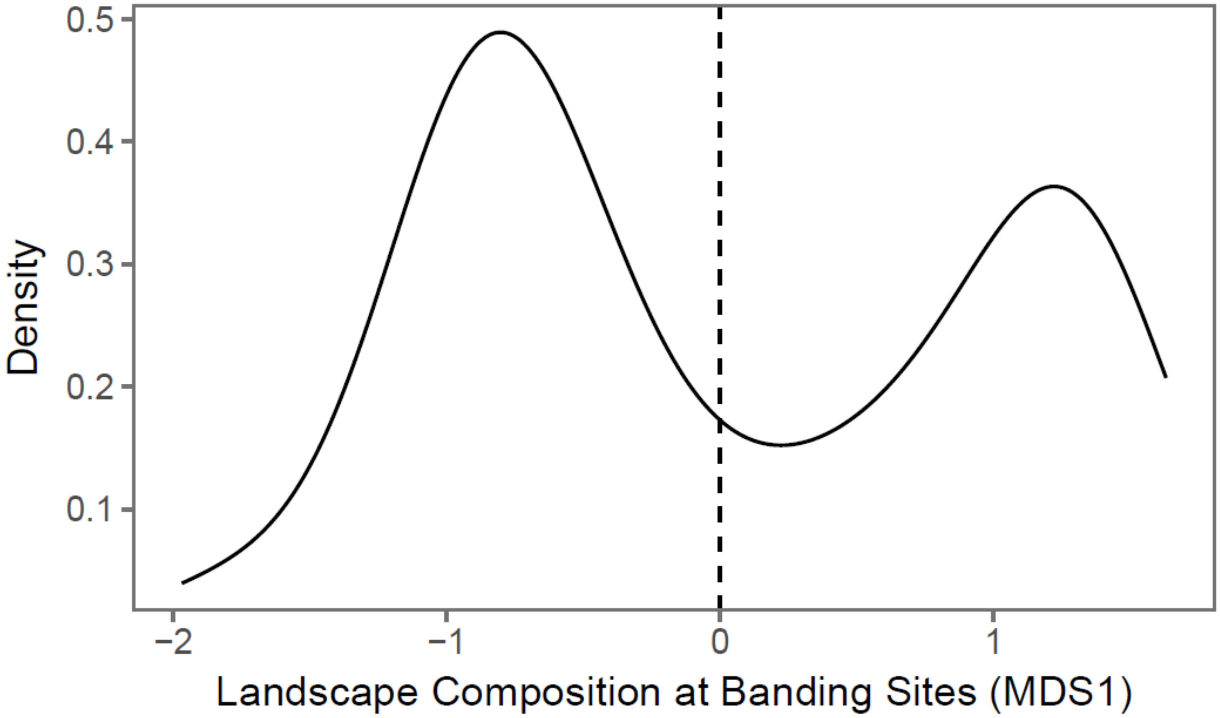

Fig. B2. Probability density of landscape composition scores at banding sites. Landscape composition at banding is highly bimodal; sites are either highly coastal (negative scores) or highly inland (positive scores). Dashed line indicates mean value, which was used to generate a categorical variable for classifying sites as either “coastal” or “inland”.

We used Landsat imagery to measure NDVI change over time across the study area, a technique previously demonstrated to accurately quantify habitat degradation at our study site (Jano, Jefferies & Rockwell 1998; Jefferies, Jano & Abraham 2005). High quality, cloud-free Landsat images were available in 1974, 1984, 1996, 2005, and 2010. We removed any effects of change in NDVI due to variation in water levels by generating a water mask for each Landsat image, merging them into an overall water mask, and removed any pixels from NDVI analysis that overlapped with any of the total water mask.

To determine an NDVI threshold for bare ground, we overlaid Brook and Kenkel's (Brook & Kenkel 2002) land cover map for our study area onto the corresponding NDVI image from 1996, the same image from which the land cover map was generated. We then extracted NDVI values associated with each land cover type. We compared distributions of NDVI values for each land cover type and determined that an NDVI threshold of 0.202 adequately separated unvegetated shoreline from other land cover types at our study site. We therefore used this as a basis for classifying unvegetated landscape.

Areas classified as unvegetated ground in 1974, prior to rapid increases in snow goose abundance, were unlikely to have been caused by destructive foraging by snow geese (Abraham, Jefferies & Alisauskas 2005; Jefferies, Jano & Abraham 2005). We therefore considered landscape condition in 1974 as a "reference" condition and calculated the proportion of pixels within 2 km of banding locations that were converted to bare ground since 1974. For years in which there were no adequate Landsat images for NDVI classification, we linearly interpolated between years in which data were available. Spatial and temporal patterns in our metric of landscape degradation were consistent with previous remote sensing studies of the area (Jano, Jefferies & Rockwell 1998; Jefferies, Jano & Abraham 2005) and with empirical trends in habitat condition based on vegetation surveys (Jefferies & Rockwell 2002; Peterson et al. 2013).

