Dynamics of pre-breeding nutrient reserves in subarctic staging Lesser Snow Geese (Anser caerulescens caerulescens) and Ross’s Geese (Anser rossii): implications for reproduction

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ABSTRACT. Phenological mismatch occurs when the timing of reproductive events and seasonal availability of resources become decoupled, and is increasing in migratory birds in response to climate change. Arctic-nesting geese acquire important nutrient reserves at spring-staging areas, but advancing springs, combined with large population increases and long-term goose-mediated habitat alteration, could induce a mismatch between optimal timing of nesting and accumulation of required reserves. From 2012 to 2019, we randomly sampled Lesser Snow (Anser caerulescens caerulescens) and Ross’s Geese (Anser rossii) throughout their spring migration near Churchill, Manitoba, Canada. Our objectives were to evaluate patterns of protein and lipid accumulation, and draw comparisons to historical estimates obtained before widespread habitat changes. We found significantly reduced pre-breeding protein reserves in Lesser Snow Geese relative to their historical values, but average protein reserve size increased somewhat with declining population size during the years of our study. Lesser Snow Geese catabolized lipid reserves, and no longer increased protein reserves during spring staging. Protein reserves were on average 17–23% smaller in 2012–2019 than in the 1970s, the deficit being equivalent to the amount of protein found in two to three eggs. In contrast, Ross’s Geese maintained lipid reserves, and accumulated protein during the staging period, irrespective of annual Lesser Snow Geese abundance. Based on patterns in gizzard hypertrophy, they appeared to be using a more digestible food source than were Lesser Snow Geese. Declines in protein reserves may hinder the ability for Lesser Snow Geese to keep nutritional pace with increasingly early springs, and could be an important underlying mechanism driving mismatches between vegetation phenology and emergence of goslings. Differences in recruitment between Lesser Snow Geese and Ross’s Geese could be related to differences in nutrient-reserve dynamics during the final stages of spring migration, which can carry over to influence annual breeding probability, clutch size, nest success, and likelihood of mismatch at a population level.

Dynamique des réserves nutritives pré-nidification chez les Petites Oies des neiges (Anser caerulescens caerulescens) et les Oies de Ross (Anser rossii) sur les haltes migratoires dans la région subarctique : répercussions pour la reproduction

RÉSUMÉ. Le décalage phénologique se produit lorsque les étapes de la reproduction et la disponibilité saisonnière des ressources sont désynchrонisées, et il s’accroît chez les oiseaux migrateurs en raison des changements climatiques. Les oies nichant dans l’Arctique acquièrent d’importantes réserves de nutriments sur les haltes printanières, mais les printemps de plus en plus hâtifs, combinés à une forte hausse de la population et à une détérioration de longue date de l’habitat par les oies, pourraient induire un décalage entre le moment optimal de la nidification et l’accumulation des réserves nécessaires pour celle-ci. De 2012 à 2019, nous avons échantillonné au hasard des Petites Oies des neiges (Anser caerulescens caerulescens) et des Oies de Ross (Anser rossii) au cours de leur migration printanière près de Churchill, Manitoba, Canada. Nos objectifs étaient de déterminer les patrons d’accumulation de protéines et de lipides, et de les comparer avec les données historiques récoltées avant les modifications d’habitat advenues à grande échelle. Nous avons constaté une réduction importante des réserves de protéines avant la nidification chez les Petites Oies des neiges par rapport aux valeurs historiques, mais la quantité moyenne de réserves de protéines a augmenté quelque peu suivant la diminution de la taille de la population pendant les années de notre étude. Les Petites Oies des neiges ont catabolisé les réserves lipidiques et n’ont plus accumulé de réserves protéiques pendant la halte migratoire du printemps. Les réserves protéiques étaient en moyenne de 17 à 23 % plus faibles en 2012-2019 que dans les années 1970, le déficit étant équivalent à la quantité de protéines présente dans deux à trois œufs. À l’inverse, les Oies de Ross ont maintenu des réserves lipidiques et accumulé des protéines pendant la halte migratoire, peu importe l’abondance annuelle des Petites Oies des neiges. D’après l’hypertrophie du gésier observée, les Oies de Ross semblaient utiliser une source d’aliments plus digestes que ne le faisaient les Petites Oies des neiges. La diminution des réserves de protéines affecte peut-être la capacité des Petites Oies des neiges d’acquérir leurs réserves nutritionnelles avec les printemps de plus en plus hâtifs, et pourrait être un mécanisme sous-jacent important à l’origine de la non-synchronie entre la phénologie de la végétation et l’éclosion des oisins. Les différences de recrutement entre la Petite Oie des neiges et l’Oie de Ross pourraient être liées à des différences dans la dynamique d’accumulation des réserves nutritives au cours des étapes finales de la migration printanière, qui peuvent se répercuter sur la probabilité de reproduction annuelle, la taille de la couvée, le succès de la nidification et la probabilité de décalage à l’échelle de la population.

Key Words: climate change; Lesser Snow Goose; mismatch; nutrient reserves; phenology; Ross’s Goose

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INTRODUCTION

Arctic-nesting geese face opposing selective pressures with respect to timing of reproduction. Early nesting is associated with increased breeding propensity (Reed and Giroux 2004, Madsen et al. 2007), and improved reproductive success overall (Lepage et al. 2000), but these fitness benefits accrue only if nutrient reserves are sufficient to produce a clutch of eggs, and to complete incubation. Thus, pressure to nest early is counter-balanced by time required to procure sufficient resources on staging areas. Over 1000 kilometres separate prairie and subarctic staging areas used by Midcontinent Lesser Snow Geese (*Anser caerulescens*) and Ross’s Geese (*Anser rossii*) and, in other geese, it has been shown that accurate prediction of annual phenology across such distances is unlikely (Tombre et al. 2008, Kölsch et al. 2017). Instead, fixed or seasonal cues such as photoperiod likely assist with timing large migratory movements between staging areas, and flights from the prairies to the subarctic are completed in a matter of hours or days (R. T. Alisauskas and D. K. Kellett, unpublished data). If migrating geese lack suitable cues to migrate earlier in years of early spring phenology in the Arctic, then they may have relatively little time to acquire sufficient resources necessary for optimal timing of nesting.

