Migration, phénologie de la nidification et succès reproducteur d'un migrateur de longue distance : la grande oie des neiges dans un environnement en changement

Thèse

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Résumé

Le moment optimal de nidification est crucial au succès reproducteur des oiseaux nichant à de hautes latitudes. Toutefois, plusieurs migrateurs de longue distance ne réussissent pas à ajuster la phénologie de leur reproduction au réchauffement climatique sur leur aire de reproduction. Un délai dans leur reproduction pourrait résulter en un décalage entre la période optimale de disponibilité de nourriture et l'éclosion des jeunes, réduisant leur croissance et leurs chances de survie. Ma thèse vise à évaluer les effets des changements environnementaux sur les patrons saisonniers du succès reproducteur de la grande oie des neiges (*Chen caerulescens atlantica*), une espèce migratrice arctique. Nous avons utilisé une base de données à long terme récoltée sur une période de plus de 25 ans sur l'île de Bylot (1991–2015) dans le Haut-Arctique canadien. Nous avons défini le succès reproducteur comme étant le nombre de jeunes survivant jusqu'à l'âge de 1 an. Nous avons étudié des changements temporels dans la date de ponte et six composantes du succès reproducteur à travers la saison de reproduction. La taille de ponte, le succès de nidification, la survie des œufs, le succès à l'éclosion, la survie pré-envol et la survie des jeunes ont été évalués en fonction de la phénologie de la reproduction, l'année et l'interaction de ces deux facteurs. Ces résultats ont été intégrés pour estimer les changements saisonniers dans le succès reproducteur global et pour évaluer les conséquences des décisions de nidification relatives à la taille et à la date de ponte. De plus, nous avons examiné si une vitesse de changement de température plus lente aux sites de haltes migratoires pouvait expliquer l'absence de réponse de la phénologie de la reproduction des oies au réchauffement climatique sur les aires de nidification. Globalement, les changements temporels dans les patrons saisonniers de la date de ponte et des composants du succès reproducteur ont été de d'ampleur et de direction différentes, particulièrement en ce qui concerne les nids initiés hâtivement et tardivement en saison. Le déclin saisonnier dans la taille de ponte a diminué dans le temps, le succès de nidification était le plus faible chez les nicheurs hâtifs et tardifs, mais s'est accru dans le temps, et la survie post-éclosion a décliné dans le temps avec les survies les plus élevées obtenues par les nicheurs les plus hâtifs. Les effets cumulatifs des changements environnementaux sur les différentes composantes ont résulté en un déclin saisonnier plus marqué du succès reproducteur avec le temps. Nous avons aussi trouvé que la date de ponte présentant le plus fort succès reproducteur survient avant la médiane de ponte de la population, mais que cette date s'est décalée vers les nicheurs les plus hâtifs tout au long de l'étude. Finalement, le taux de réchauffement a été plus élevé sous les hautes latitudes que dans les haltes migratoires tempérées des oies des neiges. La faible corrélation dans les températures rencontrées entre les haltes migratoires successives suggère que l'oie n'arrive pas à anticiper quelles seront les conditions environnementales au moment de la ponte sur l'aire de reproduction. Cette étude contribue à démontrer comment la vitesse de changement des températures rencontrée sur les routes migratoires peut représenter une contrainte importante pour l'ajustement de la date de ponte chez les migrateurs de longue distance, et les conséquences à long terme des changements environnementaux induites par le réchauffement. Nos résultats suggèrent que la pression de sélection en faveur des nicheurs les plus hâtifs va s'intensifier avec l'augmentation du réchauffement, mais que les oies pourraient être incapables d'ajuster leur phénologie reproductive, menant à un plus grand décalage trophique ayant des conséquences négatives sur la population entière.

