Decadal declines in avian herbivore reproduction: density-dependent nutrition and phenological mismatch in the Arctic

MEGAN V. ROSS,[1,4] RAY T. ALISAUSKAS,[1,2] DAVID C. DOUGLAS,[3] AND DANA K. KELLETT[1,2]

[1]*Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2 Canada*
[2]*Environment and Climate Change Canada, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4 Canada*
[3]*U.S. Geological Survey Alaska Science Center, 250 Egan Drive, Juneau, Alaska 99801 USA*

Abstract. A full understanding of population dynamics depends not only on estimation of mechanistic contributions of recruitment and survival, but also knowledge about the ecological processes that drive each of these vital rates. The process of recruitment in particular may be protracted over several years, and can depend on numerous ecological complexities until sexually mature adulthood is attained. We addressed long-term declines (23 breeding seasons, 1992–2014) in the per capita production of young by both Ross's Geese (*Chen rossii*) and Lesser Snow Geese (*Chen caerulescens caerulescens*) nesting at Karrak Lake in Canada's central Arctic. During this period, there was a contemporaneous increase from 0.4 to 1.1 million adults nesting at this colony. We evaluated whether (1) density-dependent nutritional deficiencies of pre-breeding females or (2) phenological mismatch between peak gosling hatch and peak forage quality, inferred from NDVI on the brood-rearing areas, may have been behind decadal declines in the per capita production of goslings. We found that, in years when pre-breeding females arrived to the nesting grounds with diminished nutrient reserves, the proportional composition of young during brood-rearing was reduced for both species. Furthermore, increased mismatch between peak gosling hatch and peak forage quality contributed additively to further declines in gosling production, in addition to declines caused by delayed nesting with associated subsequent negative effects on clutch size and nest success. The degree of mismatch increased over the course of our study because of advanced vegetation phenology without a corresponding advance in Goose nesting phenology. Vegetation phenology was significantly earlier in years with warm surface air temperatures measured in spring (i.e., 25 May–30 June). We suggest that both increased phenological mismatch and reduced nutritional condition of arriving females were behind declines in population-level recruitment, leading to the recent attenuation in population growth of Snow Geese.

Key words: Arctic; breeding phenology; Chen caerulescens caerulescens; Chen rossii; *climate change; density dependence; ecological mismatch; geese; nutrient reserves.*

INTRODUCTION

Animal populations fluctuate annually due to the interplay between the probability of adult survival and the per capita rate at which dead adults are replaced with new recruits. 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, high annual probability of adult survival remains relatively constant over time (Sæther and Bakke 2000, Stahl and Oli 2006). However, retrospective analyses often demonstrate that annual variation in recruitment has 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 reproductive adulthood. For birds, these states and probabilities include the propensity with which individuals attempt to breed, their fecundity (or clutch size), nest and egg survival, pre-fledging survival (i.e., before attainment of flight), and post-fledging survival until maturity. Any, and likely all, of these components respond to proximate factors before or shortly after arrival to nesting areas, and such responses in turn govern, to varying degrees, how many young are produced in a given year (Alisauskas 2002, Hoekman et al. 2002). Bottom-up regulation, driven by a reduction in per capita food supply, is most often the mechanism responsible for observed density-dependent reductions in the production of young and population growth rate (Sinclair and Krebs 2002). Resource limitation through competition can result from increases in density of conspecifics and tends to affect recruitment more than it affects adult survival (Cooch et al. 2001, Menu et al. 2002, see Koons et al. 2014).

[4] E-mail: m.ross@usask.ca

Many species of Arctic-nesting birds are long-distant migrants, and 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 toward 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 (Farmer and Wiens 1999, Cresswell et al. 2004) and recruitment (Ebbinge and Spaans 1995). Reproduction by Arctic-nesting geese, in particular, is nutritionally demanding; it requires that females store sufficient fat and protein before breeding, levels that often 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*; Ryder 1970, Bon 1997, Traylor 2010) 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 measured 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 in response to advanced vernal phenology is not ubiquitous (Guillemain et al. 2013), and earlier breeding may not translate necessarily into improved recruitment or population growth (Wilson and Arcese 2003). The selective advantage for early breeding is related to synchrony between peak resource availability and peak resource requirements by young (Visser and Both 2005). Failure to track advanced phenology of key food resources across space or trophic levels can result in phenological "mismatch" (Visser et al. 1998, Durant et al. 2007). Long-distance migrants to highly seasonal environments have a risky strategy 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 to be those most impacted by changes in climate, specifically through any advancement in plant phenology due to Arctic warming (McKinnon et al. 2012, Clausen and Clausen 2013, IPCC 2013). An improved understanding of how current climatic variability influences productivity (reviewed by Miller-Rushing et al.

2010) should inform how any future changes in climate may influence future population dynamics.

Our objective was to assess the roles of (1) density dependence, (2) pre-breeding nutrient storage, and (3) phenological mismatch behind long-term declines (23 breeding seasons) in gosling production (hereafter gosling production or annual productivity) 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. 2011, 2012). Importantly, our hypotheses address different periods of the breeding cycle: (1) density dependence on northern spring staging grounds (above the tree line) that influences pre-breeding female nutrition and (2) phenological mismatch during brood-rearing. We investigated the likely mechanisms that link the nutrition hypothesis to annual productivity by studying clutch size and probability of nest success. We specifically 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? (3) Has gosling hatch and timing of peak food resource quality become increasingly mismatched over time? (4) Has this divergence resulted from long-term changes in the dates of vegetation emergence, hatching or both?

METHODS

Study area

We 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 1994, Kerbes et al. 2014); numbers of nesting geese increased from ~408,000 in 1993 to almost 1.2 million by 2014 (Alisauskas et al. 2012, R. Alisauskas, *unpublished data*). 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).

Collection and anatomical dissections

During 1992–2014 we shot adult female geese of both species 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 ovarian follicle 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. We 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). We weighed reproductive tissues including the oviduct, ovaries, individual developing follicles (>1 g), and the oviducal egg, if present, and recorded the number of developing, atretic, and postovulatory follicles (Alisauskas and Ankney 1992).