In temperate staging areas, Arctic geese accumulate large lipid stores by feeding on waste agricultural grain (Alisauskas et al. 1988, Alisauskas and Ankney 1992). This energetic subsidy is credited with improving survival and productivity (Alisauskas 2002), resulting in a period of rapid population growth of both Lesser Snow Geese and Ross’s Geese, which in turn has led to alteration of vast areas of coastal subarctic habitat because of foraging by large numbers of geese (Abraham and Jeffries 1997, Abraham et al. 2005). Historically, coastal wetlands of James Bay and western Hudson Bay were also important sources of spring nutrition for migrating Lesser Snow Geese and Ross’s Geese (Ankney and MacInnes 1978, Wypkema and Ankney 1979). Millions of Lesser Snow Geese and Ross’s Geese staged along a relatively narrow strip of habitat (Prevett et al. 1985, Abraham et al. 2012), feeding on emerging shoots of coastal plants that were rich in protein and highly digestible (Thomas and Prevett 1982, Alisauskas and Ankney 1992). Over several weeks, protein reserves roughly equivalent to that contained in one egg were deposited, and lipid reserves were maintained, but did not increase (Wypkema and Ankney 1979).

Although their position along the endogenous-exogenous continuum is influenced by numerous factors (i.e., migration distance, geography, weather, and body size) Arctic-nesting geese must acquire at least a portion of their nutrient reserves at spring-staging areas (Alisauskas and Ankney 1992, Alisauskas 2002), or in close proximity to nesting areas (Gauthier et al. 2003, Traylor 2010, Hobson et al. 2011, Sharp et al. 2013). Overall body mass, early spring fat reserves, and pre-breeding protein reserves are all key predictors of subsequent reproductive output in Arctic-nesting geese (Alisauskas 2002, Mainey et al. 2002, Ross et al. 2017). Acquisition of protein late in spring is particularly important because it is expended at a high rate during migration (Fowler et al. 2019), and is an important constituent in eggs (Hobson et al., 2011), but its high water content (~72%) makes it an inefficient reserve to transport over long distances. Thus, in contrast to lipid reserves, Arctic-nesting geese must replenish and store protein from natural sources on the way to nesting areas, and nearer to their Arctic-nesting destinations (Alisauskas and Ankney 1992). Sufficient protein reserves are required for recrudescence of reproductive organs in both sexes, clutch formation, and to satisfy metabolic demands during incubation, when little feeding takes place and risk of nest predation can be high (Samelius and Alisauskas 2006). In Greater Snow Geese, contributions of lipid reserves to eggs is fairly low, and Gauthier et al. (2003) pointed out that although both lipid and protein reserves contribute to reproductive output, the greater reliance on endogenous protein in egg formation (compared to fat) suggests protein is a more limiting nutrient in this species. Geese must trade off early departure from staging areas and earlier arrival on breeding grounds with time allocation toward nutrient storage, because greater reserves increase clutch potential, and improve incubation constancy and nest success (Ankney and MacInnes 1978, Traylor 2010). Ankney and MacInnes (1978) remarked that heavy reliance on protein reserves in female Lesser Snow Geese and their ability to maintain egg production despite low intake of protein was unusual, but because they are quite sedentary during incubation, breast and leg muscles are less needed for locomotion and so serve as reservoirs of protein.

Per capita production of young has declined in Lesser Snow Geese and Ross’s Geese in the central Arctic because of reduced growth and survival of goslings caused by increasing phenological mismatch between plant growth and timing of nesting (Ross et al. 2018), and because protein reserves of gravid females have declined (Ross et al. 2017). We hypothesized that similar declines in protein may be occurring in the eastern Arctic, in response to large increases in population size of Midcontinent Lesser Snow Geese and Ross’s Geese (Alisauskas et al. 2009, 2012, Canadian Wildlife Service 2019), and concomitant declines in habitat quality and availability on subarctic staging areas (Abraham and Jeffries 1997, Abraham et al. 2012). Density-dependent effects from increased feeding competition in the face of declines in suitable spring-staging habitat (Conkin and Alisauskas 2017) could result in many individuals that are either physiologically unprepared to lay or incubate their eggs, or must attempt nesting in sub-optimal condition. Such a scenario could decouple the well-known relationship between early Arctic phenology and high reproductive potential in these species (Alisauskas 2002).

Between 2012 and 2019, we obtained samples of Lesser Snow Geese and Ross’s Geese during spring staging near Churchill, Manitoba, Canada. Our objective was to draw comparisons with previous work on nutrient reserves of Lesser Snow Geese near James Bay in 1976 (near Attawapiskat, Ontario; Wypkema and Ankney 1979) and at McConnell River, Nunavut, from 1971 to 1972 (Ankney and MacInnes 1978). Large numbers of Ross’s Geese migrating through our study area, and increases in this species throughout the eastern Arctic (Caswell 2009, Alisauskas et al. 2012, Nisssley et al. 2016), prompted our interest in evaluating whether there were differences in patterns of nutrient acquisition between the two species. Traylor (2010) hypothesized that Ross’s Geese may be more resilient to habitat alteration and declines in Arctic habitat quality, because they tend to have higher reproductive rates than Lesser Snow Geese (Traylor 2010), and have colonized and rapidly increased in many parts of the eastern Arctic that were previously occupied only by Lesser Snow Geese. In addition, Abraham et al. (2005) suggested that the smaller bill size of Ross’s Geese may provide foraging advantages in areas of...
low habitat quality. Thus, we hypothesized that there could be species-specific differences in patterns of protein acquisition.

The primary objectives of this research were (1) to estimate current size of pre-breeding lipid and protein reserves of Ross's Geese and Lesser Snow Goose; (2) to determine whether Lesser Snow Goose continue to increase protein reserves during their staging period along western Hudson Bay, as they did before rapid population growth occurred (Ankney and MacInnes 1978, Wypkema and Ankney 1979); and (3) to test whether patterns in nutrient reserves of each species are linked to weather, range-wide population size, and migration phenology. Our general prediction was that Lesser Snow Goose would have smaller spring protein reserves than they did in the 1970s, and that their protein reserves would not increase throughout staging periods. In contrast, we predicted that Ross's Geese would at least maintain their nutrient reserves during the spring-staging period, considering their recent range expansion and the importance of pre-breeding nutrients in annual productivity. Additional predictions about model covariates are specified and discussed below.

