ECOLOGICAL FACTORS AFFECTING MIDCONTINENT LIGHT GOOSE RECRUITMENT

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ABSTRACT

A full understanding of population dynamics requires knowledge about the relative contributions of both adult survival and recruitment to population growth rate. Avian life cycles consist of a number of reproductive stages leading to recruitment, each of which is highly susceptible to annual variability in environmental conditions. The purpose of my research was to identify key ecological factors associated with a long-term decline in the per capita gosling production of Ross's geese (*Chen rossii*) and lesser snow geese (*Chen caerulescens caerulescens*) using historical data collected from 1992-2014 at Karrak Lake, Nunavut.

I evaluated effects of (i) nutritional deficiencies of pre-breeding female Ross's geese and lesser snow geese stemming from density-dependence following large increases in nesting population size and (ii) phenological mismatch between peak gosling hatch and peak forage quality, inferred from measurements of NDVI on brood-rearing areas. Annual gosling production (i.e., proportional composition of young during brood-rearing) was reduced for both species when the mass of nutrient reserves for pre-breeding females arriving to nest were lighter. Mismatch between peak gosling hatch and peak forage quality was also related to decreases in gosling production, while delays in nest initiation negatively affected clutch size and nest success (i.e., ≥ 1 egg hatched). Vegetation phenology was significantly earlier in years with warmer spring (i.e., 25 May – 30 June) surface air temperatures. Additionally, increased mismatch over the course of the 23-year study period apparently resulted from advancing vegetation phenology without a contemporaneous advance in goose breeding phenology. I did not find evidence of a direct effect of annual nesting population size on colony gosling production.

Given an absence of information on the pre-fledging stage of the life cycle for geese originating from Karrak Lake, I studied the effect of conditions experienced during early life on the growth and survival of goslings. Time constraints due to strong seasonality at arctic-nesting grounds highlight the importance of foraging conditions (i.e., quality, quantity, availability) for offspring during brood-rearing. I found that an increase in the number of nesting geese was associated with a reduction in gosling survival for both Ross's geese and snow geese. There was weak evidence that snow goose gosling body size was negatively related to breeding population size at the colony, while no effect was detected for Ross's geese. Increasing mismatch between the seasonal peak in vegetation quality and timing of hatch was negatively related to both gosling size and survival probability; suggestive of nutritional stress. My results lend support to the notion that both global (i.e., climate change) and local (i.e., foraging/habitat conditions) phenomena may result in reduced offspring production and success, and alludes to the possibility of an eventual decline in recruitment into the breeding cohort.

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CHAPTER 1. GENERAL INTRODUCTION

1.1 The dynamics of avian productivity

The annual cycle of migratory birds is generally comprised of the breeding season, moulting (conditional on species), fall migration, the wintering period and spring migration. The breeding season, while short in comparison with the remainder of the year, is the time when new individuals are added to the population and thus, is critical to population dynamics (Johnson et al. 1992). The contribution of young to the population depends on, and is the product of, several states and transition probabilities. Avian recruitment, defined here as the per capita rate with which adults produce offspring that ultimately reproduce themselves, depends on breeding propensity, clutch size, nest success, pre-flight survival of young, and subsequent annual survival until reaching reproductive age.

Aside from variability inherent among species, the production of young depends on numerous biotic and abiotic factors that may constrain reproductive success, these may include: age or breeding experience, body condition, weather, habitat conditions, population density or geography (Johnson et al. 1992). In years when such factors are favourable (i.e., conditions improve breeding performance), subsequent recruitment is likely to increase (e.g., weather – Gullett et al. 2015, body condition – Alisauskas 2002). The effects of stochastic environmental conditions on each component of recruitment can also result in implications at the population level (Caswell 2000, Koons et al. 2014).

For migratory species destined for arctic nesting locations, breeding season length is short (later nest initiation, earlier end of brood-rearing period) relative to lower latitudes. Thus, time constraints are imposed on each individual component of recruitment in relation to the advancing summer season. This can be exemplified by species having populations that reproduce in both northern and more southerly regions. For instance, female northern pintails (*Anas acuta*), nesting in the Mackenzie Delta, NT, were not observed to re-nest following a failed attempt, whereas females breeding farther south in the parklands were more likely to lay a second clutch should the first fail (Calverley and Boag 1977). Furthermore, the timing of reproductive events relative to environmental cues within this short span is of increasing importance given observed and anticipated changes in northern climate (Brook et al. 2015, IPCC 2013).

1.2 Light goose populations

Midcontinent lesser snow geese (*Chen caerulescens caerulescens*) and Ross's geese (*Chen rossii*) are closely related species referred to and managed in aggregate as 'light geese' (Moser and Duncan 2001). Both are long-lived, highly gregarious and maintain tight associations during their annual cycles, nesting east of 115°W longitude and wintering largely in the Mississippi flyway and eastern part of the Central flyway (Leafloor et al. 2012). Geometric population growth displayed by these geese over the past three decades (Alisauskas et al. 2012) has occurred concurrently with landscape-level habitat alterations that have improved historical winter carrying capacity; mainly, increased crop yields owing to nitrogenous fertilizers (Alisauskas and Ankney 1992, Abraham et al. 2005), modern mechanized harvesting methods resulting in vast amounts of spilled grain (Krapu et al. 2004), and optimal positioning of wildlife refugia along the flyway offering more frequent stopover sites and greater flexibility in migratory pathways (Abraham et al. 2012). As a result, snow geese were designated as overabundant Canada in 1999, as were Ross's geese more recently in 2014.

Adult survival probability accounts for a greater proportion of population growth rate than does recruitment in these two species, and so is projected to have greater potential influence (Rockwell et al. 1997). Despite attempts to reduce or else stabilize populations using practical management solutions that targeted adult survival (e.g., Batt 1997, Moser 2001, Leafloor et al. 2012), efforts have been largely unsuccessful in doing so. No indication of a systematic decline in adult survival probability has been detected for either species (Alisauskas et al. 2011, Dufour et al. 2012), and the continental population size of Ross's geese has shown evidence of continued increase (Alisauskas et al. in press). However, recent assessments of population trajectories using Lincoln estimates suggest that the population growth rate for lesser snow geese began to decline in 2006 (Alisauskas et al. 2011, Leafloor et al. 2012), and that population estimates leading up to 2012 seem to have stabilized. Under these circumstances, an attenuation of the population growth rate would be consistent with a reduction in annual per-capita recruitment (Dufour et al. 2012).

Approximately 81% of all light geese nesting in Canada's central arctic are found in colonies within the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut (Kerbes et al. 2014).

One of the largest of these sympatric colonies is Karrak Lake (67° 14' N, 100° 15' W; Fig. 1.1), which contains about 40% of all nesting light geese in the Sanctuary (Kerbes et al. 2014). Colony growth here has paralleled that of the midcontinent population (Kerbes et al. 2014). The proportion of the colony composed of Ross's geese has increased slightly from 52% in the early 1990s to 58% by 2014 (R. Alisauskas, unpublished data). Furthermore, the local annual population growth rate for Ross's geese at Karrak Lake has, and currently does, exceed that of lesser snow geese (Alisauskas et al. 2011), despite a somewhat lower annual survival probability (Traylor et al. 2012). However, both species have demonstrated long-term declines in productivity (1991-2014, measured on brood-rearing areas), with Ross's geese consistently performing slightly better than lesser snow geese since the early 2000s (Fig. 1.2). Additionally, Alisauskas (2002) detected a decline in age ratios (immatures/adults) later in fall for lesser snow geese between 1962 and 1999 which has been sustained into the 2000s and similarly observed in Ross's geese (R. Alisauskas, unpublished data). End of season ratios of young:adult geese are regularly used as a metric of recruitment, offering a relative measure of offspring production among years. Consequently, understanding drivers of gosling production, and any interspecific differences present, at a well-studied and densely populated colony may offer valuable perspectives about interspecific differences in recruitment and their influence on respective population dynamics at a broader scale.

1.3 Hypotheses

Density Hypothesis. As populations approach their carrying capacity, population density may impinge on population growth (e.g., Cooch et al. 1989, Williams et al. 1993). Density-dependent factors may include increased probability of disease or predation, or involve competition for resources such as nest-sites or food supply (Newton 1998). The relationship between goose density and forage quality is not linear, but instead appears to depend on the intensity of herbivory. Low to moderate levels of grazing can be beneficial to geese, as it produces forage of greater nutritional quality for an extended period of time (Hik and Jefferies 1990, Bazely and Jefferies 1986). In contrast, high intensity foraging can decrease plant quantity by reducing primary productivity and biomass (Jefferies 1988, Slattery 2000). I hypothesized that a lower per capita supply of forage as a result of interference and exploitative competition by large numbers of geese would negatively affect the annual production of goslings. I predicted that there may be implications for fecundity (Cooch et al. 1989) or the growth and survival of goslings (i.e., reduced growth and survival; Larsson et al. 1998, Sedinger et al. 2001, Brook et al. 2015).

Pre-Breeding Nutrition Hypothesis. Lesser snow geese and Ross's geese are capital breeders (Drent and Daan 1980), meaning they acquire, store and utilize endogenous body reserves for reproduction during and after northward migration. Females that arrive to the nesting grounds with proportionally larger fat and protein reserves are able to lay earlier (Traylor 2010) and produce a larger clutch (Ryder 1970, Ankney and MacInnes 1978). Poor quality females that arrive on nesting areas with limited reserves, or that fail to spare reserves after egg production may catabolize reserves too quickly for self-maintenance and may not complete incubation (Ankney and MacInnes 1978). I hypothesized that reductions in nutrient storage (dependent in part on conditions at spring staging grounds) may contribute either directly or indirectly towards long-term (i.e., decadal) trends in reproductive performance. I predicted that a smaller nutrient mass carried by adult females would result in clutch size and nest success being smaller and lower, respectively.

Phenological Mismatch Hypothesis. Under a changing global climate, there exists considerable interest around whether breeding birds are able to keep pace with advances in spring conditions (Crick et al. 1997, Visser et al. 1998, Drever et al. 2012). This is of particular concern for long-distance migrants that must anticipate environmental conditions at the nesting grounds before departure or en-route from their wintering grounds (Møller et al. 2008, Both et al. 2010). Given shifts in the growing season, facultative adjustments to breeding phenology and the timing of resource requirement should occur in order to match the timing of greatest resource availability (Visser and Both 2005). However, reproduction may become 'mismatched' with seasonal peaks in food, resulting in potential fitness consequences (Both et al. 2010, Miller-Rushing et al. 2010). In the case of arctic-nesting geese, failure to synchronize phenologies of gosling hatch with peak seasonal forage availability would impinge on access to vegetation of the highest seasonal nutritional quality (Brook et al. 2015, Doiron et al. 2015). I hypothesized that in years when phenological mismatch was large, gosling production would decline. I predicted that reduced access to forage of adequate quality by growing young may compromise their ability to survive until achieving flight.

1.4 Thesis objectives and organization

My primary objective was to identify key factors associated with the decline in gosling production from 1992 to 2014 at the Karrak Lake colony. In Chapter 2, I examined the three above-mentioned hypotheses in relation to changes in annual productivity for both Ross's geese and lesser snow geese: (i) increased goose density, (ii) pre-breeding female nutrition, and (iii) phenological mismatch. I also aimed to understand the likely mechanisms that link nutrition to productivity by studying clutch size and apparent nest success. Finally, I was interested in evaluating aspects of phenological mismatch at Karrak Lake. I assessed whether: 1) plant phenology was predictably influenced by spring air temperature, 2) breeding geese tracked spring plant phenology, 3a) mismatch showed a temporal trend during the study period, and 3b) whether any increases to mismatch had resulted from changes in plant phenology, goose breeding phenology, or both.

Collection of information on pre-fledging gosling survival at Karrak Lake has been limited by the sheer number of nesting geese in a predominantly unmarked population, and the extremely low probability of re-encountering individually marked goslings. The only previous investigation of gosling survival spanned two breeding seasons some twenty years ago (Slattery 1994), I sought to investigate this component of the breeding cycle in greater detail (Chapter 3). I tested the density and phenological mismatch hypotheses to assess whether pre-fledging gosling survival had been reduced as a result of changes to foraging conditions (quality and availability) on brood-rearing areas. In order to evaluate if gosling survival at the annual level was in fact associated with nutritional stress, I also examined changes in gosling size over a 16-year period.

I have organized the two data chapters within this thesis as independent manuscripts intended for publication in peer-reviewed journals. Consequently, there is some repetition in certain sections, including descriptions of the Karrak Lake study area and methodologies.

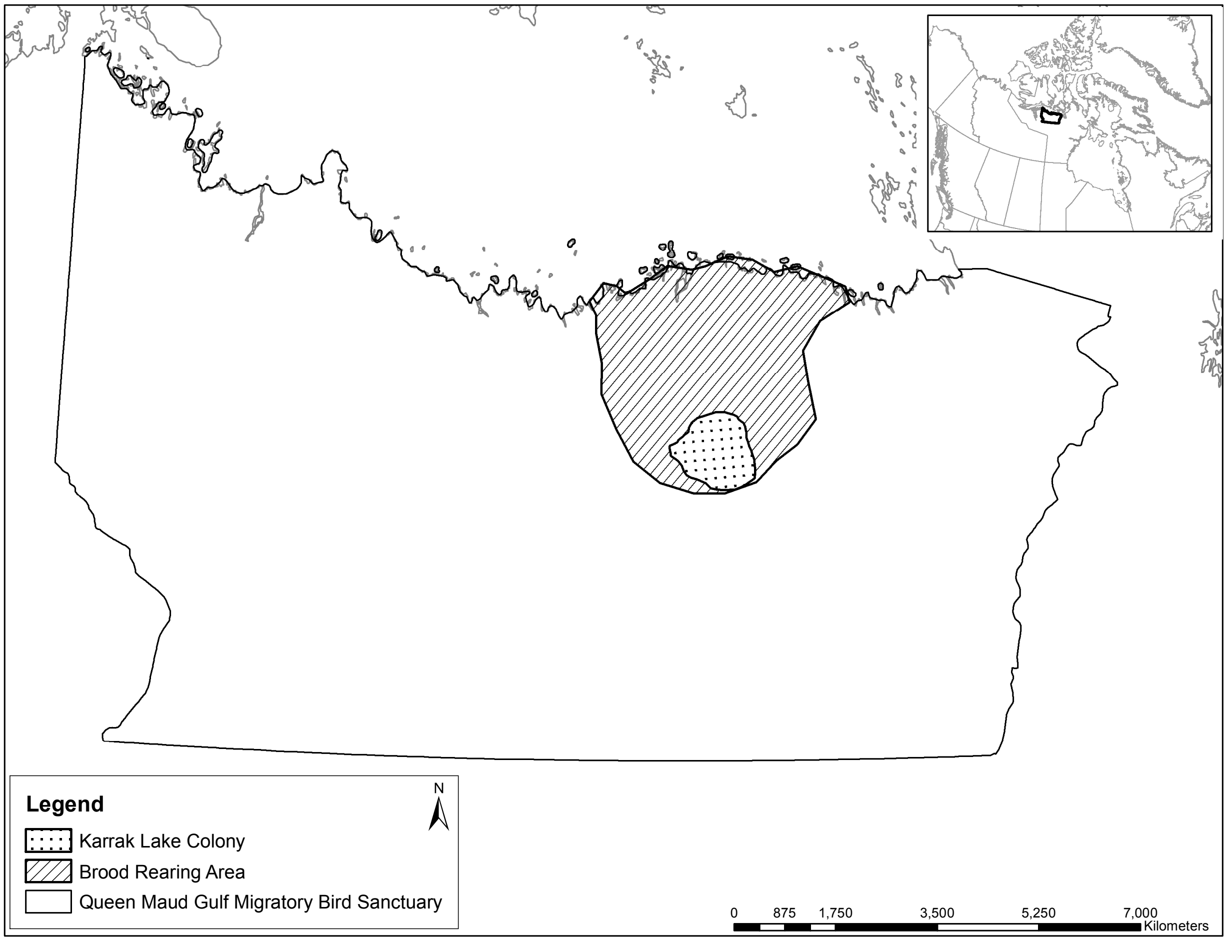

FIGURE 1.1. Map of the Karrak Lake colony and brood-rearing area within the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada.