Abstract

Optimal timing of nesting is key for the reproductive success of birds breeding at high latitudes. However, many long-distance migratory birds fail to adjust their breeding phenology to climate warming on their breeding ground. Delays in nesting may result in a trophic mismatch between the period of peak food availability and offspring hatch, reducing their growth and survival. My thesis aims to evaluate the effects of a changing environment on the seasonal patterns of reproductive success of the greater snow goose (*Chen caerulescens atlantica*), an arctic migrant species. We used a long-term dataset collected over a 25-year period on Bylot Island (1991–2015) in the Canadian High Arctic. We defined reproductive success as the number of young surviving to 1-year of age. We investigated temporal changes in laying date across the breeding season, as well as in six reproductive success components. Total clutch laid, nesting success, egg survival, hatching success and pre- and postfledging survival were examined in relation to timing of breeding, year and their interaction. These results were integrated to estimate seasonal changes in the overall reproductive success and to evaluate the consequences of breeding decisions regarding clutch size and laying dates. Additionally, we examined if a slower rate of temperature change at southern staging sites could explain the lack of response of the breeding phenology of geese to warming on its breeding ground. Overall, temporal changes in the seasonal patterns of laying date and reproductive success components were of different magnitude and directions, mainly in nests initiated the earliest and latest in the season. Seasonal decline in clutch size weakened over time, nesting success was lowest in early and late nests but increased over time and posthatch survival declined over time with the highest survival achieved in early nests. The cumulative effects of environmental changes on individual components resulted in a steeper seasonal decline in reproductive success over time. We also found that the laying date yielding the highest reproductive success occurs before the median laying date of the population, but shifted towards earlier breeders over the course of the study. Lastly, warming rates were stronger at high latitudes than at the temperate staging area of snow geese. The low association in temperature encountered between successive staging areas suggests that geese cannot anticipate in advance what will be the environmental conditions at laying time on the breeding site. This study contributes to demonstrate how the rate of temperature change encountered along the migratory route can be an important constraint for laying date adjustment in long-distance migrants, and the consequences of long-term environmental changes induced by warming. Our results suggest that selection pressure for early breeding will intensify as warming increases but that geese may be unable to adjust their breeding phenology, leading to a greater trophic mismatch with negative consequences on the entire population.

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To Moritz and Moka, coauthors of my life

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Foreword

My thesis comprises five sections describing my work on the greater snow goose. I first present a general introduction, followed by three chapters corresponding to scientific papers that include the research conducted during my doctoral studies. These studies will be published in scientific journals. I finish by presenting a general conclusion. While all these chapters are written in English, each scientific paper includes an abstract in the French language. Below, I provide some details on the scientific papers, henceforth referred to as chapters 1, 2 and 3:

Chapter 1: **Consequences of a changing environment on the breeding phenology and reproductive success components in a long-distance migratory bird**. This manuscript was published on February 21, 2020 by the journal Population Ecology. Gilles Gauthier and Guillaume Souchay are coauthors of this scientific paper.

Chapter 2: **Temporal changes in reproductive success and optimal breeding decisions in a long-distance migratory bird**. This manuscript is in preparation and requires prior acceptance of chapter 1 in a scientific journal before submission. Gilles Gauthier is coauthor of this scientific paper.

Chapter 3: **Can spring migrants anticipate conditions at sites further north from those encountered along the way? The case of the greater snow goose.** This manuscript is in preparation. Gilles Gauthier is coauthor of this scientific paper.

This thesis is an original work. I wrote the research proposal, the manuscripts and the content of this document. I participated in data collection on Bylot Island during four summers (2013–2016), cleansing and validation of the complete dataset (25 years), and performed the statistical analyses. Gilles Gauthier, my thesis director, was actively involved in all of these stages, including the original conceptual ideas, advice during the field work and data analysis and corrections and edits of various versions of the manuscripts. Joël Bêty and Jean-Pierre Tremblay were part of my doctoral committee and provided advice on the theoretical concepts, hypotheses formulation and general orientation of the thesis. Guillaume Souchay assisted me with the capture-recapture analyses in E-SURGE and provided comments on the manuscript presented in chapter 1.

Data from 1991 to 2012 was collected by different teams of postgraduate students and field technicians. Monitoring protocols were originally designed by my thesis director, Gilles Gauthier. Marie-Christine Cadieux managed and maintained the long-term dataset. Fieldwork was carried out following all applicable institutional and/or national guidelines for the care and use of animals, and the field protocols were approved by the Animal Care Committee of Université Laval. All field research was also conducted with appropriate licenses issued by Parks Canada.