Scaled nutritional condition

To compare the body composition (protein and fat) of individual females within a given year, we 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 we performed a principal components 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 skeletal size.

We 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 we 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, we controlled for each bird's nutritional investment of somatic tissue toward 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

$$\text{DOY}_{\text{NID},i} = \text{DOY}_{\text{collected},i} - x_i \times 1.3$$

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, we calculated the time (d) required for rapid follicular growth by multiplying the maximum number of developing follicles observed (6) by the laying rate (Alisauskas and Ankney 1992). This 7.8-d period corresponds to the five intervals of 1.3 d associated with the development of six follicles, plus the sixth 1.3-d interval required for the egg to travel through the oviduct to produce the albumen and shell until oviposition in the nest.

Using only geese with the maximum number of developing follicles, we estimated growth curves for rapidly developing follicles for Ross's Geese ($n = 5$) and Snow Geese ($n = 25$). We 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

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

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

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

Using these two methods (for birds with and without postovulatory follicles, respectively) to estimate NID for each collected female, we then subtracted this predicted NID from its collection date to obtain a single index for the stage of the laying cycle on the date of collection for each bird relative to its predicted NID. Negative values represented the number of days until first eggs were laid, and positive values the number of days after first eggs were laid

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

For each species, we constructed candidate sets of 16 a priori models for each fat and protein index using general linear modeling 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, we used fully saturated models based on collected females to estimate levels of fat (g) and protein (g), assuming an average apparent clutch size (four eggs), an average body size, i.e., PC1 = 0, at 3 d 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.

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 nutrition and nesting data in our study extended back to 1992 and 1991, respectively, we 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; *available online*).[5] We extracted air temperature at 2 m, relative humidity at 2 m, and total precipitation for the years, months, and locations of interest.

Following related studies (e.g., Morrissette et al. 2010), we 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. We used a PCA of mean daily temperature, relative humidity, and total precipitation during each of these intervals to obtain an index of local weather (Appendix S1: Table S1). Temperature and relative humidity from the weather station at Karrak Lake were highly correlated with the NARR values, but precipitation less so (Appendix S2: Table S1). Compared to the point location measured by our 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 Center of the National Weather Service; these values have been standardized by the standard deviation of the monthly index (data *available online*).[6] A positive phase of the AO indicates a low pressure system over the Arctic associated with cold temperatures while a high pressure system, the negative phase, produces a weaker westerly jet stream resulting in greater air movement to the south (Hurrell 1995, Thompson and Wallace 2000). While typically studied in the context of winter, others (Dickey et al. 2008) have successfully incorporated spring and summer AO values into analyses of breeding by Arctic-nesting geese. We defined two periods, spring (1 May–30 June) and summer (1 July–10 August), and calculated annual averages for each period relative to a long-term mean value (1991–2014).

Breeding success and colony size

Reproductive success and colony size have been measured annually at Karrak Lake since 1991 and 1993, respectively, following detailed methods provided by Alisauskas et al. (2012). Briefly, we 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, we 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). We 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). Negative values of ELI indicated that nest initiation was earlier than average whereas positive values indicated that it was later than average.

To test for density-dependent regulation, we 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 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).

We conducted annual capture and banding efforts on brood-rearing grounds from 1992–2014. 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 molt and the pre-fledgling stage of goslings. We determined individual age (adult vs. immature) and sex by plumage characteristics and cloacal eversion, respectively. Total numbers of adults and goslings captured each year were calculated by summing across all banding drives 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

---

[5] http://nomads.ncdc.noaa.gov/
[6] http://www.cpc.ncep.noaa.gov

$r = 0.27$ ($n = 11$), respectively (R. Alisauskas, *unpublished data*). Age ratios at banding provide a direct measure of per capita recruitment until just before 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 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).

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, we used a time series of 23 breeding seasons (1992–2014) to estimate the median date of $NDVI_{50}$ (our index of forage availability) on the brood-rearing area (~5 $\times 10^6$ km^2) north of Karrak Lake (Slattery and Alisauskas 2007, Wilson et al. 2016). Daily global NDVI grids (0.05° resolution) were obtained from two sources: the Long Term Data Record Version 3 collected by the Advanced Very High Resolution Radiometer (AVHRR) for 1982–1999 and from the Earth Science Data Record of preprocessed NDVI collected by the Moderate Resolution Imaging Spectroradiometer (MODIS) for 2000–2010 (data *available online*).[7,8] We derived 10-d maximum NDVI composites (Holben 1986) and linearly smoothed the annual NDVI phenology curves 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). We 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). We quantified phenological mismatch between geese and forage as the mean annual hatch date (of each goose species) minus the date of $NDVI_{50}$. Values closer to zero indicated that hatch was more synchronous with plant phenology.

Statistical analyses

We used general linear models (GLMs) with a normal error structure to evaluate the influence of ecological covariates on the annual production of goslings, 1992 to 2014. We modeled gosling production using the proportion of juveniles in flocks at banding, weighted by the

[7] http://ltdr.nascom.nasa.gov
[8] http://vip.arizona.edu

total number of geese captured. To avoid problems with collinearity, we 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 used together 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, we did not consider non-linear relationships and tested only interactions of interest (i.e., fat × species and protein × 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, we modeled 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 both 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: we 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 previous studies (Traylor 2010). We 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.

We 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, we considered 22 a priori models including global models that encompassed all uncorrelated effects of interest and a series of progressively less complex models that addressed the nutrition, mismatch and density-dependence hypotheses. Likewise, we constructed 12 and 15 a priori models to investigate variation in clutch size and nest success, respectively.

We 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. If geese were tracking vegetation green-up perfectly, we expected to see a 1:1 relationship between dates of hatch and $NDVI_{50}$. However, under the mismatch hypothesis we expected that in years when

spring plant phenology was early, geese might have had difficulty meeting this 1:1 relationship compared to years when it was later. We 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).

RESULTS

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 gosling proportion of captures 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; $\beta_{Snow} = -0.758$, 95% CI: -1.448, -0.069; Tables 1 and 2).