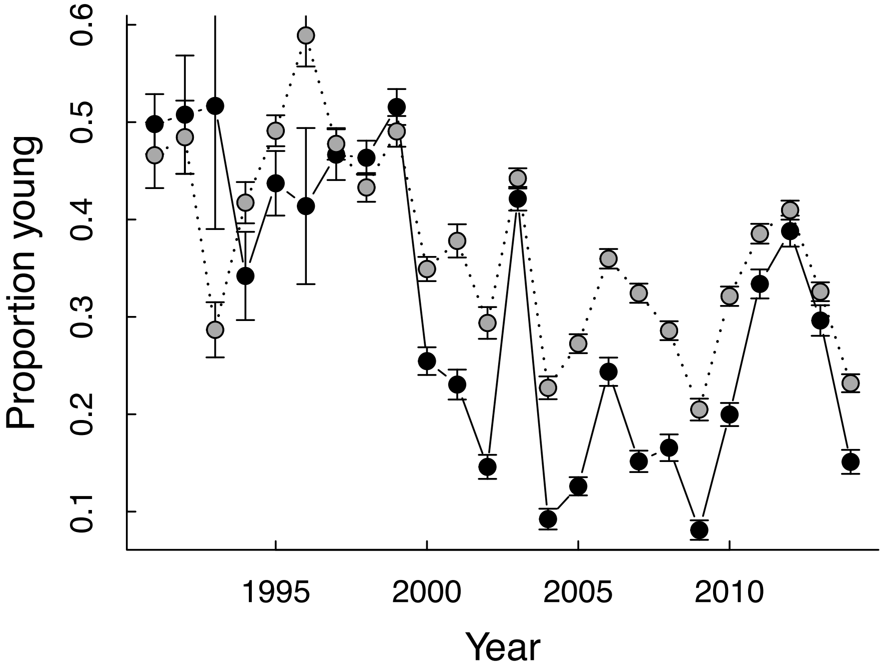

FIGURE 1.2. Proportion of geese captured as goslings during August (1991-2014) in the brood-rearing area within the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada. Ross's geese are shown in grey and lesser snow geese in black.

CHAPTER 2. DECADAL DECLINES IN GOSLING PRODUCTION IN CANADA'S CENTRAL ARCTIC: DENSITY-DEPENDENT NUTRITION AND PHENOLOGICAL MISMATCH

2.1 Introduction

Animal populations fluctuate due to the interplay between the probability of adult survival and the per capita rate at which dead adults are replaced, also known as the recruitment rate. A species' position along the r-K continuum of life history strategies affects whether proportional changes in recruitment or adult survival predictably have greater influence on population growth rate, λ, in prospective analyses (Caswell 2000). For long-lived species, the probability of adult survival is high and remains relatively constant over time (Sæther and Bakke 2000, Stahl and Oli 2006). Conversely, retrospective analyses often show that annual variation in recruitment shows greater influence on past population dynamics than does past survival (Caswell 2000, Cooch et al. 2001).

Recruitment is more complex ecologically than is adult survival because it is an outcome of various states and transition probabilities between the life stages that lead to adulthood. For birds, these include the propensity with which individuals attempt to breed, fecundity (or clutch size), nest and egg survival, pre-fledging survival and post-fledging survival until maturity. Any, and likely all, of these components respond to proximate factors experienced before or shortly after arrival to breeding grounds, and such responses in turn govern recruitment rate to varying degrees in a given year (Alisauskas 2002, Hoekman et al. 2002).

Resource limitation through competition can result from increases in density of conspecifics and tends to affect recruitment rather than adult survival (Cooch et al. 2001, Menu et al. 2002, see Koons et al. 2014). Bottom-up regulation, driven by a reduction in per capita food supply, is most often the mechanism responsible for observed density-dependent reductions in population growth rate (Sinclair and Krebs 2002).

Many species of arctic-nesting birds must acquire and store sufficient nutrient reserves to complete migration and successfully reproduce (reviewed by Drent et al. 2006). Females with proportionally larger reserves can allocate more resources towards reproduction. Across a range of arctic-breeding bird species, body condition of females before nesting has been positively associated with laying date (Traylor 2010), clutch size (Ankney and MacInnes 1978), incubation constancy (Wiebe and Martin 1997), offspring quality (Cresswell et al. 2004; Farmer and Wiens 1999) and recruitment (Ebbinge and Spaans 1995). Reproduction by arctic-nesting geese is nutritionally demanding; it requires that females store sufficient fat and protein before breeding at levels that exceed those during the rest of the annual cycle (Ankney 1982, Alisauskas and Ankney 1992). The reliance on endogenous reserves by female Ross's geese (*Chen rossii*) and lesser snow geese (*Chen caerulescens caerulescens*, hereafter, snow geese; Ankney and MacInnes 1978, Drent and Daan 1980) underscores the importance of sufficient nutrient storage during spring migration in preparation for reproduction. Alisauskas (2002) demonstrated that nutrition of snow geese in agricultural areas of prairie Canada, before their northward departure over the boreal forest to subarctic and arctic staging areas, influenced recruitment months later at a continental scale.

Recently, the effects of climate change on species' assemblages, distributions, recruitment, and phenology in particular, have become increasingly topical (Walther et al. 2002). For example, studies of whether birds adjust timing of breeding in response to advanced spring temperatures and plant phenology have gained considerable attention (Crick et al. 1997, Drever et al. 2012, Liebezeit et al. 2014). However, advancement of breeding may not translate necessarily into improved recruitment or population growth (Wilson and Arcese 2003), nor is this effect ubiquitous (Guillemain et al. 2013). The selective advantage for early breeding is related to minimized asynchrony between peak resource availability and the timing of resource requirements by young (Visser and Both 2005). Failure to keep pace with advanced phenology of key food resources across geographic space or trophic levels can result in phenological 'mismatch' (Visser et al. 1998, Durant et al. 2007). Long-distance migrants to highly seasonal environments are more 'at risk' because they are less able to assess conditions at breeding destinations than are residents or short-distance migrants (Møller et al. 2008, Both et al. 2010, Jones and Cresswell 2010). Thus, arctic-nesting migrants should be exceptionally vulnerable, and are likely those that will be most impacted by climate change, specifically advancement in plant phenology due to arctic warming (McKinnon et al. 2012, Clausen and Clausen 2013, IPCC 2013). An improved understanding of how current climate influences productivity (reviewed by

Miller-Rushing et al. 2010) is necessary to identify how changes in climate may influence future population dynamics.

My objective was to assess the roles of (i) density-dependence, (ii) pre-breeding nutrient storage and (iii) phenological mismatch behind long-term (24-year) declines in per capita gosling production (hereafter gosling production or annual productivity; see Chapter 1) for Ross's geese and midcontinent lesser snow geese breeding in the Canadian central arctic (Alisauskas 2002). These species are long-lived, closely related and undergo long-distance migrations between breeding colonies in the Canadian central arctic and wintering areas in California, Mexico and numerous states in the Central and Mississippi flyways (Mowbray et al. 2000, Jónsson et al. 2013). Both species have shown rapid increases in population size over the past three decades (Alisauskas et al. 2012). Importantly, my hypotheses address different periods of the breeding cycle: density-dependence on northern spring staging grounds (above the tree line) influencing pre-breeding female nutrition and phenological mismatch during brood-rearing. I investigated the likely mechanisms that link the nutrition hypothesis to annual productivity by studying clutch size and probability of nest success. These analyses closely reflect those that Traylor (2010) carried out at Karrak Lake until 2008. My purpose was not to repeat his work, but to extend these analyses through time. I also addressed four questions regarding phenological mismatch at the breeding colony: 1) Does spring temperature reliably predict annual phenology of forage plants? 2) Do breeding geese track spring vegetation phenology? 3a) Has gosling hatch and timing of peak food resource quality become increasingly mismatched over time? 3b) Has this divergence resulted from long-term changes in the dates of vegetation emergence, hatching or both?

2.2 Methods

2.2.1 Study area

I investigated Ross's geese and snow geese breeding at the Karrak Lake colony (67° 14' N, 100° 15' W) in the Queen Maud Gulf Migratory Bird Sanctuary, Nunavut, Canada. Karrak Lake contains approximately 40% of the continental Ross's goose population and is one of the largest known colonies of sympatrically nesting Ross's geese and snow geese (Kerbes 1994). The terrestrial area of the colony (182.8 km^2 in 2014, R. Alisauskas, unpublished data) has expanded concurrently with continental increases in the combined (Ross's and snow) goose population (Kerbes 2014); numbers of nesting geese increased from ~408,000 in 1993 to almost

1.2 million by 2014 (Alisauskas et al. 2012). Each year following hatch, successful breeders and their offspring disperse northward from the breeding colony some 10 to 60 km to brood-rearing areas located between longitude 99.5° and 101.5° W, where the habitat is characterized by sedge meadows, tundra ponds, and rock outcrops (Ryder 1972, Slattery and Alisauskas 2007).

2.2.2 Collection and anatomical dissections

During 1992-2014 adult female geese of both species were collected with a shotgun as they arrived to the nesting colony. Females were differentiated from their male counterparts by their smaller size and the presence of a rounded abdominal profile due to rapid follicular growth. Geese were identified as subadult using plumage characteristics, undeveloped ovaries, or the presence of a bursa of Fabricius (Alisauskas 2002), and were excluded from this analysis. I measured body mass including gastrointestinal contents (± 1.0 g) with a digital scale and external measurements (head length, tarsus and wing span; ± 0.1 mm) with dial calipers or a ruler. Females were dissected on location at the Research Station and their organ, lipid and muscle masses weighed (± 0.1 g). The gizzard was emptied and used in combination with the breast muscle and bone-free leg muscle from one side of the body as an index of protein. Abdominal fat mass was used to index body fat, following Gauthier and Bédard (1985). I weighed reproductive tissues including the oviduct, ovaries, individual developing follicles (if larger than 1 gram) and the oviducal egg, if present, and recorded the number of developing, atretic and postovulatory follicles.

2.2.3 Scaled nutritional condition

To compare the body composition (protein and fat) of individual females within a given year, I standardized goose anatomical data to account for predictable sources of variation. Structurally larger females have greater capacity for nutrient storage (Ankney and MacInnes 1978), so I performed a principal component analysis (PCA) on each species separately using head length, tarsus and wing span measurements to obtain a univariate index of body size. PC1 was obtained from 503 Ross's geese and 593 snow geese that had complete morphometric data. Loadings of the original variables onto the first PC axis were 0.634, 0.598 and 0.491 for Ross's geese and 0.572, 0.648, 0.502 for snow geese, and explained 49.96% and 53.98% of total variance, respectively. Thus, PC1 was a useful index of overall size.

I used each female's collection date as a continuous variable to account for differences in breeding phenology across years. Individuals preparing to lay larger clutch sizes store relatively larger reserves (Ankney and MacInnes 1978), so I calculated the apparent clutch size of each female by summing the number of developing and postovulatory follicles (Traylor 2010). The degree to which reserves are depleted as they are allocated to the clutch varies by the date of collection relative to the predicted date of nest initiation (Bon 1997, Mowbray et al. 2000). So, I controlled for each bird's nutritional investment of somatic tissue towards its clutch at the point of collection by predicting the nest initiation date (NID) for each bird relative to the day of year (DOY) it was collected. For females with at least one postovulatory follicle, NID was calculated using:

$$\mathrm{DOY}_{\mathrm{NID},i} = \mathrm{DOY}_{\mathrm{collected},i} - \mathrm{x}_i * 1.3,$$

where x is the number of postovulatory follicles for bird *i* and 1.3 is the egg-laying rate (Ryder 1971). For females with developing follicles but without postovulatory follicles, I calculated the time (days) required for rapid follicular growth by multiplying the maximum number of developing follicles (6) by the laying rate (Alisauskas and Ankney 1992). This 7.8 day period corresponds to the five intervals of 1.3 days associated with the development of six follicles, plus the sixth 1.3 day interval required for the egg to travel through the oviduct to produce the albumen and shell and be oviposited.

Using only geese with the maximum number of developing follicles, I estimated growth curves for rapidly developing follicles for Ross's geese (*n*= 5) and snow geese (*n*= 25). I used the quadratic equation for the line of best fit to predict the number of days (y_i) remaining until the first egg was laid, i.e., NID, from the largest rapidly developing follicle:

$$\mathrm{ROGO:}\ \mathrm{y}_i = 0.0028(\mathrm{mass})^2 - 0.2800(\mathrm{mass}) + 7.8034;\ \mathrm{r}^2 = 0.98$$

$$\mathrm{LSGO:}\ \mathrm{y}_i = 0.0025(\mathrm{mass})^2 - 0.2488(\mathrm{mass}) + 7.6141;\ \mathrm{r}^2 = 0.92$$

$$\text{and where, } \mathrm{DOY}_{\mathrm{NID},i} = \mathrm{DOY}_{\mathrm{collected},i} + \mathrm{y}_i.$$

Using these two methods (for birds with and without postovulatory follicles) to estimate NID for each collected female, I then subtracted this predicted NID from its collection date to obtain an index of timing of clutch formation in days. Negative values represented the number of days until first eggs were laid, and positive values the number of days after first eggs were laid:

$$\mathrm{devNID} = \mathrm{DOY}_{\mathrm{collected},i} - \mathrm{DOY}_{\mathrm{NID},i}$$

For each species, I constructed candidate sets of sixteen *a priori* models for each fat and protein index using general linear modelling in program R (Version 3.2.1, R Core Team 2015).

Select additive combinations of variables were investigated, and correlations between explanatory variables did not exceed 0.32. To make predictions uniformly across species, I used fully saturated models to estimate levels of fat (g) and protein (g), assuming an average clutch size (4 eggs), an average body size, i.e., PC1 = 0, a 3-day period before a bird's individual NID, and the observed mean NID estimated for the colony in each year. Values of fat and protein, predicted for each species for each year, were then used in all subsequent analyses.

2.2.4 Weather and climate data

An automated weather station at the Karrak Lake Research Station has recorded hourly measures of air temperature, relative humidity, wind speed and direction, and total precipitation since 2000. However, because data in my study extended back to 1991, I used quasi-observational weather data from the North American Regional Reanalysis (NARR) obtained through the National Oceanic and Atmospheric Administration National Operational Model Archive and Distribution System (NOMADS, http://nomads.ncdc.noaa.gov/). I extracted air temperature at 2 meters, relative humidity at 2 meters, and total precipitation for the years, months and locations of interest.

Following related studies (e.g., Morrissette et al. 2010), I separated the breeding cycle into distinct periods to understand the relative influence of weather variables on gosling production by calculating year and species-specific 95% interquartile ranges for the dates of (1) arrival and egg laying, (2) incubation and hatching, and (3) brood-rearing. I used a PCA of mean daily temperature, relative humidity and total precipitation during each of these intervals to obtain an index of local weather (Table A.1). Temperature and relative humidity from the weather station at Karrak Lake were highly correlated with the NARR values, but precipitation less so (Table A.2). Compared to the point location measured by the rain gauge, the reanalysis data provided an integrated estimate of precipitation over the large area represented by the colony. NARR precipitation data were found to have reasonable agreement with observations in both northwest Alberta and northern Manitoba (Choi et al. 2009, Keshta and Elshorbagy 2011; mean $r = 0.64$ and ≥ 0.52, respectively).

Daily values of the Arctic Oscillation (AO) index were obtained from the Climate Prediction Centre of the National Weather Service (http://www.cpc.ncep.noaa.gov); these values have been standardized by the standard deviation of the monthly index. I defined two periods, spring (May 1 – June 30) and summer (July 1 – August 10), and calculated annual averages for each period. A positive phase of the AO indicates a low pressure system over the polar region associated with cold temperatures and precipitation while a high pressure system, the negative phase, produces a meandering westerly jet stream resulting in greater air mixing (Hurrell 1995, Thompson and Wallace 2000). While typically studied in the context of winter, others (Dickey et al. 2008) having successfully incorporated spring and summer AO values into analyses of breeding by arctic-nesting geese.

2.2.5 Breeding success and colony size

Reproductive success and colony size have been measured annually at Karrak Lake since 1991 and 1993, respectively. For detailed methods, see Alisauskas et al. (2012). Briefly, I visited sample plots of 30 m radius located at 1 km intervals on the Universal Transverse Mercator (UTM) grid system within the colony boundary at least twice per season: once during nest initiation and/or incubation, and once after hatch. At each plot I counted the number of nests, recorded clutch size, took measurements of each egg (± 0.1 mm), and estimated incubation stage using egg candling following Weller (1956). Species of each nest was determined by egg size, following Alisauskas et al. (1998). NID of nests discovered during egg-laying was calculated as the day the nest was found minus the number of eggs, less one. Initiation date of nests discovered during incubation was calculated as incubation stage and clutch size subtracted from the date of discovery. Nests were determined to be successful if at least one egg hatched, as indicated by the presence of egg caps or membranes (Klett et al. 1988). I calculated the annual relative NID for each species by subtracting the long-term average NID from 1991 – 2014 from the mean annual NID and hereafter refer to this as an early-late index (ELI).

To test for density-dependent regulation, I included the number of geese estimated to be nesting at Karrak Lake each year (Alisauskas et al. 2012) as a continuous variable in models. Missing estimates for 1991 and 1992 were obtained using the geometric population growth equation:

$$N_t = N_0\lambda^t$$

where, N_0 was a colony estimate from a 1988 aerial survey (Kerbes et al. 2014) and the population growth rate was taken for a period of constant population growth (1993-2006).

Annual capture and banding efforts were conducted on brood-rearing grounds from 1991-2014. Geese were herded into portable corral traps with a helicopter (Timm and Bromley 1976) in early to mid-August, the timing of which corresponded with adult remigial moult and the prefledgling stage of goslings. I determined individual age (adult versus immature) and sex by plumage characteristics and cloacal eversion, respectively. Total adults and goslings captured were calculated by summing across all banding efforts within a year. This included all recaptures (those marked previously north of Karrak Lake), foreign recaptures (those originally marked elsewhere) and previously unmarked individuals. The proportion of Ross's goose and snow goose goslings at banding was correlated with the proportion of goslings estimated later the same year during fall surveys in Saskatchewan at $r = 0.49$ ($n = 22$) and $r = 0.27$ ($n = 11$), respectively (R. Alisauskas, unpublished data). Age ratios at banding provide a direct measure of per capita recruitment until just prior to fledging, and, unlike harvest age ratios, are not influenced by age, sex, or species differences in vulnerability to harvest (Dufour et al. 2012). A key assumption was that captures represented the true ratio on the brood-rearing area between young and adults. Evidence of brood patches in adult-only flocks indicated that failed-breeders remained in the area and were equally susceptible to capture. Furthermore, snow and Ross's geese that do not attempt to nest (i.e., non-breeders) are flightless in early July at Karrak Lake, and most or all have regained flight by August (Jónsson et al. 2013).