METHODS

Study area
Lesser Snow Geese and Ross’s Geese were collected along the Hudson Bay coast, within 90 km of Churchill, Manitoba (Fig. 1). The coastal portion of the Hudson Bay Lowlands in northern Manitoba remains an important spring-staging area for Lesser Snow Goose and Ross's Geese. Habitat in this area includes intertidal salt marshes, and near-coastal freshwater sedge meadows. Dominant spring forage species for geese include sedges (Carex spp.), cotton grass (Eriophorum spp.), horsetail (Equisetum spp.), marsh ragwort (Tephroseris palustris), and creeping alkali grass (Puccinellia phryganodes; Prevett et al. 1985). Based on band recoveries of female Ross’s Geese and Lesser Snow Goose shot in spring near Churchill, individuals from colonies along west Hudson Bay, Southampton Island, and Baffin Island stage in the study area during spring migration (Fig. 1). Lesser Snow Goose first arrive in northwestern James Bay, Ontario, about the last week of April (Prevett et al. 1985), and near the end of the first week of May in Churchill, Manitoba (F. B. Baldwin, personal observation). By 25 May most geese have departed the Churchill area for breeding colonies in the eastern Arctic. Nest initiation by Lesser Snow Goose typically occurs about 25 May at Cape Churchill, Manitoba (R. F. Rockwell, unpublished data), between the end of May and early June at McConnell River, Nunavut (Ankney and MacInnes 1978, Caswell 2009), early to mid-June on Southampton Island, Nunavut (Nissley et al. 2016), and around mid-June on Baffin Island, Nunavut (Kerbes 1969).

Field methods
Shotguns were used to shoot birds from flocks, without using decoys. Sampled birds were placed in sealed plastic bags, labeled with collector’s name, date of collection, area of collection, species, age, and sex if known. Birds were frozen within eight hours, and shipped frozen to our laboratory in Winnipeg, Manitoba, where morphological measurements were taken and dissections were performed. Collection of birds was carried out under a scientific permit (12-MB-SC010), and followed animal-use protocol 20050054 obtained through the University of Saskatchewan Research Services and Ethics Office. We made historical comparisons with spring nutrient reserves of female Lesser Snow Goose collected in James Bay, northern Ontario (11–17 May) in 1976 (Wypkema and Ankney 1979), and in McConnell River, Nunavut (23–31 May) in 1972 (Wypkema and Ankney 1979). We restricted comparisons to females because of the known relationship between nutrient reserves and potential clutch size, which was demonstrated by Ankney and MacInnes (1978) at McConnell River, Nunavut, 1971–72. Ross's Geese were uncommon in this area in the 1970s, and so historical comparisons are limited to Lesser Snow Goose.

Laboratory methods
We confirmed species and age of all birds in the laboratory using plumage characteristics, bill shape, and foot color, and determined sex of each individual using morphology of reproductive organs observed during dissection. We measured lengths of skull (± 0.1 mm) and tarsometatarsus bone (± 0.1 mm) with dial calipers, and measured length of flattened wing (± 1.0 mm) using a ruler so that we could use these measurements to index size of each individual (Dzubin and Cooch 1992). We excised sternal muscles (pectoralis, supracoracoideus, and coracobrachialis) and leg muscles (all muscles originating or inserting on the femur or tibiotarsus) on one side (i.e., the side least damaged from collection) and weighed each (0.1 g) using a digital scale. We removed the deposit of fat extending from the abdominal wall to the gizzard (hereafter, abdominal fat), and used its mass as an index of lipid reserves (Gauthier and Bédard 1985, Fowler et al. 2018). We severed the gizzard at the proventriculus and intestine, removed its contents, and then weighed the empty gizzard (0.1 g) using a digital scale. We doubled the mass of sternal and leg muscles and added empty gizzard mass to produce a protein reserve index (PRI) for each individual. Collectively, these muscles
represent the main sources of endogenous protein in birds and their obvious origin and insertion simplifies replication. To aid in comparison with historical work, we calculated dry mass of protein by multiplying their wet mass by 0.28, which represents mass after dehydration (R.T Alisauskas and D. K. Kellett, unpublished data). We excised reproductive organs from each individual and weighed the testes, or oviduct and ovaries (0.1 g), using a digital scale. Combined mass of oviduct and intact ovaries, or testes mass, was used as a covariate in our models to account for somatic protein that may have been allocated to reproductive development. Most females were in early stages of rapid follicle development, and no oviducal eggs or post-ovulatory follicles were observed throughout the course of the study, suggesting that any depletion of protein reserves from allocation to reproductive tissues was trivial. The early stage of follicle development observed also suggested that our sample was composed not of geese nesting locally, but rather mostly of individuals destined for colonies in Nunavut, where more than 90% of Lesser Snow Geese and Ross’s Geese nest (Kerbes et al. 2014).

Hypotheses, statistics and model development
We developed a set of predictions based on biological hypotheses for each species to account for variation in protein and fat using general linear models. We considered the following explanatory variables in models within our candidate set.

Sex
Timing of development, size of reproductive organs, and protein requirements differ greatly between sexes in geese. We considered that after controlling for differences in size, males may have greater protein reserves than females, especially if females were already converting somatic protein into eggs and oviducts (which require a larger nutrient investment than testes).

Structural size
We performed a principal-components analysis from the correlation matrix of skull length, tarsal bone length, and wing chord, and used the first principal component (PC1) as a covariate to account for the effect of individuals’ structural size on their protein and lipid reserves. We conducted separate analyses for each species, but included males and females in the same analysis so that we could distinguish sex effects from structural size effects. Loadings of original variables on PC1 were 0.61, 0.57, and 0.56 for Lesser Snow Geese, and 0.60, 0.57, and 0.56 for Ross’s Geese, respectively. This similarity in loadings of original variables suggests that PC1 represented positive covariation among them and provided a useful univariate index of structural size in each species. PC1 explained 58% of total variance in morphology measured in Lesser Snow Geese, and 56% of total variance in Ross’s Geese.