The most parsimonious model accounted for 55% of the annual variation in gosling production (Table 1; complete list in Appendix S3: Table S1), although three other models were highly competitive ($\Delta AIC_c < 2$).

Phenological mismatch was included in all competitive models. In the top-ranked model, a greater disparity between peak hatch and peak vegetation quality was associated with relatively fewer goslings during mid-August capture efforts (Fig. 1a). Models in which the mismatch effect was replaced by a colony size effect received comparatively little support ($\Delta AIC_c \geq 4.44$). Species responded similarly to protein mass (Fig. 1b), whereby larger mean annual protein reserves at arrival to the nesting grounds were positively related with the production of young. As expected, gosling production was higher in years when geese initiated nesting earlier (Fig. 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 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), while Ross's Geese were unaffected by pre-

TABLE 1. Model selection for the percentage of Ross's Goose and Lesser Snow Goose goslings observed in August on the brood-rearing areas north of the Karrak Lake colony from 1992 to 2014 ($n = 46$).

Models	k	logLik	ΔAIC_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

Notes: Shown are the number of estimable parameters (k), the log-likelihood (logLik), the Akaike Information Criterion difference with correction for small sample size (ΔAIC_c), the model weights (ω_i), and the proportion of variance explained (R^2). Model parameters are 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 1 July to 10 August relative to the long-term average for the same period; BroodWeather, PC1 of temperature, precipitation, and relative humidity from the end of the hatch period to day of year 222 (9–10 August).

TABLE 2. Parameter estimates (β) and 95% confidence intervals of the top-ranked model for the percentage of Ross's Goose and Lesser Snow Goose goslings observed in August on the brood-rearing areas north of the Karrak Lake colony from 1992 to 2014 ($n = 46$).

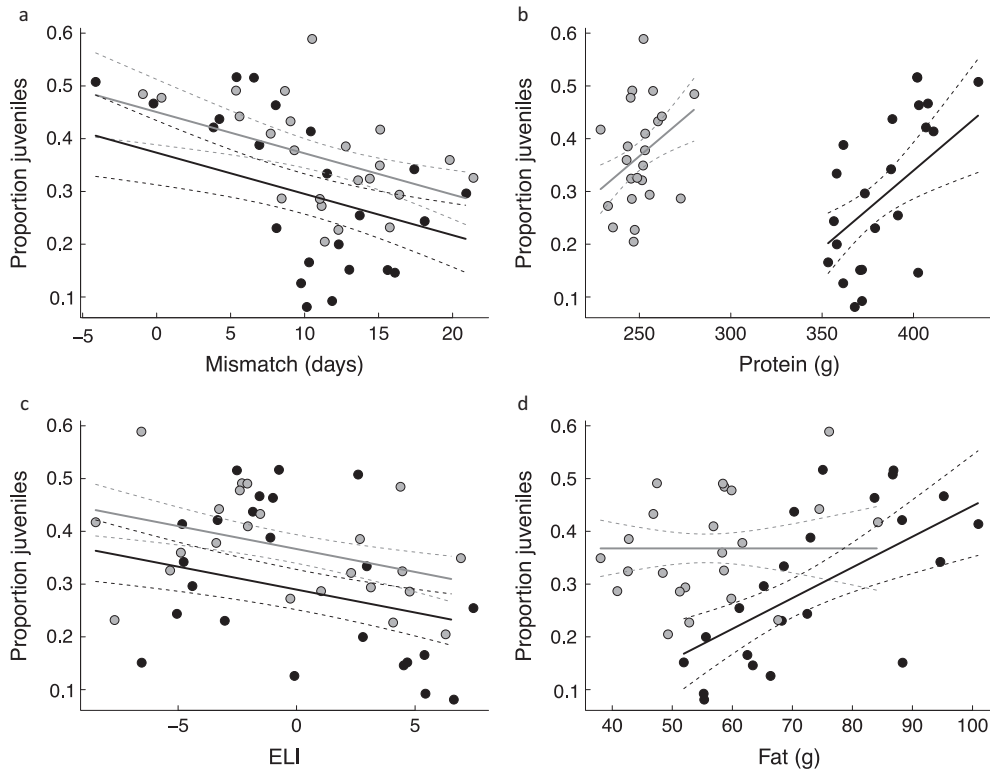| Parameters	$SPP_{Ross's}$	ELI	Mismatch	Protein	Intercept
β	0.469	-0.009	-0.008	0.003	-0.758
95% CI	0.238, 0.700	$-0.014, -0.004$	$-0.013, -0.003$	0.001, 0.005	$-1.448, -0.069$

Fig. 1. Relationships between the proportions of goslings captured annually at August banding drives from 1992 to 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 $NDVI_{50}$ (date of 50% annual maximum NDVI) is reached (hatch preceded date of $NDVI_{50}$ when negative). (b) Annual index of body protein from females collected at arrival to the colony. (c) The early-late index (ELI), a measure of relative nest initiation date among years. (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 (gray) and Lesser Snow Geese (black).

breeding fat reserves ($\beta_{spp \times fat(Ross's)} = -0.006$, 95% CI: $-0.010, -0.002$; Fig. 1d).

We 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 preferred (Appendix S3: Table S1).

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 × protein interaction (Table 3). 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. 2a). Mean clutch size predicted for Snow Geese (intercept; $\beta_{Snow} = 2.184$, 95% CI: 1.301, 3.066) was not significantly different from that of Ross's Geese ($\beta_{spp(Ross's)} = -1.179$, 95% CI: $-2.635, 0.277$), adjusted for other effects in the model. However, ranges in clutch size predicted over each species' observed range of protein mass was 3.0–3.5 for Ross's Geese and 3.2–3.6 for Snow Geese. The slope between mean clutch size and mean annual protein reserves was greater for Ross's Geese ($\beta_{spp \times protein(Ross's)} = 0.006$, 95% CI: 0.000, 0.011) relative to Snow Geese ($\beta_{Snow} = 0.003$, 95% CI: 0.001, 0.006; Fig. 3). The highest-ranked model that included 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 ($\beta_{spp(Ross's)} = 0.051$, 95% CI: 0.017, 0.085; Table 3) 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: $-0.025, -0.013$) when compared to Ross's Geese ($\beta_{spp \times ELI(Ross's)} = 0.009$, 95% CI: 0.002, 0.017; Fig. 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).