2.2.6 Plant phenology (NDVI)

Doiron et al. (2013) demonstrated that the date of 50% annual maximum Normalized Difference Vegetation Index (NDVI) could be used as a proxy for the timing of peak nitrogen availability in graminoid plants. Consequently, I used a 24-year time series to estimate the median date of NDVI_{50} (my index of forage availability) on the brood-rearing area ($\sim 5 \times 10^6$ km^2) north of Karrak Lake (Slattery and Alisauskas 2007, Wilson et al. 2016). Daily global NDVI grids (0.05-degree resolution) were obtained from 2 sources: the Long Term Data Record Version 3 collected by the Advanced Very High Resolution Radiometer (AVHRR) for 1982-1999 (http://ltdr. nascom.nasa.gov) and from the Earth Science Data Record of preprocessed NDVI collected by the Moderate Resolution Imaging Spectroradiometer (MODIS) for 2000-2010 (http://vip. arizona.edu). Ten-day maximum NDVI composites were derived (Holben 1986) and the annual NDVI phenology curves linearly smoothed to interpolate persistently cloudy periods. Details about the NDVI data processing are presented in Ward et al. (2015), and a study of sub-arctic-nesting Canada geese (*Branta canadensis*) using similar NDVI data is presented in Brook et al. (2015). I assumed that the median day of year when NDVI_{50} was attained for all vegetation was a reasonable proxy for the phenology of goose forage species alone, as have others (Brook et al. 2015). I quantified phenological mismatch between geese and forage as the mean annual hatch date (goose species specific) minus the date of $NDVI_{50}$. Smaller values indicated that hatch was more synchronous with plant phenology.

2.2.7 Statistical analyses

I used general linear models (GLMs) with a normal error structure to evaluate the influence of ecological covariates on the annual production of goslings. I modelled gosling production using the proportion of juveniles at banding, weighted by the total number of geese captured. To avoid problems with collinearity, I examined the Pearson product-moment correlation between explanatory variables. Fat and protein as well as fat and ELI variables were highly correlated ($r = \geq |0.56|$), and mismatch and colony size were moderately correlated ($r = 0.46$), so these variables were not considered as additive effects in the same models.

An intercept-only model was used as a statistical null model. Because of the importance of nest initiation date to waterfowl productivity (e.g., Traylor 2010), ELI was included in all models. Thus, the biological null model included ELI and a species term. Due to sample size constraints, I did not consider non-linear relationships and tested only interactions of interest (i.e., fat-by-species and protein-by-species). To reduce the number of explanatory variables tested within the set of candidate models, likelihood ratio tests were performed on environmental variables individually against the biological null model. The summer AO index and local weather during the brood-rearing period were retained ($p = 0.04$ and $p = 0.07$, respectively).

Using GLMs, I modelled annual mean clutch size and apparent nest success (the ratio of successful nests to total number of nests, hereafter nest success; D. Kellett and R. Alisauskas, unpublished manuscript) in a similar manner. Variables potentially explaining clutch size included species, ELI, protein, fat, colony size and local weather during arrival and egg laying. Species-specific responses to fat, protein and local weather were also tested. Similar variables were considered for nest success with some exceptions: I used local weather during incubation and hatching, included clutch size because nest success is generally higher for larger clutches (Bourgeon et al. 2006, but see Rohwer 1992), and excluded protein based on the results of previous studies (Bon 1997). I considered species interactions with ELI, clutch size, local weather, and fat. Fat, clutch size, and ELI variables were, not surprisingly, highly correlated with one another ($r = \geq |0.56|$). Accordingly, no single model included more than one of these variables.

I selected models based on an information-theoretic approach (Burnham and Anderson 2002) using Akaike's Information Criterion corrected for small sample size (AIC_c). To explain the long-term decline in the proportion of goslings, I considered 22 *a priori* models including a global model that encompassed all uncorrelated effects of interest and a series of progressively less complex models that reflected the nutrition, mismatch and density-dependence hypotheses. Likewise, I constructed 12 and 15 *a priori* models to investigate variation in clutch size and nest success, respectively. Models with ≤ 2 ΔAIC_c units were judged to have substantial support and be highly competitive. I used Akaike weights (w_i) to assess the likelihood of each model relative to others in the candidate set (Burnham and Anderson 2002).

I used simple linear regression to examine the relationship between the annual date of peak hatch and $NDVI_{50}$, in addition to detecting changes in each of these events over time. I tested whether warm spring temperatures were associated with earlier dates of $NDVI_{50}$ and assessed whether spring conditions at the breeding grounds explained the annual variation in mismatch using ten *a priori* GLM models that included the effects of year (continuous), spring AO, spring temperature (25 May-30 June), and spring precipitation (25 May-30 June). All analyses were done with Program R (Version 3.2.1, R Core Team 2015).

2.3 Results

2.3.1 Gosling production

Per capita gosling production at Karrak Lake varied annually, ranging from 20% young in 2009 to 59% in 1996 for Ross's geese ($\bar{x}_{Ross's}$ = 37%, SE = 10.1%) and from 8% young in 2009 to 52% in 1993 for snow geese ($\bar{x}_{snow}$ = 30%, SE = 9.6%). Overall, both species showed similar decadal declines in the proportion of goslings captured near fledging. However, Ross's geese appear to have had greater overall success ($\beta_{spp(Ross's)}$ = 0.469, 95% CI: 0.238, 0.700), producing more goslings per adult annually compared to snow geese (intercept; β_{Snow} = -0.758, 95% CI: -1.448, -0.069).

The best-approximating models explaining gosling production are shown in Table 1 (complete list in Table A.3). The most parsimonious model accounted for 55% of the variation (parameter estimates in Table 2.1), although three other models were highly competitive (ΔAIC_c < 2). Phenological mismatch was included in all competing models. In the top-ranked model, a greater disparity between peak hatch and peak vegetation quality was associated with fewer goslings at mid-August capture efforts (Fig. 2.1a). Models in which mismatch was replaced by colony size received comparatively little support ($\Delta AIC_c \geq 4.44$). Species responded similarly to protein mass (Fig. 2.1b), whereby larger mean annual protein reserves at arrival to the nesting grounds were positively related with the production of young. I also found an increase in gosling production in years when geese initiated nesting earlier (Fig. 2.1c).

A model that included only local weather (i.e., PCA of air temperature, relative humidity and precipitation) and climatic conditions (i.e., summer AO index) with the biological null was not well supported ($\Delta AIC_c = 21.04$). However, in addition to inclusion in lower-ranked models, the summer AO index was included in three of the four top-performing models in the candidate set. Positive values of the summer AO index were weakly related to lower annual gosling productivity ($\beta = -0.049$, 95% CI: -0.111, 0.012). The parameter for local weather during brood-rearing was poorly estimated with 95% confidence intervals consistently overlapping zero. A species-specific response in gosling production from annual variation in fat reserves ranked among the most competitive models (Table 2.1). Snow geese produced a higher proportion of young when annual levels of pre-breeding fat reserves were greater ($\beta_{Snow} = 0.006$, 95% CI: 0.003, 0.009), with no effect for Ross's geese in relation to snow geese ($\beta_{spp(Ross's)} = -0.006$, 95% CI: -0.010, -0.002; Fig. 2.1d).

I tested four *a posteriori* models: three in which ELI was removed in order to verify its ecological importance, and one in which a quadratic effect of mismatch was introduced, as it appeared to offer a better fit. However, models that retained ELI and the linear effect of mismatch were better supported (Table A.3).

2.3.2 Clutch size and nest success

Annual variation in mean clutch size was best explained by the additive effects of species, ELI, protein and a species-by-protein interaction (Table 2.2). However, an *a posteriori* model that included a quadratic effect of ELI outcompeted all others, although the quadratic effect was weak ($\beta = -0.002$, 95% CI: -0.004, 0.000; Fig. 2.2a). Mean clutch size was larger for snow geese (intercept; $\beta_{Snow} = 2.184$, 95% CI: 1.301, 3.066) than for Ross's geese ($\beta_{spp(Ross's)} = -1.179$, 95% CI: -2.635, 0.277). Larger mean annual protein reserves resulted in somewhat larger clutches for Ross's geese ($\beta_{spp*protein(Ross's)} = 0.006$, 95% CI: 0.000, 0.011), but snow geese were less sensitive to such differences in protein ($\beta_{Snow} = 0.003$, 95% CI: 0.001, 0.006; Fig. 2.3). The highest-ranked model containing mean annual fat ($\Delta AIC_c = 27.88$) suggested that for both species, clutch size increased with larger fat stores ($\beta = 0.014$, 95% CI: 0.010, 0.017).

Ross's geese exhibited greater annual mean nest success (Table 2.2; $\beta_{spp(Ross's)} = 0.051$, 95% CI: 0.017, 0.085) than did snow geese overall (intercept; $\beta_{Snow} = 0.772$, 95% CI: 0.748, 0.797). Snow goose nest success was reduced to a greater extent by delays in nest initiation ($\beta_{Snow} = -0.019$, 95% CI: -0.025, -0.013) than were Ross's geese ($\beta_{spp*ELI(Ross's)} = 0.009$, 95% CI: 0.002, 0.017; Fig. 2.2b). Warm and dry conditions during the incubation period positively influenced nest success of both species ($\beta = 0.025$, 95% CI: 0.014, 0.036). While correlated effects such as timing of nesting and clutch size generally received more support, mean annual fat reserves were also positively related to nest success ($\beta = 0.004$, 95% CI: 0.002, 0.005).

2.3.3 Vegetation and goose breeding phenology

The day of year at which NDVI$_{50}$ was reached ranged 32 days, from 12 June to 14 July with a mean of 27 June (178 ± 1.48 SE). Earlier NDVI$_{50}$ dates were associated with warmer spring temperatures ($\beta = -2.033$, 95% CI: -2.550, -1.516; Fig. 2.4a). Moreover, during this 24-year study, the timing of NDVI$_{50}$ had advanced significantly ($\beta = -0.337$, 95% CI: -0.618, -0.057; Fig. 2.4c). Annual mean hatch dates were less variable, spanning 15 days (30 June to 15 July) for Ross's geese and 13 days (1 July to 14 July) for snow geese. No long-term trend in hatch date was detected over the course of this study for either species ($\beta_{Snow} = 0.035$, 95% CI: -0.193, 0.262; $\beta_{Ross's} = 0.024$, 95% CI: -0.226, 0.274; Fig. 2.4c).

2.3.4 Phenological mismatch

Phenological mismatch, the number of days separating hatch and NDVI$_{50}$, averaged 11 ± 1.08 days (range: -1 to 21 days) for Ross's geese and 10 ± 1.19 days (range: -4 to 21 days) for snow geese. Gosling hatch preceded or coincided with the date of NDVI$_{50}$ in only two of twenty-four years (1992, 1997). I found a positive relationship between annual peak hatch and NDVI$_{50}$, suggesting that geese do respond to advanced forage phenology by nesting earlier ($\beta = 0.362$, 95% CI: 0.237, 0.486; Fig. 2.4b). According to the best-performing model, the difference (days) between hatch and NDVI$_{50}$ increased linearly through time ($\beta = 0.326$, 95% CI: 0.159, 0.493). The degree of mismatch was also greater in years with warmer spring temperatures ($\beta = 0.851$, 95% CI: 0.408, 1.293) and with negative values of the spring AO index ($\beta = -3.791$, 95% CI: -6.095, -1.486; Table 2.2).

2.4 Discussion

I found evidence to support the importance of local weather, climate and phenological mismatch to the gosling production of Ross's and snow geese at Karrak Lake. Later nesting reduced annual productivity in both goose species. Delays in nest initiation stem largely from local conditions on arctic breeding grounds (Madsen et al. 2007, Dickey et al. 2008); deep snow cover and delayed melt due to cold temperatures can impede access to nesting habitat and prolong the pre-egg laying period (Choinière and Gauthier 1995). Such delays are costly to fitness because nutrient reserves must be diverted from egg production to meet prolonged basic metabolic needs; such nutrient diversion reduces amounts available for egg production and incubation constancy (Ryder 1970, Ankney and MacInnes 1978). I found strong evidence for reduced clutch size in very late years and some evidence of a reduction in clutch size in early years. Other studies have shown that the amount of endogenous fat reserves is an important determinant for the onset of laying (Ankney and MacInnes 1978, Traylor 2010) and that clutch size declines as the season progresses (Findlay and Cooke 1982, Traylor 2010). In years when spring was relatively advanced, migratory cues may have resulted in geese departing northern staging areas prior to the completion of pre-nesting storage of fat and protein. Thus, in 'early' nesting years, a reduction in clutch size may be the result of geese laying their first eggs without having reached optimal levels of nutrient reserves. Alternatively, favourable spring conditions may result in more young birds choosing to nest for the first time, thereby inducing an age-related decline in clutch size.

Low productivity observed in years when fat reserves were reduced is consistent with findings by Alisauskas (2002), where fat acquired on the prairies was a necessary constituent for the recruitment of snow geese. In this study, gosling production by Ross's geese was more robust to the effect of fat than was gosling production by snow geese. This may relate to my finding and that of Traylor (2010) that nest success of Ross's geese was also less sensitive to delays in nest initiation. Fat reserves are metabolized during incubation to satisfy energy demands, and nest success is conditional on sufficient reserves being spared for the duration of incubation (Harvey 1971, Ankney and MacInnes 1978, Traylor 2010). As reserves are depleted, females require more frequent recesses, leaving nests exposed to predation and cooling. Delays in breeding that deplete fat reserves may be less critical for Ross's goose females because they generally build more insulated nests (McCracken et al. 1997), supplement stores with local forage (Gloutney et al. 2001) and have higher nest success despite lower attentiveness during late incubation (Craig 2000). Overall, the influence of nest initiation date on subsequent nest success is likely an important intermediary mechanism that ties pre-breeding nutrition to annual colony productivity and may provide an explanation for why Ross's geese have consistently experienced higher productivity during this study.

Similar to Dickey et al. (2008), I found that a large-scale climate index (the AO) better predicted annual gosling production in late summer while local weather conditions were better predictors of the earlier summer intermediaries of gosling production, such as nest success. Given that the AO is such a geographically broad covariate, its temporal relevance was difficult to interpret with confidence at the scale presented here. However, for short, discrete periods of time, local weather appeared to be meaningful. Warm ambient temperatures support embryonic development and survival, thereby increasing egg hatchability (van Oudenhove et al. 2014). Consequently, cooler conditions experienced during incubation recesses likely exacerbate egg cooling, placing embryos at risk of dropping below their 'thermal tolerance' (Webb 1987, van Oudenhove et al. 2014) and jeopardizing overall nest success.

Increasing mismatch over the course of my study was the result of a long-term advance in plant phenology (indexed by $NDVI_{50}$) without a corresponding advance in hatching dates by geese. Timing of both nest initiation and vegetation green-up are governed by common environmental conditions, particularly temperature and snow cover extent (Tieszen 1974, Madsen et al. 2007). Although I found that both species were able to partially adjust hatch dates by nesting earlier in years with early springs, timing of vegetation green-up responded more than did nesting females (Dickey et al. 2008). Part of the reason for this is that incubation duration in snow and Ross's geese is relatively fixed at about 22 days duration, preventing additional adjustments to hatch phenology regardless of ambient environmental conditions (Ryder 1971, 1972, Craig 2000). As well, the required storage of fat and protein prior to breeding may impose minimum time constraints that prevented earlier conditioning and nesting by both species.

Similar to Brook et al. (2015), my results demonstrated that mismatch was greatest in years when $NDVI_{50}$ was anomalously early, typically in years with high spring temperatures. Implications of such mismatches were informed by Doiron et al. (2014) who reported that experimental warming advanced plant phenology and also accelerated the rate of decline in nitrogen concentration thereafter. If unmitigated increases in greenhouse gas emissions caused arctic regions to warm as anticipated by climate projections (IPCC 2013), such a unidirectional trend of air surface temperature could result in plant phenology becoming increasingly decoupled with the hatching of goslings if adults are unable to advance their breeding chronology accordingly. Although, how geese may adapt to such changes into the future, and how populations may respond are difficult to predict.