Gonad mass
We included gonad mass of males (testes) and females (ovary plus oviduct) as individual covariates because somatic protein reserves can be depleted following allocation to gonad development, particularly in females. Alternatively, early development of ovarian follicles is thought to occur as nutrient reserves surpass some threshold, and protein reserves and ovary mass are positively correlated at this time of year (Wypkema and Ankney 1979).

Collection date (Julian)
We included Julian date of collection to determine whether reserves changed over the course of the staging period. In the 1970s Lesser Snow Geese accumulated protein during staging. However, we predicted that Lesser Snow Geese no longer increased their protein reserves during their subarctic staging period, in response to long-term depletion in vegetation availability in the Hudson Bay Lowlands (Kerbes et al. 1990, Jefferys et al. 2006, Abraham et al. 2012). We hypothesized that neither species would accumulate lipid reserves during this staging period, based on previous work that has shown fattening occurs on agricultural land on the prairies, although extent of lipid accumulation is annually variable (Alisauskas 2002).

Thaw index: Churchill
We used weather data from Churchill, Manitoba, collected by Environment and Climate Change Canada (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html) to create an annual thaw index for our study area. We used sum of daily mean temperatures above 0°C during 1–25 May as an index of annual spring warmth for the region from approximate annual arrival until northward departure of birds to large nesting colonies in Nunavut. The Hudson Bay Lowlands are an important staging area where protein acquisition takes place, so we hypothesized that local climate could influence protein reserves through its effects on food availability and possibly energy expenditure by geese. We reasoned that colder springs would reduce food availability or foraging efficiency of geese, and increase energetic costs; thus, we predicted a positive relationship between protein reserves and thaw index.

Population size
To index annual spring-foraging competition, we used population size estimates derived from annual band recoveries and estimates of continental harvest (Lincoln estimates; U.S. Fish and Wildlife Service 2021) for adult Midcontinent Lesser Snow Geese. We noted that continental abundance of Midcontinent Lesser Snow Geese based on Lincoln estimates decreased by 6%/year between 2010 and 2019 (U.S. Fish and Wildlife Service 2021), and hypothesized that such a decline could increase per capita food availability on subarctic staging areas during the course of our collection period. We excluded estimates of juveniles because poor survival after banding can produce estimates of their abundance that are biased high (Cooch et al. 2021), and because most juveniles do not survive through winter to undertake spring migration and contribute to competition. We also did not consider Lincoln estimates of Ross’s Geese because effects of Ross’s Geese on habitat alteration along Hudson Bay are less clear than for Lesser Snow Geese. As well, a large proportion of the population nests in the central Arctic, and a large fraction of their continental population likely does not use our study area during spring migration, instead migrating inland from prairie Canada to the central Arctic. We included additive effects of population size for Lesser Snow Geese adults in Ross’s Goose models because we hypothesized that there is some foraging competition between the two species, and so nutrient reserves in Ross’s Geese could be influenced by these changes in overall abundance of light geese on staging areas.
Year
We included linear effects of year in candidate model sets for each species to permit comparison with models that included population size. In separate models, we also included year as a categorical factor, because previous work demonstrated considerable year-to-year variation in nutrient reserves, but especially lipids (Alisauskas 2002). We also included an interaction between Year (factor) and Collection Date (Julian) to investigate whether nutrient reserves were stored at different rates in different years.

We used Pearson correlations to evaluate collinearity among explanatory variables. Population Size and Year (linear; \( r = -0.86, p < 0.001 \)) were strongly correlated. For Lesser Snow Geese, Collection Date and Thaw Index \( (r = 0.27, p < 0.001) \), Population Size and Gonad \( (r = 0.13, P < 0.05) \), and Population Size and Thaw Index \( (r = 0.30, P < 0.001) \) were correlated and not used in the same models. For Ross’s Geese, Collection Date and Thaw Index \( (r = 0.35, P < 0.001) \) and Population Size and Thaw Index \( (r = 0.19, P < 0.01) \) were correlated and not used in the same models.

We developed separate candidate model sets to explain variation in protein and lipid reserves for each species. We developed hypotheses a priori and used the information-theoretic approach (Burnham and Anderson 2002) and AICc to select among multiple competing models. We used a similar modelling approach for each species, wherein we constructed global models which included all uncorrelated variables, and then constructed progressively simpler models, or replaced explanatory variables that were correlated to check for substantive improvements in AICc. In addition, we checked for uninformative parameters by reviewing whether additional model parameters improved fit sufficiently to result in reduced AICc (Arnold 2010). All analyses were conducted using R, Version 3.5.1.

We used two-sample t-tests to compare our data (2012–2019) with summarized protein reserves from female Lesser Snow Goose collected at arrival in James Bay, Ontario (198.0 g, SD = 12.21, \( n = 19 \); Wypkema and Ankney 1979) and arrival to McConnell River, Nunavut (227.8, SD = 22.96, \( n = 78 \); Wypkema and Ankney 1979).

Based on preliminary results obtained during modeling of protein reserves, we used a single linear model with the explanatory variables sex, structural size, and collection date (Julian) to evaluate temporal changes in gizzard mass (dry) in each species. Changes in gizzard mass, which are positively related to feeding activity (Ankney 1977), could mask declines in leg and breast muscle mass during the staging period, because the reserve index is a composite of all of these tissues. We also compared estimates of gizzard mass (dry) to data in Ankney (1977) using two-sample t-tests.

RESULTS
Our analysis of protein and lipids included 260 adult Lesser Snow Geese (128 males, 132 females) and 204 adult Ross’s Geese (110 males, 94 females), which were collected over eight consecutive years (2012–2019). We removed a single outlier from the sample of Lesser Snow Geese, based on the assumption that this extremely large individual was a Greater Snow Goose (Chen caerulescens atlanticus). Geese were collected across an average range of 11.0 days (Lesser Snow Geese) and 8.4 days (Ross’s Geese) per year over the course of our study.