TABLE 3. Model selection for the annual variation in clutch size ($n = 46$), nest success ($n = 46$) and phenological mismatch ($n = 48$) at Karrak Lake from 1991 (mismatch analysis only) or 1992–2014 for the response variables clutch size and nest success.

Model	k	logLik	ΔAIC_c	ω_i	R^2
Clutch size					
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: Model parameters are 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 1 May to 30 June relative to the long-term average for the same period; SpringTemp, mean spring temperature from 25 May to 30 June.

Vegetation and goose breeding phenology

The day of year at which $NDVI_{50}$ was reached had a range of 32 days, from 12 June to 14 July with a mean of 27 June (178 ± 1.48 [mean ± SE]). Earlier $NDVI_{50}$ dates were associated with warmer spring temperatures ($\beta = -2.033$, 95% CI: -2.550, -1.516; Fig. 4a). Moreover, from 1991 to 2014, the timing of $NDVI_{50}$ advanced significantly ($\beta = -0.337$, 95% CI: -0.618, -0.057; Fig. 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. 4c). However, it seems that hatch dates begun advancing during the last 5 years of this time series (Fig. 4c).

Phenological mismatch

Phenological mismatch, the number of days separating hatch and $NDVI_{50}$, averaged 11 ± 1.08 d (range −1 to 21 d) for Ross's Geese and 10 ± 1.19 d (range −4 to 21 d) for Snow Geese. Gosling hatch preceded or coincided with the date of $NDVI_{50}$ in only two of 24 years (1992, 1997). We found a positive relationship between annual peak hatch and $NDVI_{50}$, suggesting that geese responded to advanced forage phenology by nesting earlier ($\beta = 0.362$, 95% CI: 0.237, 0.486; Fig. 4b). According to the best-performing model, the difference (d) between hatch and $NDVI_{50}$ increased linearly through time ($\beta = 0.326$, 95% CI: 0.159, 0.493). In years when

the date of $NDVI_{50}$ was far earlier than average, mismatch also tended to exceed the species-specific average. The degree of mismatch was 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 3).

DISCUSSION

We found evidence to support the importance of local weather, climate and phenological mismatch to the production of goslings by Ross's and Snow Geese. Later nesting reduced annual productivity in both species. Delays in nest initiation stem largely from local Snow conditions on Arctic breeding grounds (Madsen et al. 2007, Dickey et al. 2008); delayed melt due to deep snow and cold temperatures can impede access to nesting habitat and delay egg laying (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 metabolic needs during incubation (Ryder 1970, Ankney and MacInnes 1978). We 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
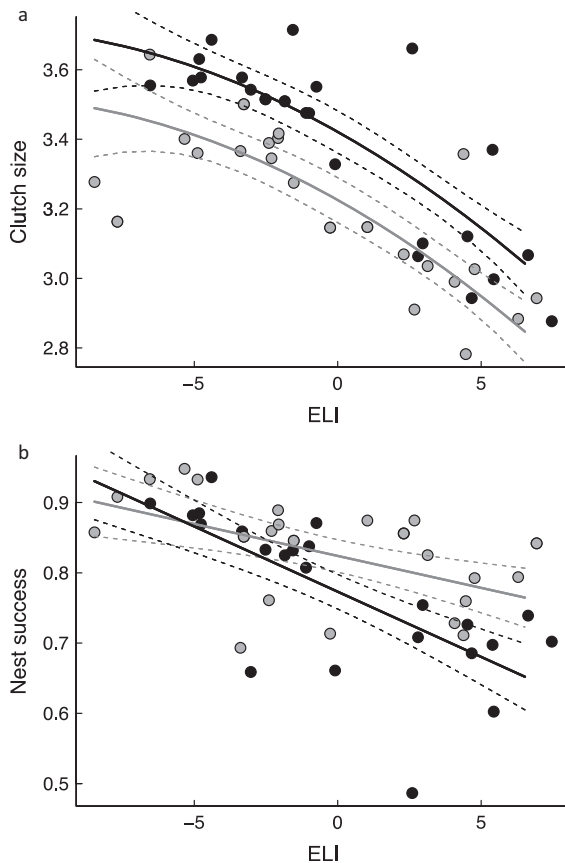
FIG. 2. The relationships between (a) mean annual clutch size and the early-late index ($n = 46$) and (b) mean annual apparent nest success and the early-late index ($n = 46$) for geese breeding at Karrak Lake, Nunavut, Canada from 1992–2014. Raw mean annual values, the model-predicted line (solid) and 95% confidence intervals (dashed) are shown for Ross's Geese (gray) and Lesser Snow Geese (black).

being spared after allocation to clutches, for the duration of incubation (Harvey 1971, Ankney and MacInnes 1978, Raveling 1979, 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 nest 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 our study.

Similar to Dickey et al. (2008), we found that a large-scale climate index (summer AO) better predicted annual gosling production while local weather conditions were better predictors of the earlier summer intermediaries of gosling production, such as nest success. Warmer temperatures during summer may improve gosling survival (Ross 2016) possibly by reducing the need for brooding, while also potentially increasing plant production. Given that the AO is a covariate with broad geographic relevance, it was difficult to interpret with confidence at some of the scales presented here. However, for short, discrete periods of time, local weather appeared to have important consequences. 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 our study was the result of a long-term trend in advancing plant

departing northern staging areas before completion of pre-nesting storage of fat and protein. Thus, in "early" nesting years, a reduction in clutch size may have been the result of geese laying their first eggs without having reached optimal levels of nutrient reserves. Alternatively, favorable 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 the degree of fat storage on the northern prairies before departure for Arctic nesting areas, in addition to Arctic climatic conditions during nesting, influenced subsequent production of Snow Geese. In this study, gosling production by Ross's Geese was less sensitive to reduced fat stores measured at arrival, than were Snow Geese. This may relate to our 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
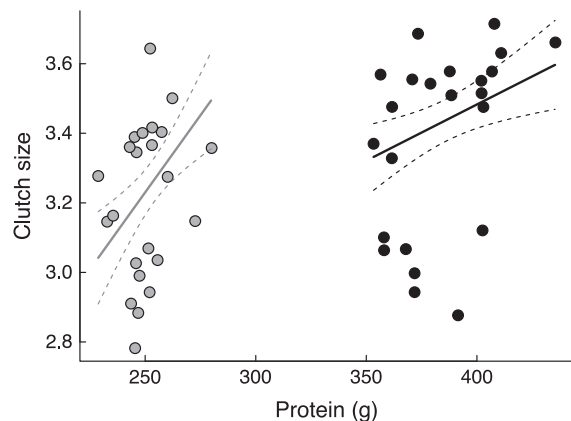