Temporal patterns in landscape degradation at each banding location confirmed that that the majority of habitat degradation largely occurred prior to 1996 (Fig. B3). Because no suitable cloud-free images of the study were area available between 1984 and 1996, it is likely that the majority of degradation had actually occurred prior to 1996 (the year in which NDVI declined dramatically at most sites). We therefore use data from 1990 onwards in our study, assuming that landscape composition has not changed drastically over this time period.

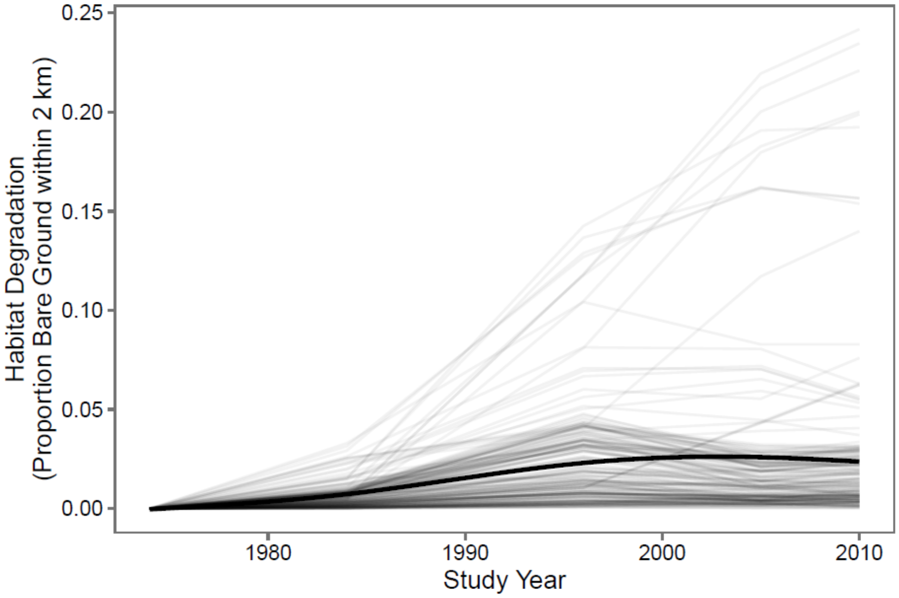

Fig. B3. Proportion of landscape degraded through time at each banding location. Each semi-transparent gray line represents a different banding location. Solid black line is average trend based on a generalized additive model.

The proportion of landscape degraded within 2 km of each banding location was highly correlated with landscape composition (i.e., position along the MDS1 axis). To control for severity of landscape degradation beyond that which is already captured by landscape composition, we regressed logit-scale landscape degradation against MDS1 using a GAM (Fig. B4) and extracted residuals for use as a covariate in productivity, gosling size, and body condition models.