Protein reserves
Lesser Snow Geese
We considered 15 models in our evaluation of protein-reserve dynamics in staging Lesser Snow Geese, and the confidence set included three models (Table 1), and accounted for all of the model weight. The top model explained 46% of variation in protein reserves of Lesser Snow Geese and included the additive effects of sex, structural size, and a linear trend in year. Even after controlling for differences in structural size, males carried larger reserves than females (\( \beta = 5.53, 95\% \text{ CI: } 1.14, 9.92; \text{ Fig. 2} \)). There was evidence that protein reserves in Lesser Snow Geese increased over the years of study (\( \beta = 2.16 \text{ g/y}, 95\% \text{ CI: } 1.19, 3.12; \text{ Fig. 2} \)), but not over collection periods within years. Larger geese carried greater protein reserves (\( \beta = 8.11, 95\% \text{ CI: } 6.44, 9.78 \)), and there was no change in body size of either sex over the study (linear regression of sex-specific body size [PC1] and year; males: \( \beta = 0.07, 95\% \text{ CI: } -0.04, 0.18 \); females: \( \beta = -0.01, 95\% \text{ CI: } -0.10, 0.09 \)) or by collection date (linear regression of sex specific body size [PC1] and collection date; males: \( \beta = -0.01, 95\% \text{ CI: } -0.05, 0.04 \); females: \( \beta = -0.02, 95\% \text{ CI: } -0.05, 0.02 \)). There was no support for year-to-year variation in protein reserves or influence of the thaw index, and we found no evidence for significant conversion of somatic protein to gonads, because inclusion of this covariate did not improve model fit. Models with Year (linear) were favored by > 4 AIC units over those with estimates of Population Size (Table 1), but the two variables are highly correlated, thus the apparent effect of year may in part reflect changes in abundance.

Table 1. Model selection for protein reserve levels in Lesser Snow Geese (Anser caerulescens caerulescens) collected near Churchill, Manitoba, from 2012 to 2019. Shown are models with a \( \Delta \text{ AICc} < 6.0 \), the null model, Akaike information criterion difference corrected for small samples size (\( \Delta \text{ AICc} \)), the number of estimable parameters (\( K \)), the log-likelihood (LL), the model weights (\( \omega_i \)), and the proportion of variance explained (\( R^2 \)). AICc value for the best model is 2134.43.

<table>
<thead>
<tr>
<th>Model</th>
<th>( K )</th>
<th>LL</th>
<th>( R^2 )</th>
<th>( \Delta \text{ AICc} )</th>
<th>( \omega_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex + Size + Year (linear)</td>
<td>5</td>
<td>-1062.1</td>
<td>0.46</td>
<td>0.00</td>
<td>0.80</td>
</tr>
<tr>
<td>Sex + Size + Pop Size</td>
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<td>0.45</td>
<td>4.13</td>
<td>0.10</td>
</tr>
<tr>
<td>Sex + Size + Collection Date + Pop Size</td>
<td>6</td>
<td>-1063.21</td>
<td>0.46</td>
<td>4.32</td>
<td>0.09</td>
</tr>
<tr>
<td>Intercept only (null)</td>
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<td>-1144.1</td>
<td>0.00</td>
<td>157.82</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Protein reserves at Churchill, Manitoba (2012–2019) were smaller than historical estimates from both James Bay, Ontario (\( T = 6.01, P < 0.001, df = 151 \), and McConnell River, Nunavut (\( T = 19.68, P < 0.001, df = 210 \). Protein reserves from 2012–2019 were, on average, 17% smaller than in James Bay, Ontario, in 1976, and 23% smaller than in McConnell River, Nunavut, in 1972 (Fig. 3).

Ross’s Geese
We considered 14 models in our evaluation of protein-reserve dynamics in staging Ross’s Geese, and the confidence set (< 6 AICc units) included seven models (Table 2). Two models from
Table 2. Model selection for protein reserve levels in Ross’s Geese (*Anser rossii*) collected near Churchill, Manitoba, from 2012 to 2019. Shown are models with a Δ AICc < 6.0, the null model, Akaike information criterion difference corrected for small samples size (Δ AICc), the number of estimable parameters (K), the log-likelihood (LL), the model weights (ω), and the proportion of variance explained (R²). AICc value for the best model is 1495.79.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>LL</th>
<th>R²</th>
<th>Δ AICc</th>
<th>ω</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex + Size + Collection Date + Year (factor) + Gonad</td>
<td>13</td>
<td>-733.94</td>
<td>0.48</td>
<td>0.00</td>
<td>0.44</td>
</tr>
<tr>
<td>Sex + Size + Collection Date + Year (factor)</td>
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<td>0.48</td>
<td>0.23</td>
<td>0.39</td>
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<tr>
<td>Sex + Size + Collection Date + Year (linear) + Gonad</td>
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<td>-743.15</td>
<td>0.45</td>
<td>5.08</td>
<td>0.03</td>
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<tr>
<td>Sex + Size + Collection Date + Gonad</td>
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<td>0.45</td>
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<td>0.03</td>
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<tr>
<td>Sex + Size + Collection Date + Year (linear)</td>
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<td>5.36</td>
<td>0.03</td>
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<td>5.55</td>
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</table>

Fig. 2. Relationship between the protein reserve index (g) of female and male Lesser Snow Geese (*Anser caerulescens caerulescens*) and year (linear). Shown is the model-predicted line for females (left) and males (right) adjusted for the influence of structural size, and the 95% confidence interval (shaded). Relative body size values represent the mean ± 1 SD of PC1.

Fig. 3. Estimates of the protein reserve index (g) and 95% confidence interval for female Lesser Snow Geese (*Anser caerulescens caerulescens*) collected during their spring-staging period at Churchill, Manitoba, James Bay, Ontario, and McConnell River, Nunavut. Estimates are colored according to the location and time period of collection, and potential clutch size (estimated by counting the number of developed and post-ovulatory follicles; Ankney and MacInnes 1978). The sample size for each period is indicated beside the point estimate.

the candidate set accounted for 83% of the model weight, and the top model explained 48% of the variation in protein reserves in Ross’s Geese (Table 2). Similar to Lesser Snow Geese, males carried larger protein reserves than females relative to their size ($\beta = 3.44$, 95% CI: 0.11, 6.77), and there was a positive relationship between protein levels and structural size ($\beta = 5.07$, 95% CI: 3.79, 6.34). In contrast to Lesser Snow Geese, year-to-year variation in protein reserves was evident in Ross’s Geese. There was no influence of population size on protein reserves. The top model
included the covariate gonad size, but it was only marginally supported, improving fit 0.23 units, but having an insignificant slope ($\beta = 0.33$, 95% CI: -0.09, 0.41). In contrast to Lesser Snow Geese, there was a positive relationship between protein reserves and collection date ($\beta = 0.66$ g/d, 95% CI: 0.18, 1.14; Fig. 4). Models with collection date were favored over those with thaw index which was an unimportant covariate.