FIG. 3. The relationship between mean annual clutch size and the mean annual protein reserve index of pre-breeding females arriving to breed at Karrak Lake from 1992 to 2014. Raw mean annual values, the model-predicted line (solid) and 95% confidence intervals (dashed) are shown for Ross's Geese (gray) and Lesser Snow Geese (black).
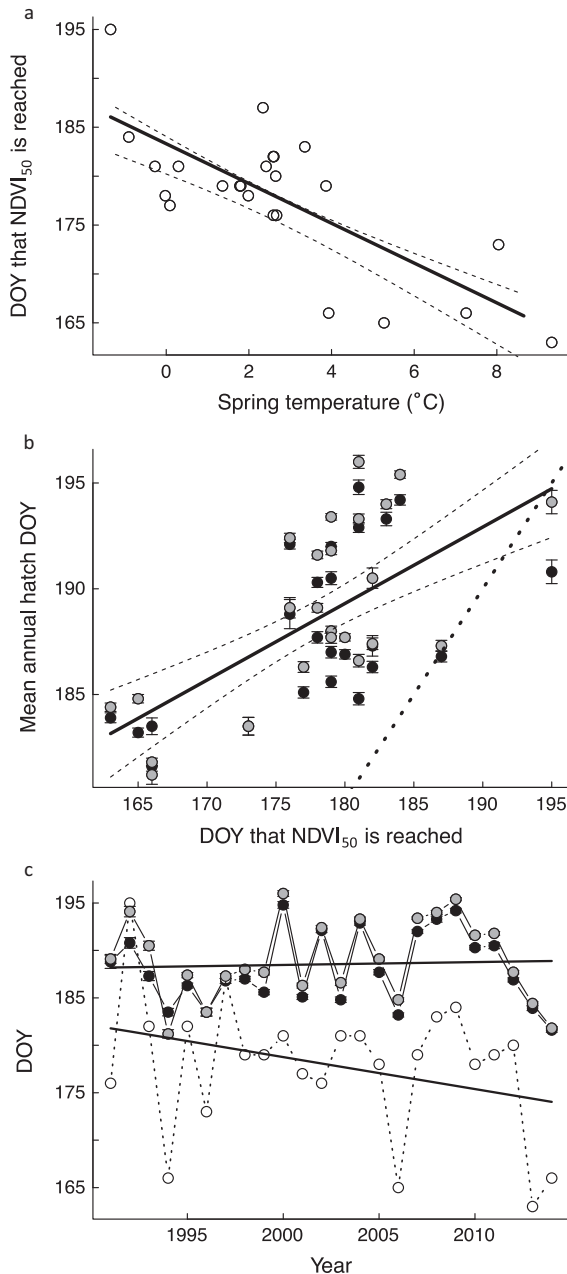
FIG. 4. (a) Relationship between the day of year (DOY) that $NDVI_{50}$ was reached and mean annual spring temperature, 1992–2014. (b) Relationship between mean annual hatch date and the day of year $NDVI_{50}$ was reached. The dotted line indicates a perfect 1:1 relationship. (c) Annual variation in the day of year that $NDVI_{50}$ was reached (open markers) and the mean annual hatch date (colored markers), 1991–2014. 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 (gray) and Lesser Snow Geese (black).

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 we found that both species were able to partially adjust hatch dates by nesting earlier in years with early springs, timing of vegetation green-up advanced more than did nesting females (Dickey et al. 2008). Part of the reason for this is because gonadal development is a function of changing day length (Bluhm 1992), which is not responsive to annual differences in spring phenology. Incubation duration in Snow and Ross's Geese is relatively fixed at about 22 d duration, largely preventing additional adjustments to hatch phenology regardless of ambient environmental conditions (Ryder 1971, 1972, Craig 2000). As well, the requisite pre-breeding storage of fat and protein may impose minimum time constraints that prevented earlier conditioning and nesting by both species. An untested hypothesis 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.

Similar to Brook et al. (2015), our 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 Arctic regions continue to warm as is anticipated, such a unidirectional trend of air surface temperature could result in hatching of goslings becoming increasingly decoupled from plant phenology if adults are unable to advance their breeding phenology accordingly. How geese may adapt to such changes into the future, and how populations may respond are difficult to predict.

The ecological consequence of advanced plant phenology was evident in our study: increased mismatch directly reduced annual productivity of geese at Karrak Lake, and was likely mediated by negative effects on 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 complete body and feather growth necessary for the attainment of flight (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 that have reduced

access to high quality foods show stunted growth and reduced body mass (Cooke et al. 1984, Sedinger and Flint 1991, 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 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), Black Brant (*Branta bernicla nigricans*; Sedinger and Chelgren 2007), as well as in Lesser Snow Geese (Francis et al. 1992) and Ross's Geese (Slattery and Alisauskas 2002) 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*). 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.

Our 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 toward the cultivation of protein-rich pulse crops (M. Ross, *unpublished manuscript*). This suggests that as large numbers of geese have converged toward breeding areas after departing prairie Canada in recent years, their ability to store protein reserves as somatic muscle tissue have been impeded compared to levels acquired historically on northern staging areas in the subarctic and Arctic (Wypkema and Ankney 1979). We 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. Our 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 at the same northern staging areas above the tree line in the Arctic plains. 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 was consistent with density-dependence detected in other regions (Cooch et al. 1989, Williams et al. 1993, Aubry et al. 2013).