The ecological consequence of this shift was evident in my study – increased mismatch directly reduced annual productivity of geese at Karrak Lake, and was likely mediated by negatively affecting gosling growth and subsequent survival. Strongly seasonal arctic environments with short growing-season length require that young-of-the-year have access to high-quality forage early enough to reach maturity before fledging (Sedinger and Raveling 1986, Both et al. 2010). Goslings preferentially select forage with high nitrogen concentration, to compensate for low processing efficiency by the gut, and to support tissue production (Sedinger 1992, 1997). A pervasive pattern in studies of arctic-nesting geese is that late-hatched goslings have reduced access to high quality foods and show stunted growth and reduced body mass (Cooke et al. 1984, Lepage et al. 1998, Brook et al. 2015, Doiron et al. 2015). Snow goose goslings raised in captivity and fed low quality (low protein) diets had reduced growth rates, reached a smaller asymptotic size, and had lower survival probability when minimum dietary requirements were not met (Richman et al. 2015). Indeed, among avian species, the rapid growth rate of geese makes them especially susceptible to mortality if food is of poor quality, often regardless of quantity (Ricklefs 1973, Aubin et al. 1986, Richman et al. 2015).

Further population-level consequences, in response to the quality and timing of forage availability relative to hatch, may occur after fledging. Structurally smaller and lighter goslings suffer reduced first-year survival rates in barnacle geese (*Branta leucopsis*; Owen and Black 1989), Canada geese (Hill et al. 2003, Brook et al. 2015), Emperor geese (*Chen canagica*; Schmutz 1993), as well as in lesser snow geese (Francis et al. 1992), leading to reduced recruitment (Sedinger et al. 1995). Smaller goslings that recruit may remain structurally smaller as adults (Cooch et al. 1991; Larsson and Forslund 1991), and may have an inherently lower ability to invest in future reproduction (i.e., breeding propensity and/or fecundity; Sedinger et al. 1995) via constraints on nutrient storage (see methods above). A long-term decline in structural body size (Alisauskas 1998, 2002) of midcontinent snow geese may have contributed to reduced production of goslings at the population level.

My results confirm the importance of adequate nutrient reserves to successful breeding by Ross's geese and snow geese. The proportion of goslings captured mid-August on brood-rearing areas was positively associated with protein reserves at arrival to Karrak Lake about two months before. Traylor (2010) reported a long-term decline in protein reserves of pre-breeding female Ross's and snow geese arriving to nest at Karrak Lake between 1993 and 2008. However, snow geese departing the Canadian prairies during spring migration between the mid 1980s/early 1990s and the early to mid 2000s have not undergone a significant decrease in protein mass, perhaps due to an agricultural shift towards the cultivation of protein-rich pulse crops (M. Ross, unpublished data). This suggests that as geese have converged towards breeding areas after departing Prairie Canada in recent years, they have not stored significant protein reserves as somatic muscle tissue compared to the levels acquired historically on northern staging areas (Wypkema and Ankney 1979). I suggest that density-dependence, a reduction in per capita food supply as a result of interference and exploitative competition, is likely occurring on these penultimate northern staging grounds as the population has continued to increase. My estimate of colony population size pertained to the number of geese breeding at Karrak Lake but did not include non-breeders near the colony; however, both breeding and non-breeding geese destined for Karrak Lake and surrounding areas likely stop to feed at the same northern staging areas above the tree line in the arctic plains. Therefore, my estimate of nesting population size likely did not accurately capture the number of foraging birds and thus, may not have been an accurate index of nutritional demand by all birds using such areas. Nevertheless, a sharp increase in population size for the region is evident (Alisauskas et al. 2012, Kerbes et al. 2014, Wilson et al. 2016) and the long-term decline in productivity appears consistent with density-dependence detected in other regions (Cooch et al. 1989, Williams et al. 1993, Aubry et al. 2013).

Increased competition under sub-optimal foraging conditions may constrain young individuals from breeding as a consequence of poor physiological condition resulting from a lack of foraging skills in comparison to older adults (the constraint hypothesis; Krapu and Doty 1979, Curio 1983). Alternatively, the restraint hypothesis (Williams 1966, Pianka 1976) proposes that younger individuals refrain from breeding to avoid reproductive costs while older individuals invest heavily in reproduction, as their time to reach senescence is reduced. The constraint hypothesis is generally more widely accepted for waterfowl species (Rohwer 1992). On some level, this remains a 'black box' in this study system, in part because the large colony size makes obtaining information at the individual level very difficult, and also because non-breeding geese were outside of the colony (Wilson et al. 2016) and not easily subject to sampling. Reed et al. (2004) found that intermittent breeding among sexually mature greater snow geese (*Chen caerulescens atlantica*) nesting on Bylot Island was common and varied depending on spring climatic conditions and extent of disturbance caused by spring conservation harvests. They also suggested that nest density and fall age-ratios offered reliable indices of breeding propensity; declines in both indices have been observed at Karrak Lake (R. Alisauskas unpublished data). Consequently, foraging competition on spring staging areas may have negatively affected breeding propensity of snow and Ross's geese, and this may have subsequently contributed to, at least in part, the long-term decline in production of young.

The effect of mean annual protein stores on gosling production appeared to be mediated partly through its effect on clutch size. As with protein stores, both species have experienced similar declines in clutch size over time (Traylor 2010). Protein is an important determinant of clutch formation, with reserves drawn from muscle groups that will be used infrequently during nesting (Ankney and MacInnes 1978). Changes in clutch size as a result of reduced protein stores were more evident in Ross's geese than snow geese. These results agree with Traylor (2010), who studied the role of nutrition in clutch size variation at the individual level, and attributed heavier reliance of reserves in smaller bodied geese to a greater proportional investment of an absolutely smaller nutrient mass (Ankney 1984). In this study, the relative size of annual pre-breeding protein reserves was unrelated to observed variation in nest success.

2.4.1 Conclusions

I have shown that declines in productivity were linked to multiple additive factors during different periods leading up to and during breeding. The parallel declines for both Ross's and snow geese in the proportion of goslings just prior to fledging indicated non species-specific responses to several environmental covariates. However, Ross's geese consistently experienced greater annual productivity over snow geese due to greater nest success. Overall, my findings support both the nutrition hypothesis, possibly stemming from density dependence on northern staging areas, and the mismatch hypothesis, due to a trend of earlier green-up of vegetation without a corresponding trend in hatch date by either species.

Sustained declines in gosling production at my study site imply reduced potential for subsequent recruitment, even if pre-reproductive survival and breeding probability remain unchanged. Kerbes et al. (2014) estimated that the number of breeding geese in the Canadian central arctic represented 45% of known breeding midcontinent snow geese and continental Ross's geese. Assuming that other large nesting colonies have experienced similar declines in production, both changes in nutrition and increasing phenological mismatch have probably influenced recent apparent changes in population trajectories. Lincoln estimates of midcontinent snow geese and continental abundance of Ross's geese appear to have attenuated in recent years (Alisauskas et al. 2011, Alisauskas et al. 2012) with no declines in adult survival over the same time period (Alisauskas et al. 2011, Wilson et al. 2016). Reduced recruitment and increased survival are predicted to alter the population age distribution toward older individuals with possible senescent effects on reproduction and momentum effects on population trajectories, possibly including population decline. I encourage continued estimation of both recruitment and survival to fully understand how each will influence future abundance of both snow geese and Ross's geese.

TABLE 2.1. (a) Model selection for the proportion of Ross's and lesser snow goose goslings (% goslings) observed in August on the brood-rearing areas north of the Karrak Lake colony from 1992-2014 (*n* = 46). Shown are the number of estimable parameters (k), the log-likelihood (logLik), the Akaike Information Criterion difference with correction for small sample size (Δ AIC$_c$), the model weights (ω_i) and the proportion of variance explained (R^2). (b) Parameter estimates (β) and 95% confidence intervals of the top ranked model.

(a) Models	k	logLik	Δ AIC$_c$	ω_i	R^2
Spp + ELI + Mismatch + Protein	6	49.039	0.00	0.278	0.55
Spp + ELI + Mismatch + Protein + Summer.AO	7	50.415	0.04	0.272	0.56
Spp + Mismatch + Spp*Fat + Summer.AO	7	49.952	0.97	0.171	0.55
Spp + ELI + Mismatch + Protein + Summer.AO + BroodWeather	8	51.169	1.48	0.133	0.57
Spp + Mismatch + Spp*Fat + Summer.AO + BroodWeather	8	50.452	2.91	0.065	0.55
Intercept (Null)	2	28.638	30.93	0.000	0.00

(b) Parameters	SPP$_{ROGO}$	ELI	Mismatch	Protein	Intercept
β	0.469	-0.009	-0.008	0.003	-0.758
95% CI	0.238, 0.700	-0.014, -0.004	-0.013, -0.003	0.001, 0.005	-1.448, -0.069

Notes: Spp = species, ELI = early-late nest initiation index, Mismatch = the difference between the mean annual hatch date and NDVI$_{50}$, Protein = annual index of body protein, Fat = annual index of abdominal fat, Summer.AO = mean annual AO value from July 1 to August 10, BroodWeather = PC1 of temperature, precipitation and relative humidity from the end of the hatch period to Julian date 222 (August 9th/10th).

TABLE 2.2. Model selection for the annual variation in clutch size (n = 46), nest success (n = 46) and phenological mismatch (n = 48) at Karrak Lake, NU from 1991 (or 1992) – 2014. Shown are the number of estimable parameters (k), the log-likelihood (logLik), the Akaike Information Criterion difference with correction for small sample size (Δ AIC$_c$), the model weights (ω_i) and the proportion of variance explained (R^2).

Response Variable	Model	k	logLik	Δ AIC$_c$	ω_i	R^2
Clutch Size	*A Posteriori Model*					
	SPP + ELI^2 + ELI + Protein + SPP*Protein	7	35.756	0.00	0.431	0.79
	SPP + ELI + Protein + SPP*Protein	6	34.241	0.24	0.383	0.78
	SPP + ELI + Protein + SPP*Protein + Pop	7	34.563	2.39	0.131	0.78
	SPP + ELI + Protein	5	30.840	4.38	0.048	0.75
	Intercept (null)	2	-2.553	63.95	0.000	0.00
Nest Success	SPP + ELI + IncWeather + SPP*ELI	6	66.108	0.00	0.494	0.61
	SPP + CS + IncWeather	5	63.893	1.78	0.203	0.58
	SPP + CS + IncWeather + SPP*CS	6	65.138	1.94	0.187	0.59
	SPP + ELI + IncWeather	5	63.225	3.11	0.104	0.56
	Intercept (null)	2	42.548	37.25	0.000	0.00
Mismatch	Year + SpringTemp + Spring.AO	5	-130.973	0.00	0.978	0.51
	Year + SpringTemp	4	-136.326	8.21	0.016	0.40
	Year + Spring.AO	4	-138.019	11.59	0.003	0.36
	SpringTemp + Spring.AO	4	-138.240	12.03	0.002	0.35
	Intercept (null)	2	-149.617	30.13	0.000	0.00

Notes: Spp = species, ELI = early-late nest initiation index, Protein = annual index of body protein, Pop = nesting population size estimate, IncWeather = PC1 of temperature, precipitation and relative humidity for the incubation and hatch period, CS = clutch size, Year = linear time trend, Spring.AO = mean annual AO value from May 1 to June 30, SpringTemp = mean spring temperature from May 25 to June 30.

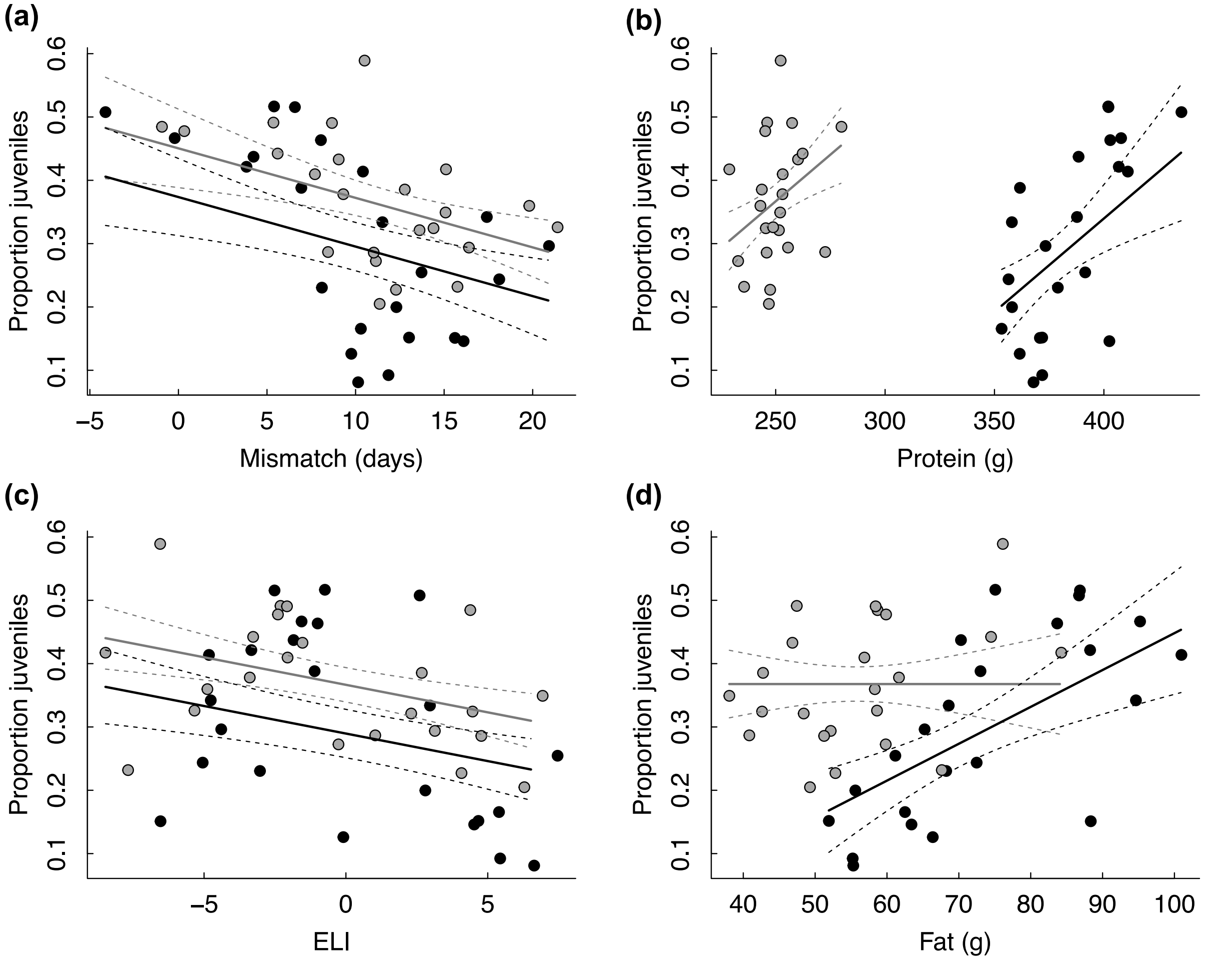

FIGURE 2.1. Relationships between the proportions of goslings captured annually at August banding efforts from 1992-2014 and the variables included in the most competitive models of the candidate set (*n* = 46). (a) Mismatch – the difference between the mean annual hatch date and the day of year $NDVI_{50}$ is reached, (b) annual index of body protein from females collected at arrival to the colony, (c) The early-late index – a measure of relative nest initiation date among years, and (d) the annual index of body fat from females collected at arrival to the colony. Raw mean annual values, the model-predicted line (solid) and 95% confidence intervals (dashed) are shown for Ross's geese (grey) and lesser snow geese (black).

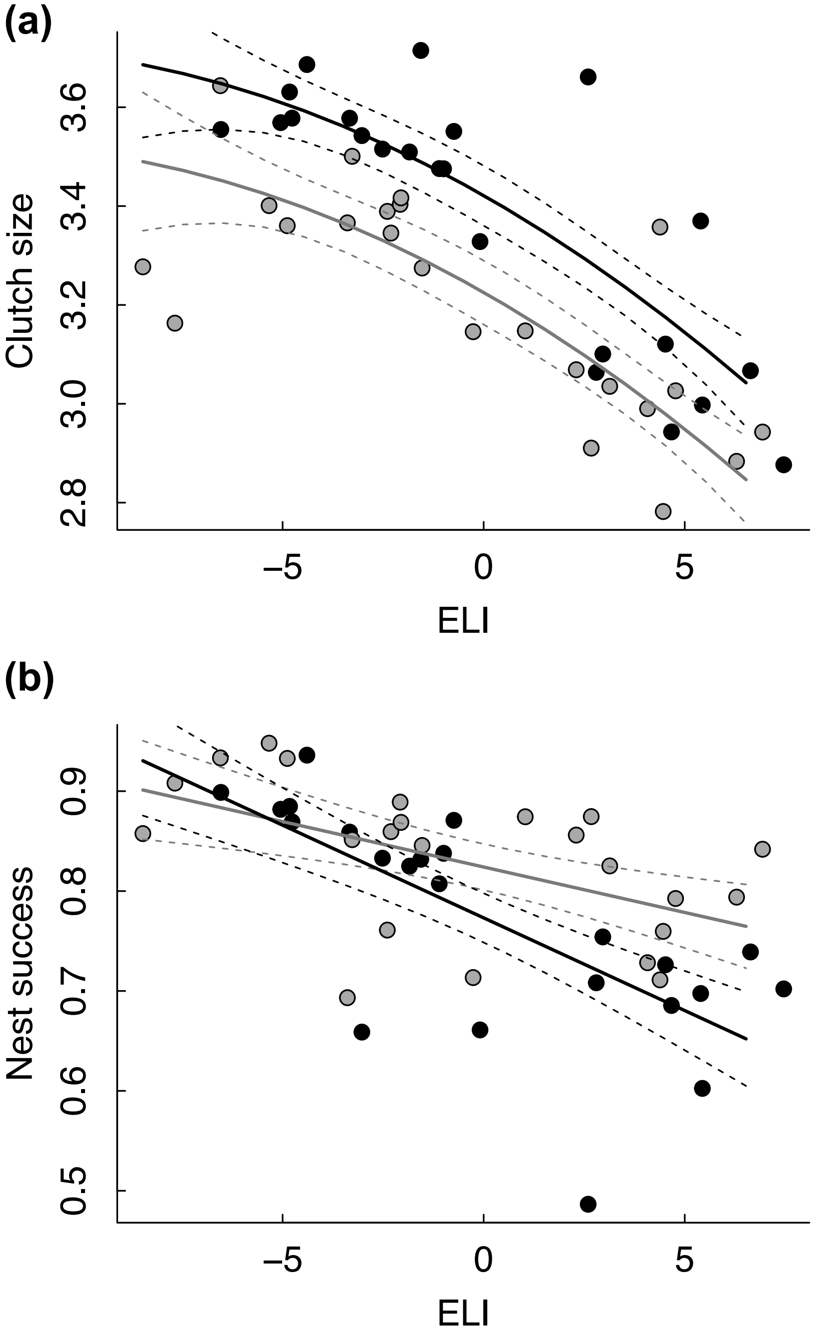

FIGURE 2.2. The relationships between (a) mean annual clutch size and the early-late-index (*n* = 46), and (b) mean annual apparent nest success and the early-late index (*n* = 46) for geese breeding at Karrak Lake, NU from 1992-2014. Raw mean annual values, the model-predicted line (solid) and 95% confidence intervals (dashed) are shown for Ross's geese (grey) and lesser snow geese (black).