Fig. 4. Relationship between the protein reserve index (g) of female and male Ross’s Geese (Anser rossii) and collection date (Julian). Shown is the model-predicted line for females (left) and males (right) adjusted for the influence of structural size (colors), and the 95% confidence interval (shaded band). Relative body size values represent the mean ± 1 SD of PC1.

Gizzard mass in Ross’s Geese and Lesser Snow Geese

Because protein reserves increased with date of collection in Ross’s Geese, but not Lesser Snow Geese, we were interested to know if there was a similar relationship between gizzard mass and collection date between species. Contrary to our expectation, we found that gizzard size increased with date of collection in Lesser Snow Geese ($\beta = 0.33$ g/d, 95% CI: 0.21, 0.45), but not in Ross’s Geese ($\beta = 0.01$ g/d, 95% CI: -0.09, 0.13; Fig. 5). Importantly, there was no significant relationship between gizzard mass and structural size in either Lesser Snow Geese ($r^2 = 0.09$, $P = 0.13$) or Ross’s Geese ($r^2 = 0.03$, $P = 0.64$), and body size did not change over the course of the study in males ($r^2 = 0.03$, $P = 0.79$) or females ($r^2 = 0.05$, $P = 0.66$). Mean gizzard mass in male Lesser Snow Geese near departure from Churchill (after 20 May) was substantially lower ($T = -5.86$, $P < 0.001$, $df = 84$) in our study (28.60 g, 95% CI: 27.40, 29.80) compared to that in birds at arrival (23–31 May) to McConnell River, Nunavut, 1971–72 (34.1 g, 95% CI: 32.73, 35.47; Ankney 1977). Separate estimates of gizzard mass from Lesser Snow Geese staging in Ontario are not available in the literature. Rather, they are included with leg and breast muscle as part of the overall protein reserve index (Wypkema and Ankney 1979).

Lipid reserves

Lesser Snow Geese

We considered nine models in our evaluation of lipid-reserve dynamics in staging Lesser Snow Geese, but only two models were included in the confidence set (< 6 AICc units; Table 3). The best model explained 16% of variation in lipid reserves, and accounted for 92% of the model weight (Table 3). Size of lipid reserves varied by year, sex (smaller reserves in males; $\beta = -15.80$, 95% CI: -24.11, -7.49), structural size (larger birds had larger lipid reserves; $\beta = 4.01$, 95% CI: 0.80, 7.23), and collection date (declining lipid reserves through time, Fig. 6; $\beta = -1.17$ g/d, 95% CI: -2.03, -0.31). There was no support for the influence of thaw index, or size of gonads. Collection date influenced lipid mass, but even after controlling for this effect, we found strong support for inclusion of a categorical year effect. This suggests the presence of interannual variation (Fig. 7) in lipids arising from
some factor not accounted for in our modeling. In addition, the low proportion of variance explained by the top model suggested that considerable individual variation because of unmeasured factors, e.g., individual energy balance.

**Table 3.** Model selection for lipid reserve levels in Lesser Snow Geese (Anser caerulescens caerulescens) collected near Churchill, Manitoba, from 2012 to 2019. Shown are models with a Δ AICc < 6.0, the null model, Akaike information criterion difference corrected for small samples size (Δ AICc), the number of estimable parameters (K), the log-likelihood (LL), the model weights (ω), and the proportion of variance explained (R²). AICc value for the best model is 2464.88.

<table>
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<tr>
<th>Model</th>
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<th>LL</th>
<th>R²</th>
<th>Δ AICc</th>
<th>ω</th>
</tr>
</thead>
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</tr>
<tr>
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<td>35.11</td>
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</tbody>
</table>

**Fig. 6.** Relationship between lipid reserves (g) of female and male Lesser Snow Geese (Anser caerulescens caerulescens) and collection date (Julian). Shown is the model-predicted line for females (left) and males (right) for an average year, adjusted for the influence of structural size, and the 95% confidence interval (shaded band). Relative body size values represent the mean ± 1 SD of PC1.

**Fig. 7.** Annual variation in lipid reserves (g) and the associated 95% confidence interval in average-sized female and male Lesser Snow Geese (Anser caerulescens caerulescens), adjusted for the collection date (Julian). Values for collection date (Julian) represent the mean ± 1 SD of PC1.

**Ross’s Geese**
We considered eight models evaluating lipid reserve dynamics in Ross’s Geese, but only two models were included in the confidence set (< 6 AICc units), with the best model explaining 15% of the variation in lipid reserves, and accounting for 88% of the model weight (Table 4). Lipid reserves varied by year; males had smaller lipid reserves than females (β = -11.49, 95% CI: -18.68, -4.30), and larger birds had larger lipid reserves (β = 3.48, 95% CI: 0.64, 6.32). There was limited support for increasing lipid reserves during spring staging. This covariate was included in our top model; however, variability was high (β = 0.35 g/day, 95% CI: -0.72, 1.42; Fig. 8). There was no support for influence of thaw index or gonad mass.

**DISCUSSION**
Proper nutrition and storage of fat and protein in late spring have long been recognized as important determinants of the production of young by Midcontinent Lesser Snow Geese and Ross’s Geese (Ryder 1970, Ankney and MacInnes 1978, Alisauskas 2002). Per capita production of young geese at nesting colonies in the Central Arctic (Karrak Lake; Fig. 1) from 1992 to 2014 was linked to annual variation in both fat and protein reserves of females arriving to breed in both Lesser Snow Geese and Ross’s Geese (Ross et al. 2017). These authors hypothesized
Table 4. Model selection for lipid reserve levels in Ross’s Geese (Anser rossii) collected near Churchill, Manitoba, from 2012 to 2019. Shown are models with a $\Delta$ AICc < 6.0, the null model, Akaike information criterion difference corrected for small samples size ($\Delta$ AICc), the number of estimable parameters ($K$), the log-likelihood (LL), the model weights ($\omega_i$), and the proportion of variance explained ($R^2$). AICc value for the best model is 1826.37.