Increased competition under suboptimal 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 appears to have more relevance to waterfowl species (Rohwer 1992), many of which require adequate nutrient storage for breeding attempts to occur (Ankney and Alisauskas 1990, Alisauskas and Ankney 1992). On some level, this remains a "black box" in our 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 so 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, increased foraging competition on spring staging areas in the Arctic and subarctic may have reduced breeding propensity by Snow and Ross's Geese and contributed to the long-term decline in production of young, in addition to reduced per capita production by breeding geese (as demonstrated herein).

Although the relative size of annual pre-breeding protein reserves was unrelated to observed variation in nest success, an effect of mean annual protein stores on gosling production appeared to be mediated partly through its effect on clutch size. As with protein stores and recruitment, 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 enter a state of disuse during nesting compared to during the spring migration (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 findings by 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 in eggs from an absolutely smaller source of stored nutrients (Ankney 1984).

Conclusions

We have shown that decadal declines in productivity were linked to multiple additive factors during different periods leading up to and during the breeding phase of two sympatric species of Geese. The parallel declines for both Ross's and Snow Geese in the proportion of goslings just before fledging indicated similar responses by both species to several environmental covariates. However, Ross's Geese consistently experienced greater annual productivity over Snow Geese due to greater nest success as well as gosling survival (Ross 2016). Overall, our findings support both the nutrition hypothesis, possibly stemming from density dependence on the final northern staging areas used during spring migration through Arctic and subarctic regions, and the mismatch hypothesis, due to a trend in earlier green-up of vegetation without a corresponding trend in hatch date by either species.

Sustained declines in gosling production at our study site imply reduced potential for subsequent recruitment to sexually mature adulthood, 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. Estimates of population size using Lincoln's (1930) method suggest that abundance of adult midcontinent Snow Geese has stabilized, although estimates for the continental abundance of adult Ross's Geese suggest continued increase in recent years (Alisauskas et al. 2011, 2012). There have been no declines in adult survival over the same time period, despite anthropogenic attempts to induce such declines (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 associated senescent reductions in reproduction and subsequent momentum effects on population trajectories. Persistence of population stability or possible decline by either or both species is likely unless there is colonization of new Arctic nesting areas currently unoccupied by these birds (see Conkin and Alisauskas 2017).

Acknowledgments

Literature Cited

Alisauskas, R. T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent lesser snow geese. Auk 115:851–862.

Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in midcontinent lesser snow geese. Journal of Wildlife Management 66:181–193.

Alisauskas, R. T., and C. D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30–61 in B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, USA.

Alisauskas, R. T., S. M. Slattery, J. P. Ryder, M. L. Gloutney, A. D. Afton, R. H. Kerbes, and M. R. McLandress. 1998. Discrimination of Ross's and lesser snow goose eggs. Journal of Field Ornithology 69:647–653.

Alisauskas, R. T., R. F. Rockwell, K. W. Dufour, E. G. Cooch, G. Zimmerman, K. L. Drake, J. O. Leafloor, T. J. Moser, and E. T. Reed. 2011. Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. Wildlife Monographs 179:1–42.

Alisauskas, R. T., J. O. Leafloor, and D. K. Kellett. 2012. Population status of midcontinent lesser snow geese and Ross's geese following special conservation measures. Pages 132–177 in J. O. Leafloor, T. J. Moser, and B. D. J. Batt, editors. Evaluation of special management measures for midcontinent lesser snow geese and Ross's geese. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C., USA and Ottawa, Ontario, Canada.

Ankney, C. D. 1982. Annual cycle of body weight in lesser snow geese. Wildlife Society Bulletin 10:60–64.

Ankney, C. D. 1984. Nutrient reserve dynamics of breeding and molting brant. Auk 101:361–370.

Ankney, C. D., and R. T. Alisauskas. 1990. The use of nutrient reserves by breeding waterfowl. Acta XX Congressus Internationalis Ornithologici:2170–2176.

Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95:459–471.

Aubin, A. E., E. H. Dunn, and C. D. MacInnes. 1986. Growth of lesser snow geese on arctic breeding grounds. Condor 88:365–370.

Aubry, L. M., R. F. Rockwell, E. G. Cooch, R. W. Brook, C. P. H. Mulder, and D. N. Koons. 2013. Climate change,

phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. Global Change Biology 19:149–160.

Bluhm, C. K. 1992. Environmental and endocrine control of waterfowl reproduction. Pages 323–364 *in* B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, USA.

Bon, R. L. 1997. Spring nutritional ecology of migrating and breeding Ross' geese (*Chen rossii*). MSc thesis. University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

Both, C., C. A. M. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, and R. P. B. Foppen. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proceedings of the Royal Society B 277:1259–1266.

Bourgeon, S., F. Criscuolo, F. Bertile, T. Raclot, G. W. Gabrielsen, and S. Massemin. 2006. Effects of clutch sizes and incubation stage on nest desertion in the female Common Eider *Somateria mollissima* nesting in the high Arctic. Polar Biology 29:358–363.

Brook, R. W., J. O. Leafloor, K. F. Abraham, and D. C. Douglas. 2015. Density dependence and phenological mismatch: consequences for growth and survival of sub-arctic nesting Canada geese. Avian Conservation and Ecology 10:1.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. Ecology 81:619–627.

Choi, W., S. J. Kim, P. F. Rasmussen, and A. R. Moore. 2009. Use of the North American regional reanalysis for hydrological monitoring in Manitoba. Canadian Water Resources Journal 34:17–36.

Choinière, L., and G. Gauthier. 1995. Energetics of reproduction in female and male greater snow geese. Oecologia 103:379–389.

Clausen, K. K., and P. Clausen. 2013. Earlier Arctic springs cause phenological mismatch in long-distance migrants. Oecologia 173:1101–1112.

Conkin, J., and R. T. Alisauskas. 2017. Conversion of tundra to exposed peat habitat by snow geese (*Chen caerulescens caerulescens*) and Ross's geese (*C. rossii*) in the central Canadian Arctic. Polar Biology 40:563–576.