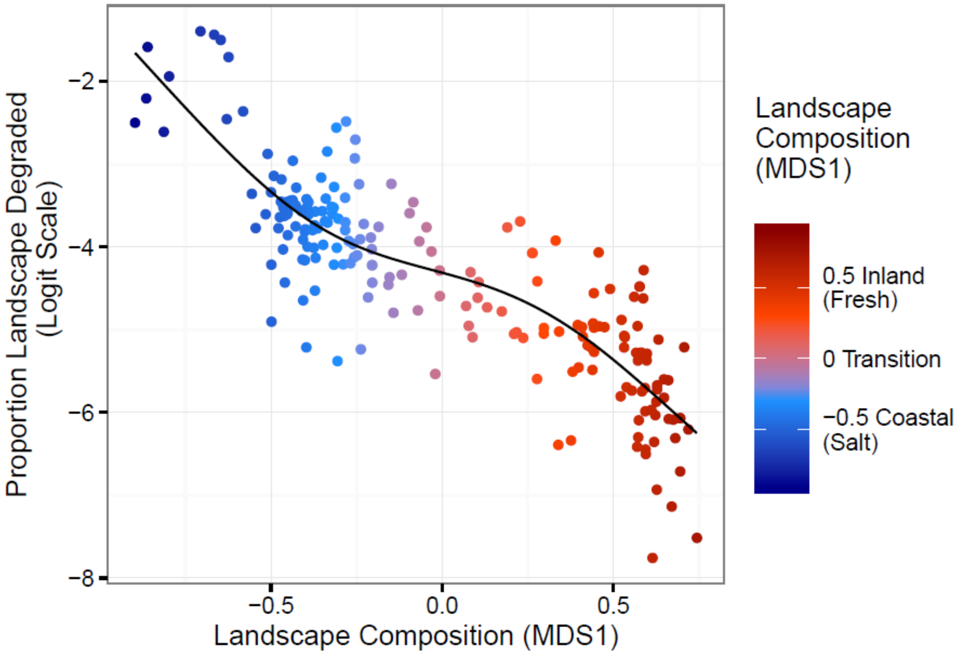

Fig. B4. Proportion of local area degraded since 1974 at each banding location in the year each banding drive was conducted. Values are represented on the logit scale since degradation is bounded by 0 and 1. Degradation is highly correlated with landscape composition and is most severe in coastal areas.

References

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

Brook, R. & Kenkel, N. (2002) A multivariate approach to vegetation mapping of Manitoba's Hudson Bay Lowlands. *International Journal of Remote Sensing,* **23,** 4761-4776.

Jano, A.P., Jefferies, R.L. & Rockwell, R.F. (1998) The detection of vegetational change by multitemporal analysis of LANDSAT data: the effects of goose foraging. *Journal of Ecology,* **86,** 93-99.

Jefferies, R.L., Jano, A.P. & Abraham, K.F. (2005) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology,* **94,** 234-242.

Jefferies, R.L. & Rockwell, R.F. (2002) Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science,* **5,** 7-16.

Peterson, S.L., Rockwell, R.F., Witte, C.R. & Koons, D.N. (2013) The legacy of destructive snow goose foraging on supratidal marsh habitat in the Hudson Bay Lowlands. *Arctic, Antarctic, and Alpine Research,* **45,** 575-583.

Appendix C – Supplementary Information for Chapter 4

Table C1. Model selection table to determine best structure for live recapture (p^A) while including an effect of published band reporting rates on dead recovery (p^D) and all environmental effects for mortality (μ).

Model Structure	df	SIC	ΔSIC
$p^A \sim Age + Time^3$	18	333075.5	0
$p^A \sim Age + Time^2$	17	333145.5	70.0
$p^A \sim Age$	15	333198.6	123.1
$p^A \sim Age + Time$	16	333208.6	133.0

Table C2. Model comparison table for different parameterizations of environmental and habitat effects on post-fledging hatch-year mortality (μ_{HY}). All models include effects of "residualized habitat degradation" and "residualized days elapsed between peak hatch and banding". Probability of live recapture (p^A) included cubic time trend and an effect of bird age, while including an effect of published band reporting rates on dead recovery (p^D). Environmental effects include seasonal warmness (*GDD₂₀₄*) and habitat (*MDS1*), measured as a continuous covariate (MDS1) based on banding location's score on a primary land cover ordination axis.

Model	df	SIC	ΔSIC
$\mu_{HY} \sim MDS1$	16	333061	0
$\mu_{HY} \sim GDD_{204}$	16	333064.9	3.8
$\mu_{HY} \sim GDD_{204} + MDS1$	17	333070.2	9.2
$\mu_{HY} \sim GDD_{204} \times MDS1$	18	333075.5	14.5
$\mu_{HY} \sim 1$	15	333127.6	66.5

Table C3. Parameter estimates (with associated uncertainty) for top-performing multistate model to estimate probabilities of live recapture (p^A), dead recovery (p^D), and mortality (μ) probability of lesser snow geese. Estimates for recapture and recovery are presented on the complimentary log-log scale, and estimates for mortality are presented on the logit scale.

Parameter	Estimate	s.e.	lcl	ucl
$p^A: Intercept$	-7.026	0.413	-7.836	-6.217
$p^A: Age\ Trend$	0.147	0.025	0.099	0.196
$p^A: Time\ Trend$	0.911	0.094	0.727	1.095
$p^A: Time\ Trend^2$	-0.063	0.007	-0.076	-0.049
$p^A: Time\ Trend^3$	0.0013	0.0002	0.0010	0.0016
$p^D_{HY}: Intercept$	-4.045	0.214	-4.464	-3.625
$p^D_{AHY}: Intercept$	-2.282	0.265	-2.801	-1.762
$p^D_{HY}: band\ reporting\ rate$	1.466	0.278	0.921	2.011
$p^D_{AHY}: band\ reporting\ rate$	1.132	0.335	0.475	1.789
$\mu_{HY}: Intercept$	0.820	0.063	0.697	0.943
$\mu_{HY}: days\ since\ hatch\ (resid)$	-0.062	0.007	-0.075	-0.049
$\mu_{HY}: habitat\ degradation\ (resid)$	-0.034	0.030	-0.093	0.025
$\mu_{HY}: habitat$	-0.069	0.033	-0.134	-0.005
$\mu_{AHY}: Intercept$	-1.371	0.069	-1.506	-1.236