<table>
<thead>
<tr>
<th>Model</th>
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<th>LL</th>
<th>$R^2$</th>
<th>$\Delta$ AICc</th>
<th>$\omega$</th>
</tr>
</thead>
<tbody>
<tr>
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</tr>
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</table>

Fig. 8. Annual variation in lipid reserves (g) and the associated 95% confidence interval in average-sized female and male Ross’s Geese (Anser rossii), adjusted for the collection date (Julian). Values for collection date (Julian) represent the mean ± 1 SD.

that nutrient deficits had increased more recently from density-dependent effects at staging areas north of the Canadian prairies. Our results support this hypothesis, although we found differing patterns of lipid and protein deposition between Lesser Snow Geese and Ross’s Geese. Lesser Snow Geese appeared to catabolize lipids during spring staging, and only maintained protein reserves, whereas nutrient dynamics in Ross’s Geese mirrored that of Lesser Snow Geese in the 1970s. Ross’s Geese were able to maintain or even increase lipid reserves, and they increased their protein reserves during subarctic staging by an amount similar to subarctic-staging Lesser Snow Geese in the 1970s (7% increase; Wypkema and Ankney 1979). Lipid reserves in both species varied annually, perhaps in response to conditions on the Canadian prairies, where annual rates of lipid accumulation can be highly variable and can explain substantial variation in subsequent continental production of young (Alisauskas 2002). Additionally, variation in hunting-related disturbance is thought to influence spring-body condition in Greater Snow Geese (LeTourneux et al. 2021), and may also contribute to such annual variation in lipid reserves in Lesser Snow Geese and Ross’s Geese.

We were unable to compare lipid reserves to estimates from the historical literature because of differences in the calculation of lipid index, but long-term comparisons were possible for protein reserves. We found evidence of significant declines in pre-breeding protein reserves of Lesser Snow Geese in the subarctic between the 1970s and 2010s, an area where they historically acquired over 60% of protein required for reproduction (Abraham et al. 2012). Protein reserves were 17–23% smaller in our study than in the 1970s at James Bay and McConnell River, respectively. And, in contrast to the earlier studies, we observed no increases in protein during the staging period. The estimated protein deficit represented the approximate amount found in two to three Lesser Snow Goose eggs (Wypkema and Ankney 1979), and the approximately 52-g difference in dry protein between the two time periods represents approximately 186 g of body mass. Although decreases in body size of Lesser Snow Geese were documented by Cooch et al. (1991; 1969–1990) and Alisauskas (2002; 1983–1993), Traylor’s (2010) analyses of size changes of breeding birds between 1991 and 2008 were inconclusive, and no change in body size of either species occurred during this study (2012–2019).

Spring-foraging activities by increasing numbers of geese have reduced forage-plant biomass, changes in soil salinity and plant community structure, and, in some cases, have resulted in complete removal of vegetation and exposure of peat and underlying sediments (Abraham et al. 2012). We believe that the reductions in protein reserves observed in this study are related to changes in coastal habitats along James Bay, and western Hudson Bay, which have been driven by large increases in goose populations (Abraham et al. 2012, Alisauskas et al. 2012). As of the late 1990s, up to 65% of intertidal salt marsh between James Bay and southern Nunavut was considered unproductive (Abraham and Jefferies 1997), and yet use of these habitats by large numbers of staging geese has continued since then. Although inland freshwater habitats in these areas are more extensive and apparently more intact, they are largely snow-covered or frozen during spring migration, and so foraging opportunities are often unavailable there during spring staging.

Half of spring diets of Lesser Snow Geese formerly consisted of portions of newly sprouted shoots, with 21% of the spring diet
composed of *P. phryganodes*, a highly digestible coastal grass (Prevett et al. 1985). *P. phryganodes* was very abundant historically on coastal brackish marshes in the James Bay area in the late 1970s, accounting for 65% of the average mass of vegetation in plots (Prevett et al. 1985), but has since declined markedly; graminoid cover in one area of the Hudson Bay Lowlands declined by 46% between 1976 and 2010 (Peterson et al. 2013). Declines have also been documented farther north on Southampton Island, Nunavut, where this important forage species has essentially disappeared from many areas, and only accounted for more than 1% of cover on two of eight vegetation transects sampled in 2010 (Abraham et al. 2020). We found gizzard mass in Lesser Snow Geese increased dramatically during spring staging, but remained substantially lower than that observed only several calendar days later in spring at McConnell River, Nunavut, 1971–72. Smaller contemporary gizzard size may reflect reduced spring feeding opportunities in the Hudson Bay lowlands, perhaps because of changes in vegetation composition or abundance. Geese may be adjusting their length of stay in response to local feeding opportunities, perhaps spending less time in James Bay than they did historically, or even arriving farther north on the Hudson Bay coast in spring, in response to habitat alteration.

### Implications for population biology and conservation

In order to optimally time nest initiation in the face of advancing spring phenology, Lesser Snow Geese and Ross’s Geese must also modify schedules of nutrient storage by either increasing their rate of protein storage, or by initiating protein storage earlier in migration. Our research demonstrates that in the case of Lesser Snow Geese, neither has occurred, and pre-breeding protein reserves have declined markedly compared to earlier studies. Phenological mismatch occurs when timing of reproductive events and seasonal availability of resources become decoupled, and is increasing in frequency in populations of migratory birds in response to climate change (Dickey et al. 2008, Both et al. 2009, Ockendon et al. 2014). In Arctic-nesting geese, timing of hatch and seasonal peaks in forage abundance and nutritional quality are increasingly mismatched, because advances in nest initiation and gosling hatch have not kept pace with advancing vegetation phenology (Ward et al. 2005, Ross et al. 2017). Adverse effects on nest success and gosling survival have been well documented across populations of Arctic-nesting geese (Brook et al. 2015, Doiron et al. 2015, Ross et al. 2018), but reduced protein reserves may predispose individuals to a novel type of mismatch, which occurs well in advance of nesting, with unstudied implications for population-level breeding propensity.