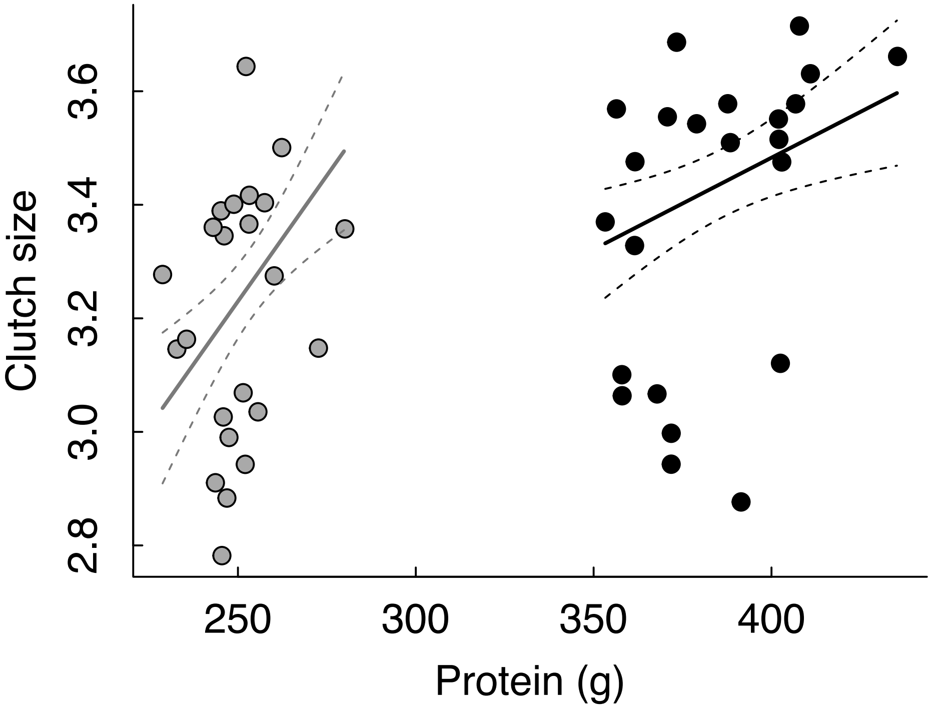

FIGURE 2.3. The relationship between mean annual clutch size and the mean annual protein reserve index of pre-breeding females arriving to breeding at Karrak Lake, NU, from 1992-2014. Raw mean annual values, the model-predicted line (solid) and 95% confidence intervals (dashed) are shown for Ross's geese (grey) and lesser snow geese (black).

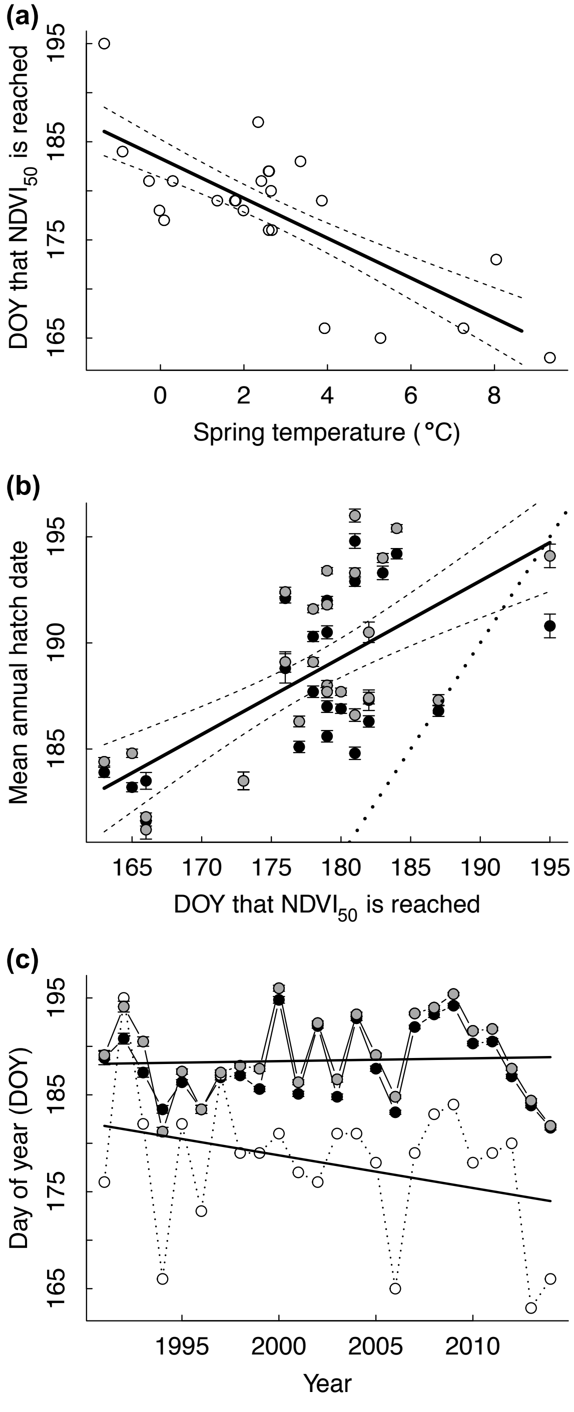

FIGURE 2.4. (a) Relationship between the day of year that $NDVI_{50}$ was reached and mean annual spring temperature, 1992-2014. (b) Relationship between mean annual hatch date and the day of year that peak nitrogen was reached. The dotted line indicates a perfect 1:1 relationship. (c) Annual variation in the day of year that $NDVI_{50}$ was reached (white markers) and the mean annual hatch date (coloured markers). Bars reflect 95% confidence intervals. Raw mean annual values, the model-predicted line (solid; species combined) and 95% confidence intervals (dashed) are shown for Ross's geese (grey) and lesser snow geese (black).

CHAPTER 3. INSIGHTS INTO PRE-FLEDGING SURVIVAL: TESTS OF BREEDING POPULATION DENSITY AND PHENOLOGICAL MISMATCH

3.1 Introduction

Offspring survival is considered a critical vital rate and component of recruitment in avian ecology, but also can be one of the most difficult to study in wild populations (Johnson et al. 1992, Sedinger 1992). Aside from maternal effects, such as body condition or clutch size, extrinsic environmental factors play important roles that account for variability in the survival of young (e.g., Blums et al. 2002). In effect, conditions experienced during early life can influence not only pre- (Williams et al. 1993, Traylor and Alisauskas 2006, Fondell et al. 2008) and post- (Owen and Black 1989, Hill et al. 2003, Aubry et al. 2013) fledging survival, but have lasting effects into adulthood (Drummond and Ancona 2015), including implications for lifetime fitness (Cooch et al. 1989, Sedinger et al. 1995, Reed et al. 2003) and population size (Brook et al. 2015).

Traditionally, survival during the pre-fledging period is estimated by repeatedly observing the number, and in some cases the identity, of offspring associated with individually-marked attendant adults. However, in large predominantly unmarked populations, tracking or recapturing marked individuals can be challenging. At Karrak Lake, Nunavut, a nesting colony of approximately 1.2 million Ross's (*Chen rossii*) and lesser snow geese (*Chen caerulescens caerulescens*, hereafter, snow geese), hundreds of thousands of goslings are hatched annually. Given that less than 1% of the estimated total adult nesting population is captured each August during banding efforts (R. Alisauskas unpublished data), the probability of recapturing previously marked goslings is exceptionally low. Here, I provide annual estimates of gosling (pre-fledging) survival probability for the Karrak Lake colony using an approach that combines information collected annually from 1993 to 2014.

Survival probability in geese has consistently been tied to body size before individuals are capable of flight (Francis et al. 1992, Schmutz 1993, Slattery and Alisauskas 2002, Hill et al. 2003, Richman et al. 2015), wherein larger individuals survive at a higher rate than those that are structurally smaller. In arctic environments where the growing-season is short, time constraints are imposed on young goslings wherein they must attain a size suitable for flight to begin southward migration. To compensate for this, arctic geese apparently have evolved some of the most rapid growth rates among precocial species (Ricklefs 1973, Aubin et al. 1986). However, gosling growth rate is remarkably variable depending on environmental, and foraging conditions in particular, that are beyond an individual's genetic potential (Cooch et al. 1991b, Larsson et al. 1998). Therefore, variation in the quality and availability of forage on brood-rearing areas can be a major contributor towards the growth and subsequent survival of young at both the individual and cohort levels (Sedinger et al. 1998, Sedinger et al. 2001, Slattery and Alisauskas 2002, Brook et al. 2015, Doiron et al. 2015).

Regular intervals of low to moderate levels of grazing can increase both plant productivity and nitrogen availability for herbivores (Hik and Jefferies 1990) and so result in a reliable supply of high quality forage within an area (Cargill and Jefferies 1984, Bazely and Jefferies 1986). However, the per-capita supply of forage may become restricted by competition associated with increases in the density of conspecifics. In 1993, the Karrak Lake colony consisted of about 408,000 nesting geese, but has since grown by 294% in just over 2 decades (Wilson et al. 2016). As a result, there are now unprecedented numbers of goslings and adults using brood-rearing areas north of the colony each year (Slattery and Alisauskas 2007). In situations of high intensity grazing due to large numbers of geese, the productivity of principal forage plants can become depressed (Jefferies 1988, Kerbes et al. 1990), and result in density-dependent effects on growth (Larsson et al. 1998, Slattery 2000), life-history traits (Cooch et al. 1989, Williams et al. 1993, Larsson and Forslund 1994) and ultimately, the population dynamics of the grazers themselves (Fondell et al. 2011).

In addition to the importance of overall quality of plant foods to gosling nutrition, growth, and subsequent survival, is the time at which forage becomes available in relation to the emergence of goslings. Timing of hatch in colonial arctic-nesting geese is generally synchronous (Findlay and Cooke 1982), with the greatest number of goslings hatching at the time when forage is readily available and is of the highest nutritional quality (Sedinger and Raveling 1986). Beyond this seasonal peak, vegetation quality declines and is of reduced value to grazers in supporting tissue production and growth (Lepage et al. 1998, Doiron et al. 2014). Thus, selection should favour early nesting to avoid late hatched goslings and the associated negative consequences for reproductive success. The ability, or perhaps inability, of birds to maintain synchrony between timing of breeding and spring phenology under changing climatic conditions has become a topic of considerable interest in recent years (Crick et al. 1997, Walther et al. 2002, Drever et al. 2012). Phenological mismatch (hereafter, mismatch) refers to a temporal decoupling of resource abundance and resource requirement, and has been studied across a diversity of avian species (Visser et al. 1998, Durant et al. 2007, Liebezeit et al. 2014). Long-term research at Karrak Lake reported an increasing disparity between the timing of gosling hatch and the seasonal peak in vegetation quality on brood-rearing areas due to the advancement of spring forage availability (Chapter 2). Such shifts in timing of food availability and quality relative to breeding phenology of adults within a season may restrict access to essential nutrients required by offspring (Doiron et al. 2014, 2015).

My objective was to assess the relative roles of the density and mismatch hypotheses on gosling survival of Ross's geese and snow geese nesting at Karrak Lake. Studies of marked populations of sub-arctic nesting species have found lower first-year survival rates with reductions to either forage quality and quantity, or the relative timing of its availability (Aubry et al. 2013, Brook et al. 2015). Therefore, I predicted that high goose density and greater annual mismatch at Karrak Lake would reduce survival during the pre-fledging period for Ross's goose and snow goose goslings. More specifically, under both hypotheses I expected that changes in survival would be an artifact of a reduction to foraging conditions on brood-rearing areas. The period for skeletal growth is finite (Cooch et al. 1991a,b) and is likely a more important investment than is body mass, because size may continue to influence a gosling's fitness into adult life (Ankney and MacInnes 1978, Alisauskas and Ankney 1990, Sedinger et al. 1995). However, gut morphology is flexible in waterfowl (Kehoe et al. 1988) and when either forage quantity or quality is sufficiently low, young may divert energy away from growth and towards gastrointestinal development in order to maximize nutrient intake and assist in counteracting low digestive efficiency (Lesage et al. 1988, Sedinger 1992, 1997, Gurney et al. 2012). Consequently, if goslings were in fact nutritionally stressed in years when mortality was high, I predicted that they would be structurally smaller, as a result of reduced assimilation of nutrients into skeletal growth.

3.2 Methods

3.2.1 Study area

The Karrak Lake nesting colony (67° 14' N, 100° 15' W) is located within the Queen Maud Gulf (QMG) Migratory Bird Sanctuary, NU, Canada. The colony covers approximately 182.8 km^2 (terrestrial area in 2014) and its growth, monitored since the early 1990s, has paralleled that of the continental population of lesser snow and Ross's geese (Kerbes et al. 2014). Following hatch, successful breeders lead their offspring north of the nesting grounds towards the coast (Slattery and Alisauskas 2007), where primary brood-rearing habitat is characterized by sedge meadows, freshwater ponds, and rock outcrops, (Ryder 1972). Goslings sampled north of Karrak Lake for this study most likely originated from Karrak Lake (Slattery and Alisauskas 2007), as the nearest colony of similar size is located >100 km to the east, near McNaughton Lake (Kerbes et al. 2014). Vegetative communities within the colony have been altered by cumulative years of foraging, nest building and trampling, with expanses of exposed peat and substrate being increasingly widespread (Alisauskas et al. 2006). Furthermore, a biodeterioration zone, within which aboveground biomass of graminoid plants is greater with increasing distance from the nesting grounds, has developed in brood-rearing habitat immediately surrounding the colony from cumulative years of use by geese (Slattery 2000, Conkin and Alisauskas 2016). Mammalian herbivores present in this region include caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*), brown (*Lemmus trimucronatus*) and collared lemmings (*Dicrostonyx groenlandicus*), ground squirrels (*Spermophilus parryii*) and red-backed voles (*Myodes rutilus*).

3.2.2 Field methods

Nesting ecology of Ross's and snow geese has been studied at Karrak Lake since 1991. Nest searching was conducted within 30 metre radius circular plots located at the intersections and midpoints of a 1-km by 1-km Universal Transverse Mercator (UTM) grid system mapped across the colony (Alisauskas et al. 2012, Wilson et al. 2016). At each plot, eggs found in nest bowls were uniquely marked and clutch sizes were recorded. A discriminant function using egg lengths and widths (± 0.1 mm) was used to assign nests to species (Alisauskas et al. 1998). A subsample of nest plots was repeatedly revisited during incubation to monitor egg loss. Incubation state was estimated by candling (Weller 1956). Nest fate was evaluated for all nests following the hatching period, where successful nests were those that produced at least one gosling, determined by the presence of egg caps or membranes (Klett et al. 1988).

Age ratios (goslings:adults) were obtained from annual mass capture and banding efforts near fledging at the end of breeding seasons. In early to mid-August when adults were flightless from remigial moult and goslings had not yet grown flight feathers, geese were herded into portable corral traps using a helicopter (Timm and Bromley 1976). Age (adult or immature) was determined by plumage characteristics and sex was verified by cloacal eversion. Annual ratios were calculated by summing the number of geese in each of the adult and immature age classes across all banding efforts within a year. Adults captured within banding efforts were assumed to have made a breeding attempt, with failed nesters and pairs subject to total brood loss being equally susceptible to capture. This is a reasonable assumption given that the percentage of adult females with brood patches for flocks tending no goslings (n = 26 flocks) was similar to flocks captured with goslings (n = 290; $\bar{x}$ = 75% and 87%, respectively). Additionally, snow and Ross's geese that do not attempt to nest (i.e., non-breeders) are flightless in early July at Karrak Lake, and most or all have regained flight by August (Jónsson et al. 2013), when we captured geese. A random sample of goslings each year was also weighed (± 5 g), and their midwing, tarsus and head length (± 0.1 mm) measured (following Dzubin and Cooch 1992).