General introduction

Reproductive success and reproductive strategies

Reproductive success and offspring survival play a key role in the maintenance of animal populations (Clutton-Brock 1988). The definition of a successful reproductive event varies in avian studies. It can be quantified as the number of offspring produced at hatching (Anderson et al. 2014), at fledging **(**Sikamäki 1998**)**, at one year of age (Brown and Brown 1988), or when offspring recruit into the breeding population (Lok et al. 2017). Reproductive success can be used as an indicator of individual fitness or to measure offspring production in populations. In this thesis, we define reproductive success as the number of offspring surviving to 1-year-old produced by an individual during a breeding season (Lepage et al. 2000).

Reproduction is a large energy investment, but not all attempts are successful. A successful reproduction in birds would require the survival of offspring from egg-laying until at least a stage when young achieve some independence from the parents. Over the course of a season, breeding birds are exposed to variable conditions that may influence differently various stages of the reproductive cycle (Öberg et al. 2014). In some environments, reproductive success follows seasonal patterns according to resources availability (Norris 1993, Verhulst et al. 1995, Sikamäki 1998). The number of offspring produced may also fluctuate from year to year in response to several intrinsic and extrinsic factors. Environmental conditions encountered by parents before a breeding attempt and by parents and offspring during breeding can both influence reproductive success (Meltofte et al. 2007).

Prior to reproduction and during egg-laying, potential breeders often need to attain a minimum threshold of body condition to start egg production (Perrins 1970, Sikamäki 1998). The degree to which birds rely on body reserves for egg production varies among species. At one end of a continuum, capital breeders rely heavily on energy reserves stored prior to a reproductive event, whereas at the other end income breeders produce eggs largely from local resources acquired during a reproductive event (Drent and Daan 1980). In birds, a pure capital or income breeding strategy is very rare. Common eiders (*Somateria mollissima*) were considered pure capital breeders in the past (Drent and Daan 1980) but in recent years tracking of nutrient sources with isotopic techniques revealed that they actually combine both strategies (Sénéchal et al. 2011). In contrast, at the other end of the continuum, an example of an almost pure income breeder is the American redstart (*Setophaga ruticilla*; Langin et al. 2006). Most avian species use intermediate strategies combining to various degrees the capital and income breeding strategies.

Later in the reproductive cycle, newly-hatched chicks must have access to abundant and high-quality food resources to obtain specific nutrients required to gain mass and grow feathers. Adequate development and growth will allow them to become independent at an optimal time and improve their chances of survival. Weather may influence both parents and young, but offspring are more vulnerable to climatic variability throughout the breeding season. During incubation, embryos can only survive within a specific thermal range and may die when exposed to extreme cold or warm temperatures (Arnold 1993, Bernsten and Bech 2016). Weather can also have a strong influence on food availability for chicks, especially in insectivorous and herbivorous birds, and thus indirectly determine their growth and ultimately their survival (Lindholm et al. 1994, Siikamäki 1998). Young birds are also more vulnerable than adults to direct exposure to extreme weather conditions because of their smaller size and immature development (Newton 1989). Severe cold weather may reduce offspring survival and even lead to widespread breeding failure (Ganter and Boyd 2000).

Species have developed strategies to cope with variable environmental conditions in order to maximize their reproductive success. Organisms may respond to environmental variability through phenotypic plasticity, which is the ability of an organism to express different phenotypes according to different environmental conditions (see Pigliucci 2001). Some species may show extensive plasticity in their phenotype, which may result in behavioral, morphological or physiological changes, or a combination of them. These responses occur within a range of possible phenotypic expressions included in the genotype of an individual. The response may be short-term and specific to conditions experienced by an individual in any given year, and may thus differ between years. The different phenotypes expressed in different environments are called reaction norms (Stearns 1992). This phenotypic plasticity allows breeding birds to advance or delay laying date, or adjust the number of eggs to lay, arguably their two most important reproductive decisions, according to prevailing environmental conditions. This ability to adjust to environmental variability is especially important for migratory birds because they use different habitats during their life-cycle, and breed in seasonal environments where timing of breeding plays a major role in their reproductive success (Perrins 1970, Verlhulst and Nilsson 2008).