Cooch, E. G., D. B. Lank, R. F. Rockwell, and F. Cooke. 1989. Long-term decline in fecundity in a snow goose population: Evidence for density dependence? Journal of Animal Ecology 58:711–726.

Cooch, E. G., D. B. Lank, A. Dzubin, R. F. Rockwell, and F. Cooke. 1991. Body size variation in lesser snow geese: Environmental plasticity in gosling growth rates. Ecology 72:503–512.

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

Cooke, F., C. S. Findlay, and R. F. Rockwell. 1984. Recruitment and the timing of reproduction in lesser snow geese (*Chen caerulescens caerulescens*). Auk 101:451–458.

Craig, L. M. 2000. Comparative incubation ecology of Ross's and lesser snow geese at Karrak Lake, Nunavut. MSc thesis. Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

Cresswell, W., S. Holt, J. M. Reid, D. P. Whitfield, R. J. Mellanby, D. Norton, and S. Waldron. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. Behavioral Ecology 15:498–507.

Crick, H. Q. P., C. Dudley, D. E. Glue, and D. L. Thomson. 1997. UK birds are laying eggs earlier. Nature 388:526–527.

Curio, E. 1983. Why do young birds reproduce less well? Ibis 125:400–404.

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

Doiron, M., P. Legagneux, G. Gauthier, and E. Lévesque. 2013. Broad-scale satellite normalized difference vegetation index data predict plant biomass and peak date of nitrogen concentration in arctic tundra vegetation. Applied Vegetation Science 16:343–351.

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

Doiron, M., G. Gauthier, and E. Lévesque. 2015. Trophic mismatch and its effects on the growth of young in an arctic herbivore. Global Change Biology 21:4364–4376.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Drent, R. H., A. D. Fox, and J. Stahl. 2006. Travelling to breed. Journal of Ornithology 147:122–134.

Drever, M. C., R. G. Clark, C. Derksen, S. M. Slattery, P. Toose, and T. D. Nudds. 2012. Population vulnerability to climate change linked to timing of breeding in boreal ducks. Global Change Biology 18:480–492.

Dufour, K. W., R. T. Alisauskas, R. F. Rockwell, and E. T. Reed. 2012. Temporal variation in survival and productivity of midcontinent lesser snow geese and survival of Ross's geese and its relation to population reduction efforts. Pages 95–131 *in* J. O. Leafloor, T. J. Moser, and B. D. J. Batt, editors. Evaluation of special management measures for midcontinent lesser snow geese and Ross's geese. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C., USA and Ottawa, Ontario, Canada.

Durant, J. M., D. Ø. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271–283.

Ebbinge, B. S., and B. Spaans. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied Brent Geese *Branta b. bernicula* in the high arctic. Journal of Avian Biology 26:105–113.

Farmer, A. H., and J. A. Wiens. 1999. Models and reality: time-energy trade-offs in pectoral sandpiper (*Calidris melanotos*) migration. Ecology 80:2566–2580.

Findlay, C. S., and F. Cooke. 1982. Breeding synchrony in the lesser snow goose (*Anser caerulescens caerulescens*). I. Genetic and environmental components of hatch date variability and their effects on hatch synchrony. Evolution 36:342–351.

Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992. Long-term changes in survival rates of lesser snow geese. Ecology 73:1346–1362.

Gauthier, G., and J. Bédard. 1985. Fat reserves and condition indices in greater snow geese. Canadian Journal of Zoology 63:331–333.

Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2001. Foraging time and dietary intake by breeding Ross's and lesser snow geese. Oecologia 127:78–86.

Guillemain, M., et al. 2013. Effects of climate change on European ducks: What do we know and what do we need to know? Wildlife Biology 19:404–419.

Harvey, J. M. 1971. Factors affecting blue goose nesting success. Canadian Journal of Zoology 49:223–234.

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

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management 66:883–900.

Holben, B. N. 1986. Characteristics of maximum-value composite images from temporal AVHRR data. International Journal of Remote Sensing 7:1417–1434.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic oscillations: regional temperatures and precipitation. Science 269:676–679.

Jones, T., and W. Cresswell. 2010. The phenology mismatch hypothesis: Are declines of migrant birds linked to uneven global climate change? Journal of Animal Ecology 79:98–108.

Jónsson, J. E., J. P. Ryder, and R. T. Alisauskas. 2013. Ross's Goose (*Chen rossii*). Account 162 *in* A. Poole, editor. The birds of North America online. http://bna.birds.cornell.edu/bna/species/162

Kerbes, R. H. 1994. Colonies and numbers of Ross's Geese and Lesser Snow Geese in the Queen Maud Gulf Migratory Bird Sanctuary. Canadian Wildlife Service Occasional Paper 81: 1–47.

Kerbes, R. H., K. M. Meeres, and R. T. Alisauskas. 2014. Surveys of nesting lesser snow geese and Ross's geese in Arctic Canada, 2002–2009. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C., USA and Ottawa, Ontario, Canada.

Keshta, N., and A. Elshorbagy. 2011. Utilizing North American regional reanalysis for modeling soil moisture and evapotranspiration in reconstructed watersheds. Physics and Chemistry of the Earth 36:31–41.

Klett, A. T., T. L. Shaffer, and D. H. Johnson. 1988. Duck nest success in the prairie pothole region. Journal of Wildlife Management 52:431–440.

Koons, D. N., G. Gunnarsson, J. A. Schmutz, and J. J. Rotella. 2014. Drivers of waterfowl population dynamics: from teal to swans. Wildfowl Special Issue 4:169–191.

Krapu, G. L., and H. A. Doty. 1979. Age-related aspects of mallard reproduction. Wildfowl 30:35–39.

Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619–636.

Lepage, D., G. Gauthier, and A. Reed. 1998. Seasonal variation in growth of greater snow goose goslings: the role of food supply. Oecologia 114:226–235.

Liebezeit, J. R., K. E. B. Gurney, M. Budde, S. Zack, and D. Ward. 2014. Phenological advancement in arctic bird species: relative importance of snow melt and ecological factors. Polar Biology 37:1309–1320.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. Circular 118. U.S. Department of Agriculture, Washington, D.C., USA.