$\mu_{AHY}: S\ rank\ from\ Koons\ et\ al. 2014$	-0.029	0.005	-0.038	-0.019
$\mu_{AHY}: Year\ 2002\ (outlier\ effect)$	0.276	0.129	0.023	0.530

Table C4. Model comparison for rates of change in mean (μ) and standard deviation (σ) of seasonal warmness (GDD_{204}) between 1932 and 2015.

Model	df	SIC	ΔSIC	SICw	AICc	ΔAICc	AICw
μ~Year, σ~Year	4	996.6	0.0	0.59	987.4	0.0	0.82
μ~Year, σ~1	3	997.9	1.3	0.31	991.0	3.5	0.14
μ~1, σ~Year	3	1000.3	3.7	0.09	993.4	6.0	0.04
μ~1, σ~1	2	1004.6	8.0	0.01	999.9	12.4	<0.01

CURRICULUM VITAE

David Iles
Department of Wildland Resources and the Ecology Center
5230 Old Main Hill
Utah State University
Logan, Utah 84322-5230
Email: david.thomas.iles@gmail.com

Employment

2017-present	Postdoc Researcher Tufts University	Studying the responses of bumblebee populations to landscape change.

Education

2017	Ph.D. in Ecology Utah State University	Studied responses of natural populations to climate change, with a focus on climate-driven changes in snow goose demography
2012	M.S. in Ecology Utah State University	Studied patterns in long-term nest success of common eider ducks at La Pérouse Bay, Mantioba, Canada.
2008	B.S. in Ecology University of Guelph	Dean's Honor Roll.

Peer-Reviewed Publications

Gormezano, L.J., S.R. McWilliams, D.T. Iles, and R.F. Rockwell. 2016. Costs of locomotion in polar bears: when do the costs outweigh the benefits of chasing down terrestrial prey? *Conservation Physiology* 4: cow045 (Online version).

Mulder, C.P.H., D.T. Iles, and R.F. Rockwell. 2016. Increased variance in temperature and lag effects obscure phenological responses to rapid warming in a subarctic plant community. *Global Change Biology* 23: 801-814.

Koons, D.N., D.T. Iles, M. Schaub, and H. Caswell. 2016. A life history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecology Letters* 19: 1023-1031.

Iles, D.T., R. Salguero-Gomez, P.B. Adler, and D.N. Koons. 2016. Linking transient dynamics to biological invasion success. *Journal of Ecology* 104: 399-408.

Iles, D.T., S.L. Peterson, L.J. Gormezano, R.F. Rockwell, and D.N. Koons. 2013. Terrestrial predation by polar bears: not just a wild goose chase. *Polar Biology* 36: 1373-1379.

Iles, D.T., R.F. Rockwell, and D.N. Koons. 2013. The effects of predators, alternative prey, and climate on common eider nesting success. *Journal of Animal Ecology* 82: 683-693.

Conference Papers

Mattingly, M., A. Barnas, S. Ellis-Felege, R. Newman, **D.T. Iles**, and T. Desell. Developing a citizen science web portal for manual and automated ecological image detection. (In review for *Proceedings of the 12th IEEE International Conference on eScience*).

In Preparation

Iles, D.T., R.F. Rockwell, and D.N. Koons. Fitness consequences of joint vital rate responses to environmental variation across life histories. (In preparation for submission to *Oikos*).

Iles, D.T., C.P.H. Mulder, R.F. Rockwell, and D.N. Koons. Resource diversity reduces demographic sensitivity to climate for a keystone herbivore. (In preparation for *Global Change Biology*).

Iles, D.T., R.F. Rockwell, and D.N. Koons. Climate change improves suitability of novel habitats for a keystone herbivore. (In preparation for *Journal of Animal Ecology*).

Teaching

NR 6580 – Data Analysis and Programming for Natural Resource Managers. 2017. Lead instructor. 15 students.

NR 6580 – Data Analysis and Programming for Natural Resource Managers. 2016. Lead instructor. 18 students.

NR 6580 – Data Analysis and Programming for Natural Resource Managers. 2015. Teaching assistant. 15 students.