Laying date and clutch size are linked and both will influence the reproductive outcome. When energy stores acquired by individuals for breeding are adequate, they can determine the energy that can be allocated to egg production and when to start laying. Clutch size sets the upper limit of the number of potential offspring for a given reproductive attempt. Reaction norms predict that in seasonal ecosystems, late breeders should have a lower clutch size than birds nesting earlier (Klomp 1970). Rowe et al. (1994) proposed a model that provides a unifying framework to explain seasonal variation in clutch size and laying date in relation to body condition and environmental conditions. The model is based on phenotypic plasticity and reaction norms expressed in variable environments. According to the model, individuals will exhibit different combinations of clutch size and laying date to maximize their reproductive success under specific conditions. Due to time constraints, reproductive success declines over the season, which may force individuals not able to initiate laying early enough to trade-off additional eggs in their clutch for an earlier hatching to improve success. Rowe et al. (1994) model, which is very general, potentially applies to many groups of birds and support for it has been found in geese (Bêty et al. 2003) and common eiders (Descamps et al. 2011)

Time constraints in long-distance migrants

Migration allows birds to exploit predictable food resources seasonally available across different latitudes (Alerstam et al. 2003, Shaffer et al. 2006). Migration may also confer additional benefits, such as breeding in environments with a low risk of nest predation (McKinnon et al. 2010). Migratory movements are usually timed to match seasonal patterns of resources availability in specific areas. In some species, these movements imply long-distance migration, where individuals move thousands of kilometers between their wintering and breeding grounds. Since their life-cycle is often a complex succession of multiple events, to make this possible they must be at the right time and right place for each of these events. Spring migration is especially important in the life cycle of birds because it is the prelude to the upcoming reproductive event. Migration is energetically costly and exposes birds to numerous hazards along the way. For instance, adverse weather can slow down or delay migration, increase energetic cost and in the worst case increase mortality risk (Newton 2007). To endure the journey, most long-distance migrants need to stop at staging areas to refuel and store energy to complete the next leg of the migration and eventually arrive on the breeding ground in good body condition. However, some staging areas may also be challenging for migrant birds and expose them to predators or competitors for food resources (Newton 2007).

Multiple factors control the life cycle of birds, including endogenous mechanisms. These internal mechanisms, which are under hormonal control, respond to change in day-length (i.e. photoperiod) and trigger several annual events in the life cycle. In long-distance migratory birds, change in photoperiod regulates the onset of migration (Gwinner 1996, Both and Visser 2001). Once the migration has started, environmental cues encountered along the route can provide additional information to individuals to adjust their length of stay at staging areas and when it is time move to the next one. Environmental cues may become increasingly important compared to photoperiod as birds approach their breeding grounds. Among these cues, food availability is particularly relevant during spring migration, because it will determine feeding conditions at staging areas and ultimately the total amount of body stores individuals can acquire for the next migration leg. Refueling conditions encountered at staging areas can thus have a strong influence on migratory decisions and speed, and ultimately on arrival time on the breeding ground, with possible carry-over effects on the subsequent reproduction (Studds and Marra 2005, Legagneux et al. 2012, Harrison et al. 2013). Timing and speed of migration are important because arriving too early or too late to a staging area or the breeding ground entails a cost (Sergio et al. 2014). An early arrival to staging areas may expose birds to extreme weather, low temperatures and lack of food resources. On the contrary, late migrants may arrive to these areas when resources are depleted by earlier migrants.

Temperature is another important environmental factor during migration. Temperature has a strong influence on food availability through its effects on vegetation greening and insect emergence, and thus can indirectly control migration speed (Tøttrup et al. 2010, Ovaskainen et al. 2013, Haest et al. 2018). In herbivores, feeding opportunities will be strongly affected by plant phenology, which is closely related to temperature. Herbivorous birds travel across a latitudinal gradient in the timing of spring onset, as temperature triggers plant growth at different times depending of latitude, creating a 'green wave' of successive peaks of food availability for migrating birds (Drent et al. 1978). According to this theory, nutritive quality of plants peaks sequentially with latitude, which provides a continuum of suitable foraging conditions at successive staging areas. Recent studies with individually radio-tracked geese confirmed that some populations, mostly grazers, follow the 'green wave' of food availability (Van Wijk et al. 2012, but see Wang et al. 2019). Individuals that time their migration to successfully ride on this 'green wave' should arrive on the breeding ground in optimal body condition and at the right time to maximize their reproductive success.