Long-distance Arctic migrants are particularly susceptible to scheduling errors in migration timing because their Arctic breeding grounds are warming at a greater rate than are temperate wintering areas, and there is no consistent correlation in seasonal cues when the distance between these areas is great (Tombre et al. 2008, Nolet et al. 2019). Mismatches can result from missed or inappropriate interpretation of cues during spring migration, but they can also occur through intrinsic limitations. In the case of Arctic-nesting geese, intrinsic cues such as photoperiod and body condition may constrain timing of ovarian follicle development (Bluhm 1992), and location and rate of pre-breeding nutrient acquisition may be relatively inflexible because of specific forage requirements. Thus, physiological and environmental limitations impede advancement of breeding schedules in Lesser Snow Geese and Ross’s Geese, and this is likely most apparent in the Arctic where the rate of climatic change is greatest (Serreze and Francis 2006). We propose two hypotheses to explain differences in nutrient dynamics between these sympatric species.

### Constraints on the timing and location of protein acquisition

High energetic costs of carrying protein reserves suggests that there are advantages to delaying protein acquisition until late in spring migration, i.e., in the subarctic. Nevertheless, individuals must optimize arrival on staging areas to match timing of favourable foraging conditions; otherwise, they risk catabolizing lipid reserves while attempting to accumulate protein reserves. In addition, schedules for nutrient accumulation are likely constrained by strong selective pressure to arrive on the breeding grounds early, motivating migration ahead of full snowmelt before spring green-up, and peak nutrition of vegetation. Ross et al. (2017) found that clutch sizes in Lesser Snow Geese and Ross’s Geese were reduced in years of earliest nesting, and suggested that this effect could be related to individuals leaving northern staging areas before they have stored optimum levels of nutrient reserves. We found no evidence that protein reserves were influenced by phenology of vernal melt (i.e., our annual thaw index) in either species, perhaps because weather on subarctic staging areas is not predictable from temperate spring-staging areas farther south. If migration schedules to subarctic areas are driven largely by formerly adaptive endogenous cues (e.g., day length), these may impede responses to advances in phenology, thereby reducing time available for replenishing reserves. Ross’s Geese currently show greater nest success (Kellett and Alisauskas 2019), and higher recruitment of young relative to Lesser Snow Geese (Ross et al. 2017). The superior ability of Ross’s Geese to maintain or increase lipid and protein reserves during the spring-staging period could be an important additional factor that explains the reproductive resiliency to late springs which have been observed in Ross’s Geese (Traylor 2010).

### Declines in per capita availability and nutritional quality of subarctic vegetation

Although Lesser Snow Geese increased rapidly in abundance throughout the 1990s until the mid-2000s, the Midcontinent population has since declined considerably to levels of the late 1990s (Cooch et al. 2021), when special measures were enacted to reduce the population. Despite unprecedented regulatory changes designed to increase kill by hunters, population declines were unrelated to harvest or other forms of mortality (Alisauskas et al. 2011, Calvert et al. 2017), and are instead thought to be associated with declines in production (Calvert et al. 2017), driven by increasing frequency of phenological mismatches, and reduced nutrient reserves (Ross et al. 2017). We found that pre-breeding protein reserves of Lesser Snow Geese increased annually during our study, concomitant with their recently declining population size. We interpret this recent increase in protein reserves as support for a density-dependent response to reduced per capita foraging competition. Although Lesser Snow Geese did not increase protein reserves during spring staging in the subarctic, perhaps there was a carry-over effect from reduced competition in previous...
seasons. We found opposite patterns in gizzard hypertrophy between species, and hypothesize that Lesser Snow Geese used more fibrous, less nutritious foods than Ross’s Geese because, despite increases in gizzard mass through the spring-staging period, their protein reserves did not increase (Kehoe et al. 1988). Ross’s Geese require absolutely fewer nutrients to satisfy metabolic demands in comparison to Lesser Snow Geese, and possess a bill morphology better adapted to exploit higher-quality forage such as remnant swards of *P. phryganodes*.

**CONCLUSION**

Arctic-nesting geese have evolved life-history attributes adaptive for coping with effects of unpredictable spring-weather conditions. Among these adaptations, stored energy reserves have been particularly important in the long-term growth of these populations, in addition to enhanced adult survival. However, recent declines in productivity of both species have been associated with reduced pre-breeding protein reserves as well as phenological mismatch (Ross et al. 2017). Our study suggests that inadequate protein reserves may be widespread in Lesser Snow Geese, because our collected specimens were obtained within several weeks of nesting, and represent a random sample of birds from colonies across the eastern Arctic. Although protein reserves in Lesser Snow Geese may have increased slightly in response to recent population declines, Lesser Snow Geese still face a large protein deficit relative to levels four to five decades previously. Attempted protein storage in subarctic staging areas appears to involve lipid catabolism (in Lesser Snow Geese), perhaps through elevated energy expenditure associated with extra foraging effort. Alternatively, the origin of oxaloacetate (required for lipid catabolism; Hanson 1962) may have shifted away from exogenous sources, and might be increasingly derived from protein reserves instead (Ankney 1977). Declines in protein reserves relative to historic levels may reflect an inability for geese to keep nutritional pace with increasingly earlier springs, and, later in the annual cycle, could contribute to mismatches between vegetation phenology and emergence of goslings, with negative effects on gosling survival and per capita production of young geese (Ross et al. 2017, 2018).

Agricultural subsidies in temperate regions of North America released populations of Lesser Snow Geese and Ross’s Geese from historical constraints of population growth, but our study suggests that northern staging habitats remain an important energetic bottleneck for proper nutritional conditioning by these populations, likely because these habitats provide no anthropogenic nutritional replacement. Differences in recruitment between Lesser Snow Geese and Ross’s Geese could be related ultimately to differences in nutrient-reserve dynamics during the final stages of spring migration, which can carry over to influence annual breeding probability, clutch size, nest success, and likelihood of mismatch at a population level. A key uncertainty remains whether nutritional deficits can be reversed, or compensated for, through feeding opportunities farther north by changes in the summer distribution of these geese. Future research should aim to resolve this important question.

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