3.2.3 Colony gosling production and survival

The annual number of goslings hatched within the study area from 1995-2014 was estimated using: {no. of goslings = [no. of nests] × [mean (apparent) nest success] × [mean clutch size] × [mean egg survival] × [hatching success]} for each species separately. Egg survival was considered as the probability that an egg within a clutch survived the incubation period, given that the nest was successful This was calculated for each species by dividing the number of eggs found in the nest on the visit before hatch by the maximum number of eggs found in the nest. Nests with eggs damaged by investigator handling procedures were excluded (n = 6). The estimate of overall mean egg survival across all years was used in place of missing values for 1993 and 1994. Hatching success was not estimable from observed nests because nests often were not visited for a number of days following the hatching period to reduce observer travel through the nesting colony and so to reduce disturbance to geese as they began to make their way towards brood-rearing areas. Consequently, unsuccessful eggs may have been eaten or cached by foxes in the interim. Thus, I used estimates of hatching success from a long-term study of lesser snow geese at La Pérouse Bay, Manitoba, Canada (Rockwell et al. 1997).

An index of gosling survival was calculated for each year as the ratio between the number of goslings per adult captured during banding in mid-August and the number of goslings per adult at hatch, calculated above.

3.2.3.1 Assumptions of survival index

a) *Closure of adult population (i.e., absence of emigration and death) between hatch and banding efforts.* Failure to meet this assumption may impose a bias if, for example, pairs that experience total nest failure depart the study area to moult elsewhere, as has been observed in greater snow geese nesting on Bylot Island, NU (Reed et al. 2003). No similar study has been conducted at Karrak Lake. However, evidence of brood patches in adult-only flocks captured on the brood-rearing area indicate that failed-breeders do remain in the area, although it cannot be inferred with certainty at which stage of reproduction they may have failed, but only that they attempted to nest. Adult survival probability during the breeding season can reasonably be assumed to be very nearly 1.0 given that predation by arctic foxes is very low (Samelius and Alisauskas 2000). Survival from spring to summertime in greater snow geese is 0.989 (Gauthier et al. 2001). Hunter harvest does not occur during the breeding period, and there are no records of severe mass mortality events due to disease as has been the case with other colonial arctic nesting species (e.g., common eiders (*Somateria mollissima)*; Descamps et al. 2012).

b) *Unbiased sampling effort during August banding efforts*. Ratios calculated from August banding efforts must be representative of the true ratio of young to adults. Thus, sampling effort, or selection of flocks of flightless geese, should be independent of the annual variation in gosling production. Decisions of which flocks to select and band on brood-rearing areas mostly depend on the terrain they occupy (preferably dry, flat and consisting of graminoid vegetation) and total group size. Additionally, the number of banding efforts made in a season was unrelated to the number of goslings available to be captured, meaning that there were not fewer banding efforts in years when there were fewer goslings.

c) *No change in the methodology/protocols for nest surveys and banding efforts.* Despite more plots having been added to the sampling grid as the Karrak Lake colony has expanded in terrestrial area, the nest searching protocol and methodology used to extrapolate nesting densities across the colony have remained unchanged. Likewise, capture during banding operations have been unaffected by a substantial increase in the number of geese banded annually.

3.2.4 Explanatory variables

Quasi-observational weather conditions were retrieved from the North American Regional Reanalysis (NARR) obtained through the National Oceanic and Atmospheric Administration National Operational Model Archive and Distribution System (NOMADS, http://nomads.ncdc.noaa.gov/). [See Chapter 2 for the reliability of NARR data in comparison with conditions measured by the automated weather station at the Karrak Lake research station]. Adverse weather conditions after hatch have frequently been tied to high mortality of precocial young [e.g., ducks (Mendenhall and Milne 1985), geese (Flint et al. 1995), grouse (Gilbert et al. 2010]. I expected that goslings would experience reduced survival during cool and wet conditions due to an inability to thermoregulate properly (MacInnes et al. 1974, Sedinger 1992, Fondell et al. 2008). Principal component analysis (PCA) was used to derive an index of local weather up to three weeks after mean hatch using air temperature at 2 meters, relative humidity at 2 meters and total precipitation. Loadings for the first principal component axis were [-0.629, 0.661, 0.410] for each weather measurement respectively, explaining 68% of the total variation. To include a more regional measure of climate, I obtained daily Arctic Oscillation (AO) index values from the Climate Prediction Centre of the National Weather Service (http://www.cpc.ncep.noaa.gov); these values have been standardized by the standard deviation of the monthly index. I defined a summer period (July 1 – August 10), when goslings would have hatched and begun foraging, for which I calculated an annual average AO index value.

Annual breeding population estimates derived from colony nest plot surveys were used as an index of goose density on brood-rearing areas. I estimated the timing of peak nitrogen availability, indicative of the highest quality forage, using the median date of NDVI_{50} – the date at which 50% of the annual maximum Normalized Difference Vegetation Index (NDVI) was attained (Doiron et al. 2013) on the brood-rearing area (~5 x 10^6 km^2) north of Karrak Lake (Slattery and Alisauskas 2007, Wilson et al. 2016). The difference between the mean annual hatch date and NDVI_{50} (i.e., hatch date – date of NDVI_{50}) was used to quantify phenological mismatch. NDVI data were obtained from 2 sources: the Long Term Data Record Version 3 collected by the Advanced Very High Resolution Radiometer (AVHRR) for 1982-1999 (http://ltdr. nascom.nasa.gov) and from the Earth Science Data Record of preprocessed NDVI collected by the Moderate Resolution Imaging Spectroradiometer (MODIS) for 2000-2010 (http://vip. arizona.edu) [see Chapter 2 for details].

I also explored the role of pre-breeding female body condition on annual gosling survival. The interplay between local snow conditions and stored lipid reserves largely determine the timing of nest initiation (Ankney and MacInnes 1978). I previously showed that earlier nesting positively influenced annual breeding productivity measured just before fledging (Chapter 2). Consequently, I predicted that gosling survival would also be positively influenced by fat reserve mass. Nutrition data were obtained from annual collections and dissections of geese arriving to Karrak Lake. Geese identified as subadult (Alisauskas 2002), were excluded. Each female's abdominal fat mass was used to index body fat, following Gauthier and Bédard (1985) and was standardized for variation in structural size, apparent clutch size, investment of somatic tissue towards its clutch at the point of collection and breeding phenology across years [methods described in Chapter 2]. Thus, remaining variation in female condition was due to annual differences in environmental conditions.

3.2.5 Statistical analyses

Annual gosling survival was considered normally distributed and was analyzed using general linear modeling. First, I constructed an a priori set of candidate models to explain survival as a function of the density and mismatch hypotheses. Banding dates can be constrained by helicopter availability and considerable annual variation exists around the timing of hatch relative to banding efforts. Thus, I controlled for annual differences in the mean age of goslings at banding by including the number of days between peak hatch for each species and the mean banding effort date into a biological null model. This model also included a species term and the intercept. Models with hypothesized effects were built on top of the biological null except in cases of collinearity between explanatory variables. Correlated variables were not considered in the same model (gosling age/fat, and gosling age/summer AO; r's $\geq |0.51|$). Finally, species-specific responses in gosling survival to goose density and mismatch were considered.

I used general linear mixed effects models to test whether goslings were structurally smaller in years with high goose density and during greater mismatch between hatch and forage availability. A random effect of banding effort was included in each model to account for dependences among related goslings and among flocks utilizing similar habitats or experiencing similar foraging conditions. I used PCA to obtain an integrated, univariate measure of gosling size using midwing, tarsus and head length measurements. This was done separately for each sex to remove variation in structural size owing to sexual differences in growth rates. Following methods by Hill et al. (2003), I estimated gosling age for each individual by subtracting the mean annual hatch date from its date of capture. A similarly-structured biological null model as was used for gosling survival (intercept, gosling age and species) was included in the candidate set. A density × mismatch interaction and species-specific responses to these two hypotheses were considered. Absolute values of correlations between explanatory variables did not exceed 0.12.

I assessed the relative support of models using an information-theoretic approach (Burnham & Anderson 2002) based on Akaike's Information Criterion corrected for small sample size (AIC_c). Progressively less complex models refined for hypothesis testing were derived from global models that included all possible effects and interactions. Models with ≤ 2 ΔAIC_c units were judged to have substantial support and be highly competitive. I used Akaike weights (w_i) to assess the likelihood of each model relative to others in the candidate set. I present parameter estimates from the best performing model rather than model-averaged coefficients in cases of model uncertainty because of collinearity among explanatory variables in the candidate set (Cade 2015). All analyses were done with Program R (Version 3.2.1, R Core Team 2015).

3.3 Results

3.3.1 Gosling survival

The index for gosling survival probability displayed considerable variability among years (from 0.24 to 0.93 for Ross's geese and from 0.09 to 0.80 for snow geese). Ross's goose goslings had a higher annual survival probability ($\beta_{spp(Ross's)} = 0.139$, 95% CI: 0.059, 0.219) than did snow geese (intercept; $\beta_{Snow} = 0.324$, 95% CI: -0.018, 0.666). The best-supported model accounted for 58% of the variation in gosling survival probability, although three similar models offered an equivalent fit to the data ($\Delta AIC_c < 2$). The top ranked model included the effects of goose density, phenological mismatch and local weather conditions, together with the biological null (Table 1). There was a positive effect of mean gosling age on survival probability ($\beta = 0.013$, 95% CI: 0.005, 0.022). I had expected the opposite result, given that fewer days between hatch and banding should leave a greater number of younger goslings available for capture. However, this finding was likely confounded by positive effects of earlier hatch date on survival in years when goslings were older during banding. Gosling survival was reduced in years when $NDVI_{50}$ was reached well before the mean annual hatch date for the colony ($\beta = -0.016$, 95% CI: -0.025, -

0.007; Fig. 3.1a). The survival of goslings was also negatively related to the annual index of goose density on brood-rearing areas (β = -0.020, 95% CI: -0.036, -0.004; Fig. 3.1b). The effect of local weather was weak, as indicated by its absence from the second-ranked model (ΔAIC_c = 0.04) but cool, damp and rainy conditions appeared to result in lower survival probability (β = -0.022, 95% CI: -0.050, 0.005). A model where gosling age was replaced by the pre-breeding fat mass of females was well supported (ΔAIC_c = 1.49) and indicated that larger reserves of prospective breeding females subsequently increased gosling survival in the same year (β = 0.004, 95% CI: -0.001, 0.008). Although the addition of a species-by-density interaction was competitive (ΔAIC_c = 1.73), it was not very well estimated ($\beta_{Ross's}$ = 0.015, 95% CI: -0.013, 0.044). Moreover, the summer AO variable was not retained among the top models ($\Delta AIC_c \geq$ 2.09).

3.3.2 Gosling size

Each year from 1999-2014, between 151 and 555 goslings were successfully captured and measured. The first principal component axis for gosling size accounted for 83% of the total variation in morphometric measurements made on male and female goslings. Loadings of midwing, tarsus and head length were [0.533, 0.603, 0.593] and [0.530, 0.602, 0.597] for males and females, respectively. After adjusting for the effects of sex and the random effect of banding effort, the preferred model for predicting gosling structural size included both goose density and phenological mismatch. Differences in structural size were discernable between species ($\beta_{spp(Snow)}$ = 2.331, 95% CI: 1.956, 2.702) with Ross's geese being smaller overall (intercept; $\beta_{Ross's}$ = -4.544, 95% CI: -5.163, -3.925). As expected, older goslings were larger than younger goslings (β = 0.159, 95% CI: 0.144, 0.174). Gosling size for both species was negatively affected by phenological mismatch (β = -0.068, 95% CI: -0.082, -0.054; Fig. 3.2a). However, the effect of density was only important (ΔAIC_c of second ranked model = 0.32) when including a species-by-density interaction. The structural size of snow goose goslings appeared to be reduced in years with high goose density ($\beta_{spp*density(Snow)} = \beta$ = -0.072, 95% CI: -0.108, -0.035; Fig. 3.2b) while Ross's goose goslings were insensitive to such differences in breeding population size ($\beta_{Ross's}$ = 0.001, 95% CI: -0.044, 0.046; Fig. 3.2b).

3.4 Discussion

As predicted, my results demonstrated that survival of Ross's and snow goose goslings on brood-rearing areas north of Karrak Lake depended on conditions relating to both the quality and availability of food plants. Foraging by dense aggregations of herbivores beyond some defined carrying-capacity can become detrimental, as plant biomass is reduced and this can result in habitat degradation from the perspective of food availability (Jefferies 1988, Kerbes et al. 1990). Furthermore, larger colonies generally reduce local resource productivity to a greater extent than colonies consisting of fewer individuals (Hamilton and Watt 1970). Since the biodeterioration zone surrounding the colony was described by Slattery (2000), the nesting population has continued to grow (Wilson et al. 2016), which has likely increased grazing intensity and further reduced the quality of locally-available forage. Under such conditions, I might have expected some species-specific differences in gosling performance. Ross's geese have a smaller body size (MacInnes et al. 1989) and, thus, smaller gastrointestinal organs (i.e., a shorter retention time in the gut; Sibley 1981) and a higher mass-specific metabolic rate. Consequently, this species should fare poorly on a low-quality diet and instead, require higher-quality forage to offset these limitations and assimilate nutrients at a rate comparable to snow geese (Demment and van Soest 1985, Richman et al. 2015). However, I found that Ross's goose goslings had a higher survival probability with increasing goose density compared to the larger-bodied snow geese. Interestingly, while the structural size of snow goose goslings appeared to be slightly reduced in years of high goose density, that of Ross's goose goslings was not. Likely, this was related to interspecific differences in the time required for growth (longer for larger species – snow geese; MacInnes et al. 1989) in addition to selective advantages of morphological features and strategies for dispersal from the nesting colony.

Among the traits that distinguish Ross's geese from closely-related snow geese is the size and shape of the bill (Jónsson et al. 2013). While the longer bill of snow geese has adapted for grubbing roots and tubers, the shorter bill of the Ross's goose is better able to graze short swards of vegetation (Johnson and Raveling 1988, Jónsson et al. 2013). This ability to crop vegetation very close to the ground may enable them to exploit habitats that are depleted for meeting snow goose requirements, and where snow geese have since been excluded.

Slattery (1994) found that Ross's and snow geese differed in their dispersal patterns from the colony. Ross's goose broods dispersed a mean distance of 42.1 km from the colony towards the coast while snow goose broods dispersed only 16.1 km on average (*n* = 11 and 5, respectively). Goslings reared at a greater distance were structurally larger and in better condition (i.e., larger mass corrected for body size) than those reared nearer the colony (Slattery 1994, Aubry et al. 2013). Historically, it seems that Ross's geese have occupied more coastal regions in the QMG (Gavin 1947, Hanson et al. 1956). Natal philopatry refers to the tendency for young to return as adults to the brood-rearing habitat they were led to by their parents (Cooke and Abraham 1980, Larsson and Forslund 1992). Fidelity to foraging sites visited in previous years can be profitable because it reduces costs associated with dispersing to forage in an unfamiliar area (e.g., predation risk; Greenwood et al. 1980). However, once the resource quality of a site becomes degraded, returning to the area can be nutritionally disadvantageous or 'maladaptive' (Cooch et al. 1993, Aubry et al. 2013).

While a more recent assessment of species-specific dispersal distances from radio telemetry data is not available, observations made during banding in mid-August continue to indicate that Ross's goose broods are detected closer to the coast than are snow goose broods (K. Drake personal communication). Thus, either an innately shorter dispersal distance, philopatric behavior that constrains snow geese to be close to or within the biodeterioration zone (see also Conkin and Alisauskas 2016), or avoidance of areas with high densities of Ross's geese may have contributed towards diminished offspring growth and survival. In contrast, the long distances travelled by Ross's geese may have enabled broods to bypass the most heavily degraded areas and avoid density-dependent effects of resource limitation.

Consequently, reduced survival of Ross's goose goslings stemming from colony population size must, rather, be the result of other mechanisms associated with a greater density of conspecifics within an area. For example, it is generally accepted that parasite transmission rates and abundances are positively related to host density, as each individual parasite has an increased chance of coming into contact with a suitable host (Anderson and May 1978, Arneberg et al. 1998). In effect, Slattery (2000) found that while the structural size of Ross's goose goslings on Karrak Lake brood-rearing areas was unaffected by parasite load, first-year survival was reduced, and reasoned this was likely due to an inability to accumulate the nutrient reserves necessary for migration. Moreover, large colonies of geese are attractive to predators such as arctic foxes (*Vulpes lagopus*); foxes were found to be more abundant within the boundary of the Karrak Lake colony and to occur in higher breeding densities than in areas outside of the colony

(Samelius et al. 2011). Following the hatching period, foxes breeding at Karrak Lake forage on newly-hatched geese, having been observed returning to den sites with goslings (É. Bouchard personal communication).