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

McCracken, K. G., A. D. Afton, and R. T. Alisauskas. 1997. Nest morphology and body size of Ross' geese and lesser snow geese. Auk 114:610–618.

McKinnon, L., M. Picotin, E. Bolduc, C. Juillet, and J. Bêty. 2012. Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the high arctic. Canadian Journal of Zoology 90:961–971.

Menu, S., G. Gauthier, and A. Reed. 2002. Changes in survival rates and population dynamics of greater snow geese over a 30-year period: implications for hunting regulations. Journal of Applied Ecology 39:91–102.

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

Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences USA 105:16195–16200.

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

Mowbray, T. B., F. Cooke, and B. Ganter. 2000. Snow Goose (*Chen caerulescens*). Account 514 *in* A. Poole, editor. The birds of North America online. http://bna.birds.cornell.edu/bna/species/514

Owen, M., and J. M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. Journal of Animal Ecology 58:603–617.

Pianka, E. R. 1976. Natural selection of optimal reproductive tactics. American Zoologist 16:775–784.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Raveling, D. G. 1979. The annual cycle of body composition of Canada geese with special reference to control of reproduction. Auk 96:234–252.

Reed, E. T., G. Gauthier, and J.-F. Giroux. 2004. Effects of spring conditions on breeding propensity of greater snow goose females. Animal Biodiversity and Conservation 27:35–46.

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

Ricklefs, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177–201.

Rohwer, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pages 486–539 *in* B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Ross, M. V. 2016. Ecological factors affecting midcontinent light goose recruitment. Thesis. Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

Ryder, J. P. 1970. A possible factor in the evolution of clutch size in Ross's goose. Wilson Bulletin 82:4–13.

Ryder, J. P. 1971. Distribution and breeding biology of the lesser snow goose in central arctic Canada. Wildfowl 22:18–28.

Ryder, J. P. 1972. Biology of nesting Ross' geese. Ardea 60: 185–213.

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

Schmutz, J. A. 1993. Survival and pre-fledging body mass in juvenile emperor geese. Condor 95:222–225.

Sedinger, J. S. 1992. Ecology of prefledging waterfowl. Pages 109–127 *in* B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, editors. Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, Minnesota, USA.

Sedinger, J. S. 1997. Adaptations to and consequences of an herbaceous diet in grouse and waterfowl. Condor 99:314–326.

Sedinger, J. S., and N. D. Chelgren. 2007. Survival and breeding advantages of larger black brant (*Branta bernicla nigricans*) goslings: within- and among-cohort variation. Auk 124:1281–1293.

Sedinger, J. S., and P. L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. Ecology 72:496–502.

Sedinger, J. S., and D. G. Raveling. 1986. Timing of nesting by Cackling Canada Geese in relation to the quality and availability of their food plants. Journal of Animal Ecology 55:1083–1102.

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

Sinclair, A. R. E., and C. J. Krebs. 2002. Complex numerical responses to top-down and bottom-up processes in vertebrate populations. Philosophical Transactions of the Royal Society of London B 357:1221–1231.

Slattery, S. M., and R. T. Alisauskas. 2002. Use of the Barker model in an experiment examining covariate effects on first-year survival in Ross's Geese (Chen rossii): a case study. Journal of Applied Statistics 29:497–508.

Slattery, S. M., and R. T. Alisauskas. 2007. Distribution and habitat use of Ross's and lesser snow geese during late brood rearing. Journal of Wildlife Management 71:2230–2237.

Stahl, J. T., and M. K. Oli. 2006. Relative importance of avian life-history variables to population growth rate. Ecological Modelling 198:23–39.

Thompson, D. W. J., and J. M. Wallace. 2000. Annular modes in the extratropical circulation. Part I: month-to-month variability. Journal of Climate 13:1000–1016.

Tieszen, L. L. 1974. Photosynthetic competence of the subnivean vegetation of an arctic tundra. Arctic and Alpine Research 6:253–256.

Timm, D. E., and R. G. Bromley. 1976. Driving Canada Geese by helicopter. Wildlife Society Bulletin 4:180–181.

Traylor, J. J. 2010. Comparative breeding ecology in arctic-geese of different body size: an example in Ross's and lesser snow geese. Dissertation. University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

van Oudenhove, L., G. Gauthier, and J.-D. Lebreton. 2014. Year-round effects of climate on demographic parameters of an arctic-nesting goose species. Journal of Animal Ecology 83:1322–1333.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B 272:2561–2569.

Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society B 265:1867–1870.

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

Ward, D. H., J. Helmericks, J. W. Hupp, L. McManus, M. Budde, D. C. Douglas, and K. D. Tape. 2015. Multi-decadal trends in spring arrival of avian migrants to the central Arctic coast of Alaska: effects of environmental and ecological factors. Journal of Avian Biology 46:1–11.

Webb, D. R. 1987. Thermal tolerance of avian embryos: a Review. Condor 89:874–898.

Weller, M. V. 1956. A simple candler for waterfowl eggs. Journal of Wildlife Management 20:1111–1113.

Wiebe, K. L., and K. Martin. 1997. Effects of predation, body condition and temperature on incubation rhythms of white-tailed ptarmigan *Lagopus leucurus*. Wildlife Biology 3:219–227.

Williams, C. J. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687–690.

Williams, T. D., E. G. Cooch, R. L. Jefferies, and F. Cooke. 1993. Environmental degradation, food limitation and reproductive output: juvenile survival in lesser snow geese. Journal of Animal Ecology 62:766–777.

Wilson, S., and P. Arcese. 2003. El Niño drives timing of breeding but not population growth in the song sparrow *Melispiza melodia*. Proceedings of the National Academy of Sciences USA 100:11139–11142.

Wilson, S., R. T. Alisauskas, and D. K. Kellett. 2016. Factors influencing emigration of Ross's and snow geese from an arctic breeding area. Journal of Wildlife Management 80:117–126.

Wypkema, R. C. P., and C. D. Ankney. 1979. Nutrient reserve dynamics of lesser snow geese staging at James Bay, Ontario. Canadian Journal of Zoology 57:213–219.

SUPPORTING INFORMATION