Breeding decisions in highly seasonal environments

The first reproductive decision taken by an individual is to breed or not in a given year (i.e. breeding propensity). This decision will be based on a combination of intrinsic and extrinsec factors experienced by each individual prior to and at arrival to the breeding ground. Temperature is a major driver of avian reproductive phenology and can act both directly and indirectly on individuals (Dunn 2004). In boreal and arctic environments, temperature regulates the timing of snowmelt, which in turn determines the start of the growing season. Snowmelt also provides access to nesting areas and food, with the potential of delaying or advancing the breeding season for birds. Temperature can also play a role during incubation by influencing the behavior of brooding parents, which in turn can increase vulnerability of nests to predation (Conway and Martin 2000). Seasonality increases with latitude and the length of the growing season becomes progressively shorter at higher latitudes. In the arctic tundra, harsh and long winters with cold temperatures contrast with the short but productive summer season that is used by many migratory species for breeding. During the summer, the tundra provides offspring with long feeding hours and high quality food that allow them to grow fast. However, these food resources peak during a brief period after which they can decline rapidly. Decisions made early in the reproductive season, at laying time, can thus influence the synchrony between offspring and their food.

Weather and resources availability in the Arctic may also fluctuate significantly from one year to the next and can be subject to extremes. To succeed in these environments, organisms linked by trophic interactions should respond adequately to these fluctuations. For long-distance migratory birds, this means they should be able to adjust their breeding phenology to environmental conditions encountered at arrival on the breeding ground to ensure optimal growing conditions for their offspring. Indeed, because the energetic demand of offspring is high, they must have access to the best food resources possible in order to grow and develop fast before the end of the short arctic summer. In seasonal environments, offspring that are in synchrony with the period of high food availability grow faster and have higher survival than those hatched too early or too late in the season (Verhulst and Nilson 2008, Doiron et al. 2015, Figure 1.a). For insectivorous migratory birds breeding in temperate forests, such as great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*), their reproductive success is dependent on a good synchrony between hatching time of their offspring and the short peak of caterpillar abundance. Likewise, caterpillars hatching time should coincide with the newly emerged leaves of trees. Timing is important because caterpillars are only available for birds while they are feeding on leaves, before pupation.

In migratory herbivores like geese, high plant nutritive quality in the form of nitrogen content is essential to maximize offspring growth and survival (Mattson 1980). In order to maximize their protein intake, geese must have access to highly nutritious plants. However, in environments like the arctic tundra, abundance and quality of food resources follow different trajectories over the growing season. Plants abundance gradually increase after the snowmelt, and peaks in mid-summer but nutritive quality of plants peaks soon after the onset of plant growth and gradually declines throughout the summer (Doiron et al. 2013). Synchronizing the period of high energy demand of goslings with the peak in nitrogen concentration allows them to grow fast and enhances their survival. Because this peak occurs early in the summer, goslings hatched early typically have a better growth than those hatched later in the season (Lindholm et al. 1994, Lepage et al. 1998). Yet, regardless of the food resources consumed by birds breeding in seasonal environments (i.e. insects or plants), failure to match the timing of chick hatch with the period of highest food availability may result in a trophic mismatch leading to negative consequences such as reduced growth (McKinnon et al. 2012, Doiron et al. 2015).