Despite snow goose goslings being seemingly more sensitive to increases in the breeding population size at Karrak Lake, a temporal lack of available high quality forage due to phenological mismatch affected the survival probabilities of both species in a similar manner. My results indicated that a greater mismatch between peak forage quality and the hatching period negatively affected gosling growth (a sign of nutritional stress) and that this likely had subsequent implications for survival during the pre-fledging period. Selective foraging by adults and goslings on plants with high protein content (i.e., those rich in nitrogen) during brood-rearing is essential for gosling development (Sedinger 1992, 1997), and also the rebuilding of adult flight muscles for the fall migration. Using dates of $NDVI_{50}$, plant nitrogen availability at Karrak Lake peaked annually around mid-June to early July. Following the peak in forage quality, plant nitrogen content declines steadily throughout the rest of the period that geese spend in this ecosystem before fall departure (Sedinger and Raveling 1986, Manseau and Gauthier 1993). Consequently, in years when mean hatch date was late relative to the peak in forage quality, goslings would have had access to vegetation that was nutritionally inferior to the younger and more digestible plants available earlier. Brook et al. (2015) and Doiron et al. (2015) similarly found a reduction in gosling growth stemming from phenological mismatch in sub-arctic nesting Canada geese (*Branta canadensis*) and arctic-nesting greater snow geese (*Chen caerulescens atlantica*), respectively, and were able to relate smaller structural size to decreases in survival later in the first year of life. However, in this study, mismatch was found to affect survival prior to departure from the brood-rearing grounds. Mortality during the pre-fledging period has been attributed to gosling malnutrition in other species of geese (e.g., Hill et al. 2003). Smaller and nutritionally stressed offspring have lower feeding efficiency and increased difficulty with motor skills (e.g., sprinting or endurance) which can affect their ability to evade predators (Swennen 1989, Anderson and Alisauskas 2001). I suspect that the energy expenditure required to keep pace with parents during dispersal from the nesting grounds may impose additional nutritional stress on goslings, rendering them more susceptible to exhaustion and eventual mortality before fall migration due to starvation or predation.

The degree of mismatch incurred by geese nesting at Karrak Lake has increased throughout this study as warmer spring air temperatures have led to earlier dates of peak nitrogen availability in forage plants (Chapter 2). Furthermore, recent evidence suggests that declines in plant nitrogen following the seasonal peak can become accelerated under warmer than average conditions (Doiron et al. 2014). As alluded to by Dickey et al. (2008) and Brook et al. (2015), warm and early springs also favour increased breeding propensity and improved nesting success in geese (Reed et al. 2004, van Oudenhove et al. 2014). Consequently, in such years, the number of goslings leaving nests should be greater, strengthening density-dependence during the brood-rearing period. Thus, advances in spring phenology at the nesting grounds due to changes in climate may impose restrictions on gosling growth and survival via the combined effects of both mismatch and density-dependence.

Later in summer, cool and wet weather conditions can negatively affect survival due to greater thermoregulatory costs imposed on down-covered young (Sedinger 1992, Schmutz et al. 2001). Indeed, I found that goslings survived at a higher rate when conditions were warmer and drier, as have others (Doiron et al. 2015). However, the strength of this effect may not have been as great as initially expected because rainfall during the brood-rearing period can improve foraging conditions, leading to increased growth rates and a higher first-year survival probability (Brook et al. 2015).

3.4.1 Conclusions

This study has provided some of the most in-depth information to date on gosling survival probabilities at the Karrak Lake colony. During the brood-rearing period, lesser snow and Ross's goose goslings appear to be impacted by the combined effects of population density and phenological mismatch. The survival of young in early life is typically the first vital rate to be affected by nutritional stress (Eberhardt 2002). In fact, increased competition for forage among geese during brood-rearing has been tied to long term declines in gosling survival for snow geese (Williams et al. 1993) and in population size of Canada geese (Brook et al. 2015) at sub-arctic nesting areas. The results presented here clearly demonstrate that advanced forage availability relative to goose breeding phenology can strongly negatively influence both growth and survival of goslings. Moreover, gosling size is correlated with their final size as adults (Cooch et al. 1991a, Larsson and Forslund 1991), leading to lagged density dependent effects on adults which include reduced breeding propensity or fecundity for small geese (Sedinger et al. 1995) and further population level implications.

Ross's goose goslings appear to have higher survival probability than snow geese at Karrak Lake as a result of a combination of behavioural strategies and physical characteristics. These results align with previous work that reported Ross's geese to have higher overall breeding productivity (measured when goslings are approximately four weeks of age; Chapter 2). Effectively, these findings mirror what has been observed at the continental population level. Given that the number of breeding geese in the Canadian central arctic represents approximately 45% of known breeding midcontinent snow geese and most continental Ross's geese (Kerbes et al. 2014), these findings may have broader, large-scale relevance to population-level dynamics for these two species. Lincoln estimates of midcontinent snow geese appear to have attenuated in recent years while estimates for Ross's geese have continued to increase at a rapid rate (Alisauskas et al. 2011, Alisauskas et al. 2012). This may relate in part to an eastward range expansion by Ross's geese (Kerbes et al. 2006) and population growth in those colonies formerly occupied solely by snow geese. Over the same time period, adult survival of snow geese has not declined (Alisauskas et al. 2011, Wilson et al. 2016), and so this recent change in trajectory must relate to conditions at the breeding grounds that have resulted in reduced recruitment into the breeding cohort, possibly stemming in part from changes in gosling survival.

TABLE 3.1. Model selection for annual Ross's and lesser snow goose gosling survival probability at Karrak Lake, NU 1993-2014 (*n* = 44). Shown are the number of estimable parameters (k), the log-likelihood (logLik), the Akaike Information Criterion difference with correction for small sample size (Δ AIC$_c$), the model weights (ω_i) and the proportion of variance explained (R^2).

Model	k	logLik	Δ AIC$_c$	ω_i	R^2
Spp + Age + Mismatch + Pop + Weather	7	29.302	0.00	0.255	0.58
Spp + Age + Mismatch + Pop	6	27.863	0.04	0.250	0.56
Spp + Fat + Mismatch + Pop	6	27.137	1.49	0.121	0.55
Spp + Age + Mismatch + Spp*Pop + Weather	8	29.938	1.73	0.107	0.58
Spp + Age + Spp*Mismatch + Pop + Weather	8	29.769	2.07	0.091	0.58
Spp + Summer.AO + Mismatch + Pop	6	26.836	2.09	0.090	0.54
Spp + Age + Mismatch + Weather	6	25.948	3.87	0.037	0.52
Spp + Summer.AO + Mismatch + Pop + Weather	7	27.093	4.42	0.028	0.53
Spp + Age + Mismatch	5	23.880	5.31	0.018	0.49
Spp + Age + Pop + Weather	6	22.854	10.06	0.002	0.45
Spp + Age + Pop	5	21.250	10.57	0.001	0.42
Spp + Age + Weather	5	17.953	17.17	0.000	0.33
Spp + Age	4	15.412	19.70	0.000	0.27
Spp	3	9.350	29.39	0.000	0.07
Intercept	2	7.577	30.63	0.000	0.00

Notes: Spp = Species, Age = number of days between peak hatch and banding, Mismatch = the difference between the mean annual hatch date and the day of year peak nitrogen is reached, Pop = nesting population size, Fat = annual index of body fat, Weather = PC1 of temperature, precipitation and relative humidity for three weeks following peak hatch, Summer.AO = Mean annual AO value from July 1 to August 10.

TABLE 3.2. Model selection for Ross's and lesser snow goose gosling structural size (*n* = 5,325) corrected for sex differences in growth rate from 1999-2014. Each model includes a random effect of banding effort. Shown are the number of estimable parameters (k), the log-likelihood (logLik), the Akaike Information Criterion difference with correction for small sample size (Δ AIC_c) and the model weights (ω_i).

Model	k	logLik	ΔAICc	ω_i
Spp + Age + Mismatch + Spp*Pop	8	-7085.533	0.00	0.526
Spp + Age + Mismatch	6	-7087.696	0.32	0.450
Spp + Age + Mismatch + Pop	7	-7090.023	6.97	0.016
Spp + Age + Spp*Mismatch + Spp*Pop	9	-7089.436	9.81	0.004
Spp + Age + Spp*Mismatch	7	-7091.729	10.39	0.003
Spp + Age + Mismatch*Pop	8	-7091.694	12.32	0.001
Spp + Age + Spp*Mismatch + Pop	8	-7094.062	17.06	0.000
Spp + Age + Spp*Mismatch + Spp*Pop + Mismatch*Pop	10	-7093.288	19.52	0.000
Spp + Age + Spp*Pop	7	-7122.373	71.67	0.000
Spp + Age	5	-7124.681	72.28	0.000
Spp + Age + Pop	6	-7127.361	79.64	0.000
Intercept	3	-8684.183	3187.28	0.000

Notes: Spp = Species, Age = number of days between peak hatch and capture date, Mismatch = the difference between the mean annual hatch date and the day of year peak nitrogen is reached, Pop = nesting population size.

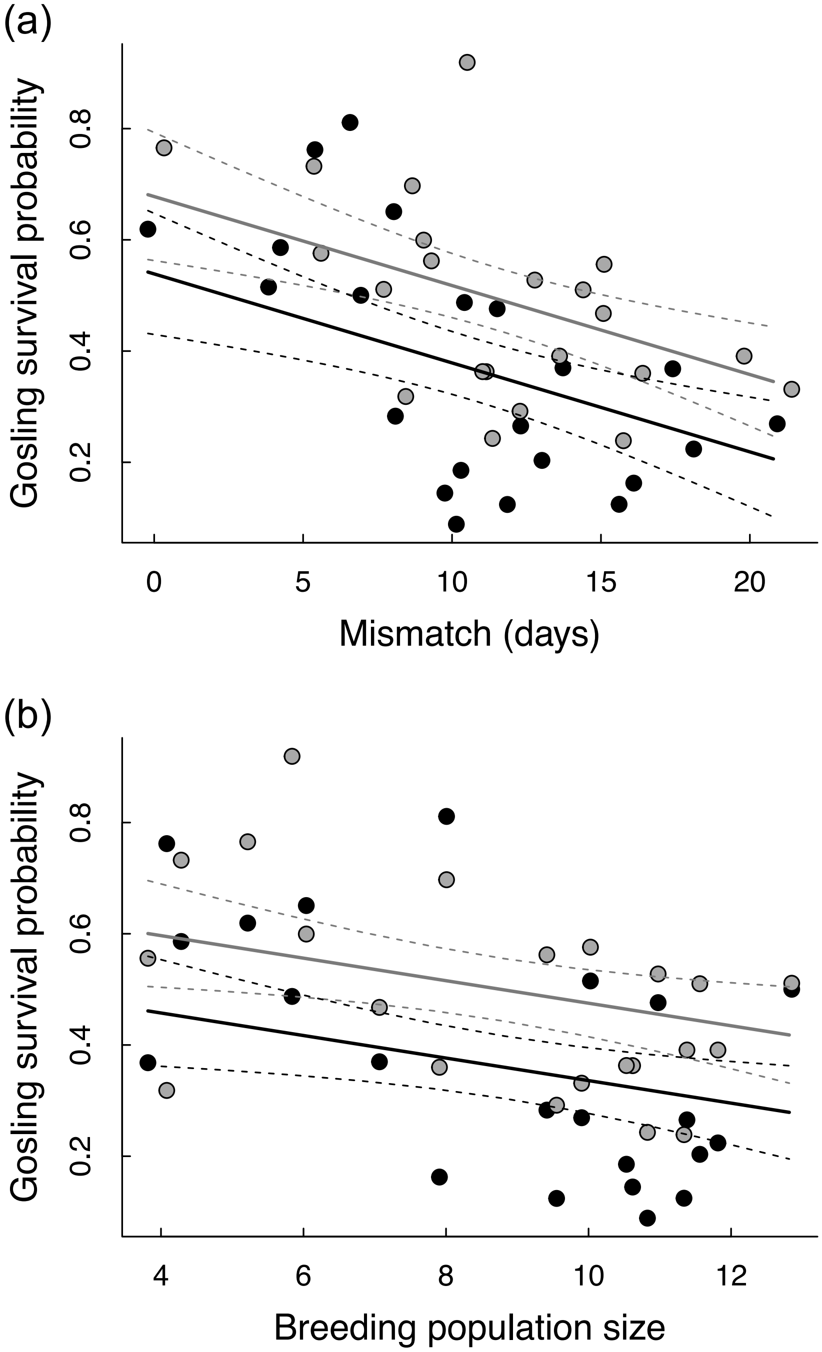

FIGURE 3.1. Relationships between annual gosling survival probability and (a) mismatch between peak hatch and $NDVI_{50}$ and (b) breeding population size at the Karrak Lake nesting colony from 1993-2014. Population size is indicated in the 100,000s. Raw annual values, the model-predicted line (solid) and 95% confidence intervals (dashed) are shown for Ross's geese (grey) and lesser snow geese (black).

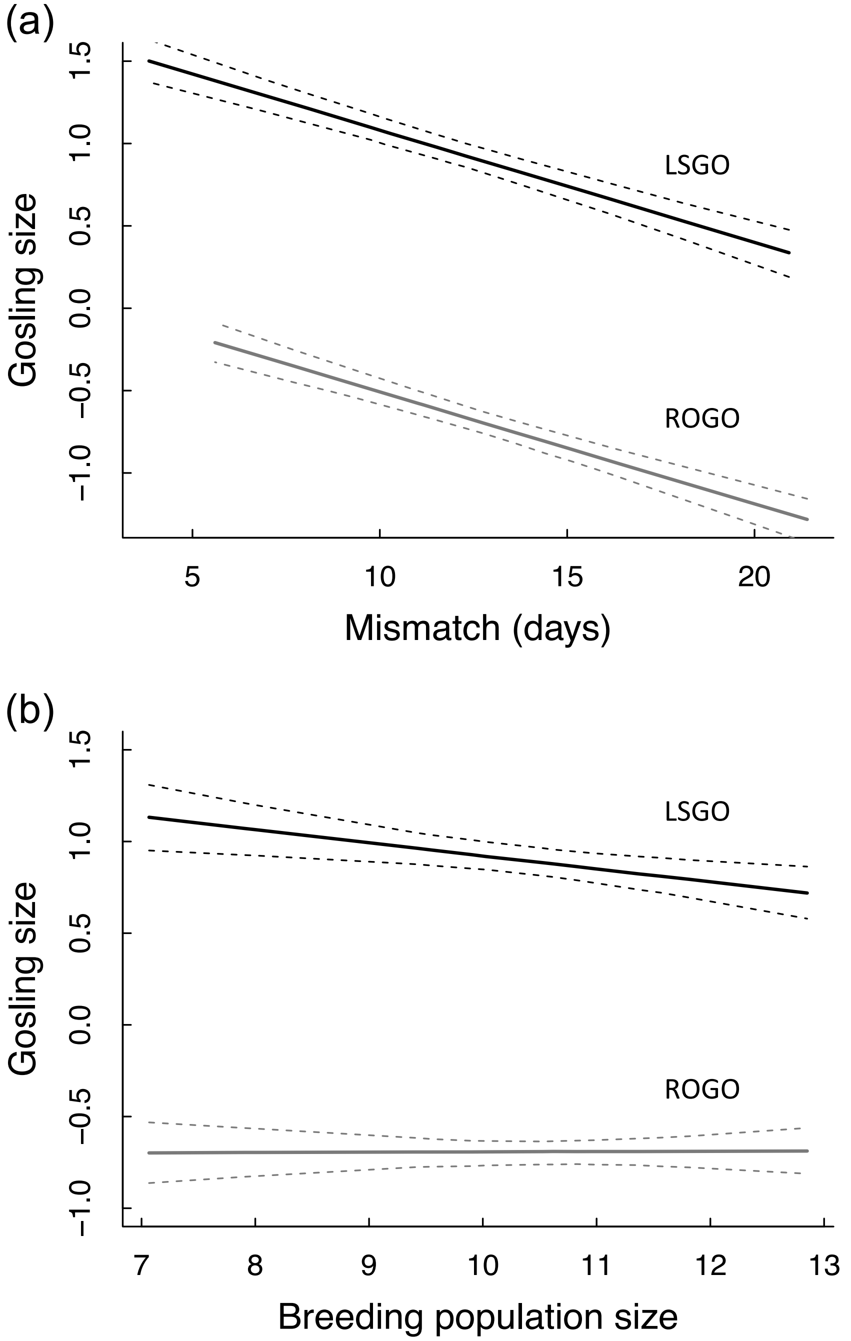

FIGURE 3.2. Relationship between gosling size (n = 5,325) and (a) mismatch and (b) breeding population size for goslings raised in brood-rearing areas north of Karrak Lake, NU, from 1999-2014. The model-predicted line (solid) and marginal 95% confidence intervals (dashed) are shown.

CHAPTER 4. SYNTHESIS

Ecological factors, originating from local variability or global change, can influence breeding productivity from year to year. Using a long-term dataset from one of the largest nesting colonies in the Queen Maud Gulf Migratory Bird Sanctuary, I addressed a declining trend in gosling production for Ross's geese and lesser snow geese (hereafter, snow geese). I considered three non-mutually exclusive hypotheses: 1) density, 2) pre-breeding nutrition, and 3) phenological mismatch. Although the focus of this research was to understand key factors that could have directly influenced end of season gosling production, I also analyzed three separate components of recruitment (clutch size, apparent nest success and pre-fledging survival) to better understand the mechanisms behind my hypotheses in relation to variation in gosling production. Below, I outline the primary findings of each, and provide direction for future research.