WILD 6770 – Plant Community Ecology. 2014. Teaching assistant. 25 students.

WILD 3810 – Plant and Animal Populations. 2012. Teaching assistant. 45 students.

Conference Presentations and Abstracts (*Selected*)

Iles, D.T., R.F. Rockwell, and D.N. Koons. 2015. Linking transient dynamics and life history to biological invasion success. Ecological Society of America 100th Annual Meeting. Baltimore, Maryland, USA.

Koons, D.N., D.T. Iles, and M. Schaub. 2015. Estimating demographic drivers of transient population dynamics in changing environments: Towards a holistic understanding. Ecological Society of America 100th Annual Meeting. Baltimore, Maryland, USA.

Iles, D.T., A. Kleinhesselink, E. LaMalfa, R. Mann, A. Tredennick, and P. Adler. 2015. Plant population responses to historical climate variation in sagebrush steppe. Society for Rangeland Management Annual Meeting. Sacramento, CA, USA.

Iles, D.T. and D.N. Koons. 2013. Stochastic population dynamics of common eiders at La Pérouse Bay, Manitoba, Canada. Ecology and Conservation of North American Waterfowl Conference. Memphis, Tennessee, USA.

Iles, D.T., D.N. Koons, and R.F. Rockwell. 2011. Effects of boom-bust nesting success on common eider population dynamics: inferences from a long-term study in La Pérouse Bay, Manitoba, Canada. 4th International Sea Duck Conference. Seward, Alaska, USA.

Iles, D.T., D.N. Koons, and R.F. Rockwell. 2011. Lesser snow goose nest proximity affects common eider nest survival. 12th North American Arctic Goose Conference. Portland, Oregon, USA.

Iles, D.T. and D.N. Koons. 2010. Impacts of variable nesting success on common eider population dynamics. The Wildlife Society 17th Annual Conference. Snowbird, Utah, USA.

Other Professional Experience

Journals Reviewed For

The Auk (2), Biological Conservation (1), Biological Invasions (1), Global Change Biology (2), Journal of Ecology (1), Mammalian Biology (1), Oecologia (1), Ornis Fennica (1)

Service / USU Campus Involvement

USU Ecology Center Seminar Committee Member (2011/2012 and 2015/2016)
Demographic Advancements in Ecology and Evolution Meeting Group (organizer; 2016)
USU College of Natural Resources Graduate Student Council Member (2011-2016)

- Wildland Resources Department Representative
- On-Campus Educational Development Chairperson

Research Experience for Undergraduate Mentor (summer 2014)
Wildland Resources Research Symposium Volunteer (2011-2015)

Grants, Scholarships, and Awards

2016

Graduate Researcher of the Year – Utah State University (finalist)
Graduate Researcher of the Year - USU Quinney College of Natural Resources (awarded)
Graduate Enhancement Award – Utah State University - **$4,000**

2014-2015

Richard H.G. Bonnycastle Graduate Fellowship in Wetland and Waterfowl Biology (Institute for Wetland and Waterfowl Research – Ducks Unlimited Canada) - **$28,000**

2013
Dennis Raveling Scholarship for Waterfowl Research- **$500**
Parks Canada – secured approx. **$30,000** in equipment and logistical support

2012
Quinney Foundation PhD Fellowship - **$80,000**

2011
Delta Waterfowl Research Support Award **- $4,000**
Intermountain Graduate Research Symposium Presentation Award **- $100**
North American Arctic Goose Conference Student Travel **Award - $400**
International Sea Duck Conference Student Travel Award **- $500**
International Sea Duck Conference Student Presentation Award

2010
Delta Waterfowl Research Support Award - **$1,000**
Ecology Center Research Support Award - **$4,000**
Frank M. Chapman Research Grant - **$1,000**

2009
Quinney Foundation Master's Fellowship - **$30,000**

Media Coverage

Popular Media
June 8, 2016 – *National Geographic* – "What Do Polar Bears Eat on Land?"
March 2, 2015 – *Conservator* - "Warm Warnings"
Sep 22, 2014 – *New York Times* - "For Polar Bears, a Climate Change Twist"
Jan 28, 2014 – *Audubon Magazine* - "The Arctic Omnivore's Dilemma"
Jan 27, 2014 – *New York Times* - "Polar Bears Turn to Snow-Goose Egg Diet"
Dec 3, 2013 – *The Nature Conservancy* - "Will Polar Bears Die Out Because Of Climate Change?"
Oct 21, 2013 – *National Geographic* - "Watching Polar Bears Eat Goose Eggs in Warmer Arctic"
June 1, 2013 – *The Economist* - "Sacred Geese"