As early hatching of chicks is essential to maximize reproductive success in seasonal environments, delays in nest initiation can be costly in terms of offspring survival. The mechanism of trading-off additional eggs for an earlier hatching date (using the model from Rowe et al. 1994) can be used to adjust breeding phenology to environmental variability. This is because offspring from eggs laid early in the season will hatch early and match better the peak in food availability than those from eggs laid later in the season. As egg-value decreases over the season due to declining food availability, initiating incubation with a lower clutch size early in the season may lead to higher offspring survival than delaying the onset of incubation by a few days to lay more eggs. Thus, the number of surviving offspring from a large brood hatched late in the season could be equal to or even lower than those surviving from a smaller brood hatched earlier (Lepage et al. 2000).

Climate change effects on bird reproduction

Although migratory birds have some mechanisms to cope with environmental variability, temperature has considerably increased at a global scale in recent decades due to climate change. Evidence shows that warming trends vary greatly across regions, being stronger at high latitudes than at low latitudes (IPCC 2014, Francis et al. 2017). Uneven temperature change across latitudes may thus be a factor preventing migratory birds from anticipating warmer temperatures at their breeding grounds when they depart from wintering sites and during migration. In this thesis, temperature is therefore considered a constrain to the ability of birds to anticipate changing temperature conditions on their breeding grounds while they are still at more southern locations. Climatic models predict that warming will continue to increase in the next decades, particularly at high latitudes. Moreover, the rate of temporal and spatial warming also varies between seasons, with some seasons warming more than others (Ovaskainen et al. 2013). Heterogeneous warming has led to different responses among populations of the same species, such as in great tits and blue tits (*Cyanistes caeruleus*; Visser et al. 2003). This occurred because populations responded to local warming rates on their respective breeding grounds during prelaying and breeding periods. Across trophic levels, responses to warming also differ and may disrupt the trophic dynamics of the entire community (Voigt et al. 2003, Both et al. 2009, Ovaskainen et al. 2013). Organisms at lower trophic levels typically adjust faster to warming than those at higher levels (Voigt et al. 2003, Both et al. 2009, Post et al. 2009, Ovaskainen et al. 2013). For instance, in the boreal forest, caterpillars have shown a stronger response to warming temperature than birds (Visser et al. 2006, Both et al. 2009). Weak responses in the breeding phenology of these birds may result in a trophic mismatch between offspring and the peak food availability (Both et al. 2009, McKinnon et al. 2012, Doiron et al 2015, Figure 1.b).

Responses of migratory birds to warming may include changes in geographical distribution, behavior or diet, but the most common response found is phenological change (Post et al. 2009, Ovaskainen et al. 2013, Dunn and Møller 2014). Adjustments at the population level in response to climate change can be detected with long-term monitoring data, which is available for many temperate species, especially in passerines. Some studies suggest that short-distance migratory birds have shown stronger responses to warming than long-distance migrants (Both et al. 2010). However, most of these phenological adjustments have been insufficient to match the magnitude of environmental change experienced by populations breeding in seasonal environments (Both et al. 2009, McKinnon et al. 2012). An advancement of laying date of 10 days was documented in a pied flycatcher population of the Netherlands, but this was not enough to match the advancement of caterpillar emergence, which was greater, leading to a decline in reproductive success and an increase in selection for earlier laying (Both and Visser 2001). Similar evidence of increased selection for early laying was also found in populations of great tits in the Netherlands (Visser et al. 1998, Gienapp et al. 2006) and the United Kingdom (Charmantier et al. 2008). These adjustments in laying date in response to environmental change have been possible through individual phenotypic plasticity (Charmantier et al. 2008, Gienapp et al. 2008). This mechanism accounts for most of the documented responses to climate change possibly due to the lack of more detailed studies in wild populations at the genetic level (but see Berteaux et al. 2004 for mammals).

Negative consequences of climate change are exacerbated in long-distance migrants because the start of migration is largely determined by photoperiod, whereas stopovers located at higher latitudes are likely warming at a faster rate than their wintering areas. Temperature warming of different magnitude between successive stopovers increases the risk of mismatch between timing of migration and of food availability at those sites (Both and te Marvelde

2007). Moreover, interactions of climate change with human-transformed landscapes may intensify the impacts of climate warming on migratory species. For instance, the interaction between habitat fragmentation and warming has had a negative effect on the number of young produced in the indigo bunting (*Passerina cyanea*) and the Acadian flycatcher (*Empidonax virescens*, Cox et al. 2013). In the Arctic, plant phenology is sensitive to temperature increase and early snowmelt, and is advancing with warming. When migratory birds like geese arrive, it may already be too late to synchronize the hatch of their offspring with peak food availability. Some populations of long-distance migratory birds have even remained unresponsive to warming temperatures as they did not show any change in migration speed, arrival time or breeding phenology (Visser et al. 1998, Both and Visser 2001, Møller et al. 2008, Post et al. 2009). Failure to adjust to warming temperatures may reduce reproductive success and ultimately population size (Both et al. 2006, Møller et al. 2008).