Annual variation in productivity is of particular interest in species where adult survival is both high and stable (Sæther and Bakke 2000, Stahl and Oli 2006), because retrospectively, it has a greater contribution towards population dynamics (Cooch et al. 2001). In chapter 2, I evaluated three hypotheses that related to variation in gosling production at the Karrak Lake colony by examining an index of breeding productivity measured near the end of the pre-fledging period, in addition to clutch size and apparent nest success. I considered nesting population size because of possible density-dependent effects (Cooch et al. 1989, Williams et al. 1993), pre-breeding female nutrition because of the importance of fat and protein reserves to reproduction (egg production and incubation; Ankney and MacInnes 1978), and phenological mismatch due to changes in global climate (IPCC 2013) and recent findings for other arctic-breeding geese (e.g. Doiron et al. 2015). Ross's geese demonstrated greater annual productivity, overall. I found that gosling production was reduced in both species in years of increased phenological mismatch. This tended to be when spring vegetation phenology was unusually early, which was positively correlated with warmer spring air temperatures. At the annual level, geese appeared to at least partially track spring conditions, having earlier hatch dates in years when vegetation phenology was advanced. However, across the 23-year study period, the degree of mismatch has increased: green-up has become progressively earlier while hatching dates have not shown a similar advancing trend, suggesting that geese have not been fully able to adjust their breeding phenology to match that of their environment. Compared to nest initiation dates, Ross's and snow geese are relatively constrained by low variation in incubation duration of 21.8 ± 0.90 (SD) days (Ryder 1972). Thus, little can be done to adjust nesting phenology after egg-laying should spring conditions ameliorate (Dickey et al. 2008).

An untested hypothesis with additional effects that may have contributed to increased mismatch more recently relates to cumulative decadal effects of grazing by the growing numbers of geese themselves. Possibly, continued grazing in the same brood-rearing area over the course of this study induced a shift in plant communities from those with later, to those with earlier, emergence phenologies. If so, then part of the increase in mismatch may have been the result of a dependence on goose density leading to changes in plant community composition, in addition to demonstrated advances in spring warming.

Gosling production was directly and positively related to the mass of protein stores carried by pre-breeding females arriving to nest at the colony and negatively related to delays in nest initiation. Mean fat mass of arriving females was highly correlated with the relative timing of nest initiation. Local conditions at breeding grounds, such as deep snow and slow rate of melt, delay nest initiation by reducing access to nesting habitat (Choinière and Gauthier 1995, Madsen et al. 2007) while diverting stored reserves from reproduction (i.e., clutch formation and incubation) towards satisfying basic metabolic needs. These effects were perceived as being intermediary and, thus, warranted investigation as prospective mechanisms. Both species experienced reductions to clutch size in years when the mean date of nest initiation was delayed, but also in years when it was particularly early. Snow geese had significantly larger mean annual clutch sizes compared to Ross's geese. Greater mean annual protein reserves resulted in larger clutches for both species, but this effect was more pronounced for Ross's geese than for snow geese. Traylor (2010) found a similar result, and reasoned that the smaller bodied Ross's goose was likely required to invest a greater proportion of its available reserves (Ankney 1984). Nesting success was reduced to a lesser extent in Ross's geese than in snow geese when mean annual nest initiation was late relative to average. I suspect that depletion of fat reserves in 'late' years affected the incubation ability of Ross's goose females less so because of superior nest construction (McCracken et al. 1997) and a tendency to balance losses with local foraging during incubation recesses (Gloutney et al. 2001). This may also partially explain why Ross's geese experienced higher annual nest success compared to snow geese. Lastly, desirable weather (warm and dry) during the incubation period had a similar positive effect on the nesting success of both species.

I did not find an effect of nesting population size among my top-ranking models for gosling production. However, a long-term decline in the protein mass of pre-breeding females (Traylor 2010) suggests that a restriction of per-capita resource supply before females arrive to the colony may have occurred. Additional work is needed to explore whether increased density on penultimate staging areas from those geese nesting not only at Karrak Lake, but throughout the QMG have contributed indirectly via constraints on nutrient storage towards changes in productivity.

Season length constraints limit the capacity for goslings of arctic-nesting species to grow sufficiently large to fledge for migration without suitable habitat conditions. Aside from a genetic component, growth rates in geese can be exceptionally sensitive to environmental conditions on brood-rearing areas (Cooch et al. 1991b, Larsson et al. 1998). Therefore, the role of annual variation in forage quality and quantity as well as availability towards growth and survival is particularly non-trivial (Sedinger et al. 1998, Slattery and Alisauskas 2002).

Consequences stemming from the phenological mismatch and density hypotheses should become apparent in the gosling, or pre-fledging, stage of the life cycle. Therefore, I felt it merited attention and so became the focus of chapter 3. Under nutritional stress, goslings should divert energy from skeletal growth and towards increased digestive efficiency (e.g., Gurney et al. 2012). Consequently, to reinforce whether changes in survival might be related to resource limitation, I also examined whether goslings were of smaller structural size in years of high mortality. In the absence of marked goslings, I used ratios derived at hatching and banding as an index of gosling survival probability. Overall, at the annual level, Ross’s goose goslings tended to survive at a higher rate than did snow goose goslings. I found that mean gosling age had a positive effect on survival probability. As the number of nesting geese at Karrak Lake increased, gosling survival declined. However, Ross’s geese maintained a higher probability of survival compared to snow geese. Interestingly, the structural size of Ross’s goose goslings was unaffected by changes in goose density while size was reduced in higher-density years for snow goose goslings. I expect that this may have had to do with interspecific differences in bill morphology (Jónsson et al. 2013), or alternatively, to differences in dispersal strategies from the nesting colony. Ross's goose broods tend to disperse farther towards the coast than do snow goose broods, resulting in snow goose goslings being reared within the spatial extent of the biodeterioration zone where forage is of reduced nutritional quality (Slattery 1994, 2000).

Gosling structural size and survival were reduced in years with greater mismatch between the seasonal peak in forage quality and the hatching period in both species. Goslings in late-hatch years have access only to vegetation that has passed a point of maximum nutritional value. Young which are then smaller or nutritionally stressed have reduced foraging efficiency and mobility (Anderson and Alisauskas 2001), which likely becomes problematic for survival given dispersal distances once leaving the nest.

The local weather variable included in my top-performing model for gosling survival indicated that cool and wet conditions during brood-rearing negatively affected the survival of young. This is likely imposed via thermoregulatory costs (Sedinger 1992) and agrees with findings from other arctic-nesting species of geese (Doiron et al. 2015). However, the degree of competitiveness between the first and second-ranked model, where the effect of local weather was removed, indicated some uncertainty. In effect, wet conditions in the form of precipitation falling as rain may actually benefit growing vegetation and thus, improve foraging conditions for geese (Brook et al. 2015).

Parallelism apparent in the variation in annual productivity between Ross's geese and snow geese throughout this study (Fig. 1.2) implies that species responded similarly to common ecological factors. Statistically, my results support this, as I did not find species-specific responses to variables included in the top-ranking model describing gosling production. However, a strong species effect indicated that Ross's geese consistently outperformed snow geese. A combination of advantages throughout the breeding portion of the annual cycle that were investigated here (i.e., improved nest success and higher gosling survival) likely contributed towards superior reproduction by Ross's geese compared to snow geese at Karrak Lake.

From this study, it is apparent that no single variable could be isolated as the sole cause for long-term declines in gosling production at Karrak Lake. Instead, there appeared to be a multitude of factors that took effect at various stages of the life cycle to collectively reduce productivity. Indeed, I found support for each of the three hypotheses explored in this thesis, although a significant effect of each was not found for every component of recruitment analyzed here. Additional work might investigate how these hypotheses relate to other demographic parameters, such as (i) breeding propensity, defined as the probability that a sexually mature adult will attempt to nest, and (ii) perhaps a delayed age of first breeding.

Future research should also examine any lagged effect of the three aforementioned hypotheses on the post-fledging, or juvenile, survival of Ross's geese and snow geese. The first long-distance flight from brood-rearing areas towards wintering grounds by juveniles (geese that have fledged until 1 year later) has been identified as a critical time where considerable mortality can occur (Owen and Black 1989, Francis et al. 1992, Traylor et al. 2012). For geese leaving the Karrak Lake colony, this consists of a non-stop flight over the boreal forest towards prairie staging grounds (~ 1600 km; R. Alisauskas, unpublished data). Using retrospective analysis for lesser snow geese nesting at La Pérouse Bay, Cooch et al. (2001) found that juvenile survival accounted for the largest proportion of the variation inherent in recruitment rate among years. Changes in juvenile survival have also frequently been tied to environmental conditions experienced during the brood-rearing period (Slattery and Alisauskas 2002, Brook et al. 2015, Doiron et al. 2015). Thus, this single component of the breeding season represents potentially the most influential vital rate leading up to the recruitment of young into adulthood.

At the continental level, species population trajectories have begun to differ; Ross's goose populations have increased at a much faster rate when compared to the estimated rate of growth for snow geese (Alisauskas et al. 2011, Alisauskas et al. 2012). In effect, evidence from Lincoln's (1930) method suggests that the midcontinent population of snow geese may have stabilized, i.e., λ = approximately 1, at 13-15 million adults (R. Alisauskas personal communication). In the absence of declines in adult survival for either snow geese or Ross's geese (Alisauskas et al. 2011, Traylor et al. 2012, Wilson et al. 2016), a reduction in recruitment may be responsible for this attenuation in population growth (Dufour et al. 2012). While this thesis does not attempt to address this question at continental scales, my results lend support to the idea that disparities in trajectory may be related to species differences in productivity. Growth of Ross's goose populations has likely been aided by an eastward expansion of the breeding range (Kerbes et al. 2006) into colonies previously occupied exclusively by snow geese. Ross's geese tend to form large mixed flocks with snow geese (Alisauskas 2001). Coupled with a high affinity for dispersal (Drake and Alisauskas 2004, Wilson et al. 2016), this is expected to have enabled the spread of Ross's geese to new nesting sites. Dispersal has occurred into eastern arctic areas such as McConnell River, Southampton Island and western Baffin Island (Caswell 2009, J. Leafloor, personal communication), where reproduction has apparently been highly successful (Caswell 2009). Consequently, if advantages in gosling production held by Ross's geese over snow geese occur at other nesting colonies, then this has likely assisted in maintaining continental population growth by Ross's geese despite declining productivity at Karrak Lake.

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APPENDIX 1

TABLE A.1. Loadings obtained from the first axis (PC1) of principal component analyses (centred and scaled) based on weather variables during the arrival and egg laying, incubation and hatch and brood rearing periods in lesser snow geese and Ross's geese from 1991-2014. Also shown is the amount of variation accounted for by the first principal component in each period.

Period	% Variation	Variable	Loading: PC1
Arrival & Egg laying	73.40%	Mean T°	0.619
		Mean RH	-0.649
		Total Precipitation	-0.442
Incubation & Hatch	76.73%	Mean T°	0.607
		Mean RH	-0.616
		Total Precipitation	-0.502
Brood-Rearing	65.23%	Mean T°	0.640
		Mean RH	-0.670
		Total Precipitation	-0.377

TABLE A.2. Annual relationships between local weather variables measured by the weather station at Karrak Lake (y) and the NARR data (x) from 2000 – 2013. Data were sorted by three distinct periods of the breeding cycle for each species. Variables are mean temperature (T°), relative humidity (RH) and total precipitation (Precip). Shown are results of simple linear regressions, the number of years available to be compared (n), adjusted proportion of variance explained (R^2) and *p*-value.

Species	Variable	Period	Model	n	R^2	p
Snow Geese	Mean T°	arrival & egg laying	y = 1.04 + 0.56x	8	0.88	0.0004
		incubation & hatch	y = 0.44 + 0.82x	12	0.94	< 0.0001
		brood-rearing	y = 1.31 + 0.82x	6	0.94	0.0008
	Mean RH	arrival & egg laying	y = 68.69 + 0.23x	7	0.28	0.1260
		incubation & hatch	y = 34.04 + 0.68x	11	0.81	< 0.0001
		brood-rearing	y = 36.77 + 0.60x	5	0.91	0.0070
	Total Precip	arrival & egg laying	y = 24.34 + 0.05x	8	0.00	0.9800
		incubation & hatch	y = 5.54 + 1.24x	12	0.20	0.0807
		brood-rearing	y = 56.84 + 0.14x	6	0.00	0.9150
Ross's Geese	Mean T°	arrival & egg laying	y = 1.55 + 0.51x	9	0.91	< 0.0001
		incubation & hatch	y = 0.0014 + 0.86x	12	0.96	< 0.0001
		brood-rearing	y = 0.82 + 0.86x	6	0.95	0.0061
	Mean RH	arrival & egg laying	y = 76.80 + 0.11	8	0.00	0.4333
		incubation & hatch	y = 31.90 + 0.72x	11	0.85	< 0.0001
		brood-rearing	y = 34.37 + 0.64x	5	0.93	0.0053
	Total Precip	arrival & egg laying	y = 17.57 + 0.56x	9	0.00	0.7340
		incubation & hatch	y = 7.68 + 1.34x	12	0.39	0.0175
		brood-rearing	y = 55.70 + 0.15x	6	0.00	0.9050

TABLE A.3. (a) Model selection for the proportion of Ross's and lesser snow goose goslings (% goslings) observed in August on the brood-rearing areas north of the Karrak Lake colony from 1992-2014 ($n = 46$). Shown are the number of estimable parameters (k), the log-likelihood (logLik), the Akaike Information Criterion difference with correction for small sample size (Δ AIC$_c$), the model weights (ω_i) and the proportion of variance explained (R^2). (b) *A Posteriori* model set. (c) Parameter estimates (β) and 95% confidence intervals of the top ranked model in (a).

(a) Models	k	logLik	Δ AIC$_c$	ω_i	R^2
Spp + ELI + Mismatch + Protein	6	49.039	0.00	0.278	0.55
Spp + ELI + Mismatch + Protein + Summer.AO	7	50.415	0.04	0.272	0.56
Spp + Mismatch + Spp*Fat + Summer.AO	7	49.952	0.97	0.171	0.55
Spp + ELI + Mismatch + Protein + Summer.AO + BroodWeather	8	51.169	1.48	0.133	0.57
Spp + Mismatch + Spp*Fat + Summer.AO + BroodWeather	8	50.452	2.91	0.065	0.55
Spp + Pop + Spp*Fat + Summer.AO	7	48.217	4.44	0.030	0.52
Spp + ELI + Mismatch + Summer.AO	6	45.789	6.50	0.011	0.48
Spp + Mismatch + Spp*Fat	6	45.235	7.61	0.006	0.47
Spp + ELI + Pop + Protein + Summer.AO	7	46.619	7.63	0.006	0.49
Spp + ELI + Pop + Protein	6	45.212	7.65	0.006	0.47
Spp + ELI + Protein	5	43.776	7.87	0.005	0.45
Spp + ELI + Mismatch	5	43.709	8.01	0.005	0.44
Spp + ELI + Protein + Summer.AO	6	45.015	8.05	0.005	0.46
Spp + Spp*Fat + Summer.AO	6	44.485	9.11	0.003	0.45
Spp + ELI + Spp*Protein	6	44.083	9.91	0.002	0.44
Spp + Pop + Spp*Fat	6	43.836	10.41	0.002	0.43
Spp + Spp*Fat	5	40.394	14.64	0.000	0.36
Spp + ELI + Pop	5	39.528	16.37	0.000	0.33
Spp + ELI + Summer.AO + BroodWeather	6	38.518	21.04	0.000	0.29
Spp + ELI (biological null)	4	34.963	22.98	0.000	0.21
Spp	3	31.920	26.66	0.000	0.11
Intercept (Null)	2	28.638	30.93	0.000	0.00
(b) *A Posteriori* Models					
Spp + Mismatch + Protein	5	43.213	9.00	0.003	0.43
Spp + Mismatch + Protein + Summer.AO	6	46.650	4.78	0.023	0.50
Spp + Mismatch + Protein + Summer.AO + BroodWeather	7	46.798	7.28	0.007	0.49
SPP + ELI + Mismatch^2 + Mismatch + Protein	7	49.193	2.49	0.072	0.54

(c) Parameters	SPP$_{ROGO}$	ELI	Mismatch	Protein	Intercept
β	0.469	-0.009	-0.008	0.003	-0.758
95% CI	0.238, 0.700	-0.014, -0.004	-0.013, -0.003	0.001, 0.005	-1.448, -0.069

Notes: Spp = species, ELI = early-late nest initiation index, Mismatch = the difference between the mean annual hatch date and NDVI$_{50}$, Protein = annual index of body protein, Fat = annual index of abdominal fat, Pop = nesting population size estimate, Summer.AO = mean annual AO value from July 1 to August 10, BroodWeather = PC1 of temperature, precipitation and relative humidity from the end of the hatch period to Julian date 222 (August 9th/10th).