The greater snow goose: an arctic breeder in a changing environment

The greater snow goose (*Chen caerulescens atlantica*) is a long-distance arctic migrant that winters on the Atlantic coast of the United States and breeds in the eastern Canadian High Arctic. During the spring migration, birds stage for several weeks in the St. Lawrence valley area in Quebec, Canada, their most important and longest stopover (Gauthier et al. 2005). Moving northwards they have a few more, but brief, stops in Nunavik (LeHenaff et al. 1995) and in Baffin Island (Matt Evans, pers. comm.), before they reach their arctic breeding grounds. Young and adults are strict herbivores, but for gosling growth it is critical to have access to plants with high nitrogen content, which are available for only a short period of time during the summer (Lepage et al. 1998, Doiron et al. 2015). They nest colonially in the tundra and typically lay 2–7 eggs in a single nesting attempt per season. Egg production relies on a mix of capital/income resources and a large proportion of nutrients invested in the eggs is acquired by feeding during the prelaying period on the breeding ground (Gauthier and Tardif 1991, Gauthier 1993, Gauthier et al. 2003). Predation by arctic foxes (*Vulpes lagopus*) is the main cause of nest failure, accounting for the largest losses of eggs and young. Avian predators also contribute to egg and young losses, mostly through partial predation of nests (Bêty et al. 2001, Lecomte et al. 2008).

This species has been the focus of a long-term study since 1989 at its main breeding colony on Bylot Island. Breeding activity, from laying to hatching, is monitored annually on a sample of several hundred nests. Several thousands adults and young are also marked during mass-banding drives every year in late summer. Lepage et al. (2000) unveiled the seasonal patterns of six components of reproductive success in the early years of this long-term study, using data from 1991 to 1997. This study found a seasonal decline in the components clutch size, prefledging survival and postfledging survival, which, once combined, resulted in a strong seasonal decline in overall reproductive success. The analysis of Lepage et al. (2000) showed that early breeders performed better than those breeding late (i.e. after the median population date), except for the few birds breeding earliest. They also showed that greater snow geese may trade-off a lower clutch size for earlier laying to maintain or increase reproductive success, in accordance with Rowe et al. (1994) model. The high success of early breeders is due to a good match between the period of high nutrient demand of goslings and the brief peak in food quality, measured by the plant nitrogen content (Lepage et al. 1998). This was further tested in a supplementary food experiment in which goslings receiving a high quality supplement grew faster and became heavier than unsupplemented goslings feeding on natural food (Lindholm et al. 1994). Recently, Doiron et al. (2015) demonstrated that warm temperature in spring increases the mismatch between gosling hatch and the peak in nutritive quality of food, leading to reduced growth and body mass of goslings near fledging. This is because in years with warm spring temperature and early snowmelt, the peak in nutritive quality of food occurs too early with respect to the period of gosling hatch. Consequently, in those years goslings are exposed to food of deteriorating quality throughout their growing period.

From 1989 to 2011, Bylot Island experienced a strong warming trend with an increase of 2.8°C in spring and summer temperatures (Gauthier et al. 2013). Despite this warming trend, the mean laying date of geese remained unchanged (Gauthier et al. 2013), increasing the potential for trophic mismatch between goslings and their food (Doiron et al. 2013, Doiron et al. 2015). This may suggest changes in the seasonal pattern of variations of individual components and of the overall reproductive success previously documented by Lepage et al. (2000).

Thesis objectives and structure

This study uses the greater snow goose breeding in the Canadian Arctic as a model. Nonetheless, the results presented in this thesis are relevant to understanding the potential effects of climate change on the reproductive success of many other long-distance migratory birds, and especially those breeding in the Arctic. My analysis covers a 25-year period, which is still a relatively short period on an evolutionary time scale considering that geese are long-lived; this corresponds to about 4 generations as generation time is about 6 years in the species (Gauthier and Lebreton 2004). For my work, I used data and previous knowledge from one of the most complete long-term population studies of arctic geese available.

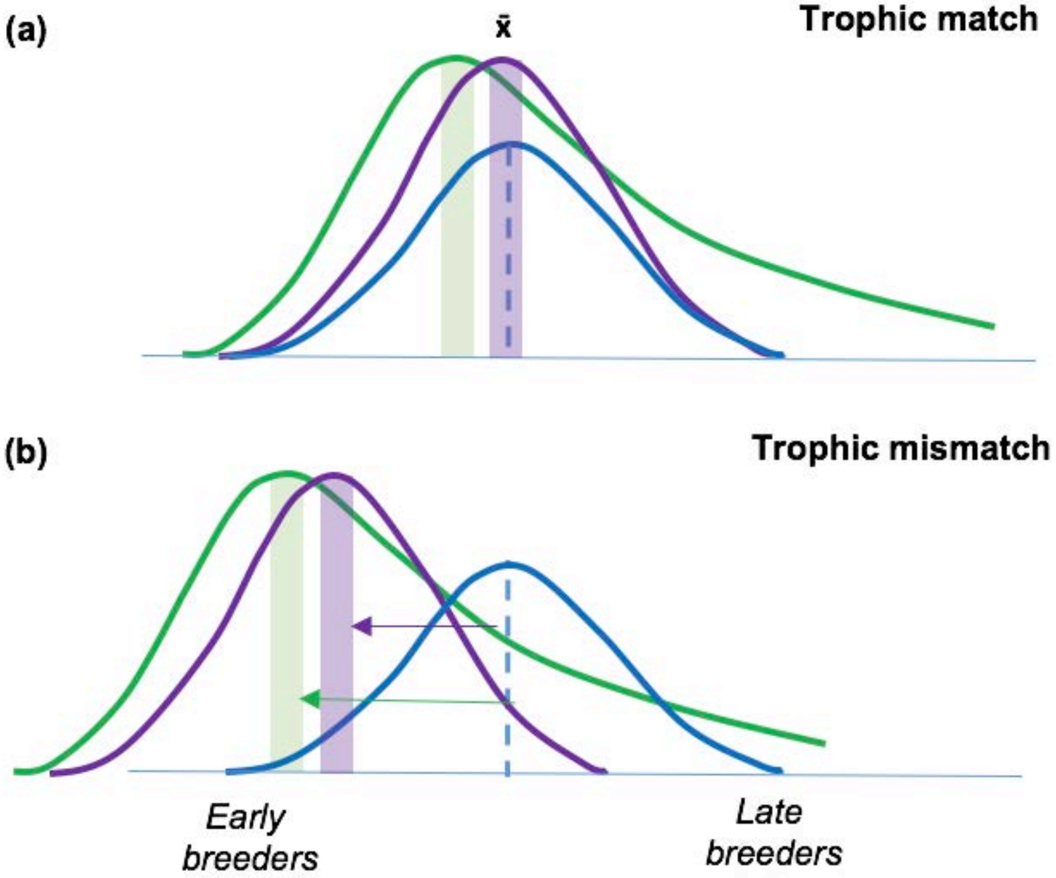
The main objective of this thesis was to evaluate the effects of a changing environment on the seasonal variations in reproductive success of the greater snow goose. In doing so, I expanded the results of Lepage et al. (2000) by adding a multi-year dimension to their seasonal analysis of reproductive success in the context of a changing environment. For this thesis, I analyzed greater snow goose reproductive data collected on Bylot Island over the period 1991 to 2015. Based on previous studies in this population, I made a series of predictions on possible long-term effects of a changing environment on specific components of the reproductive success of this population, from the number of eggs laid by the female to the first-year survival of offspring. I also investigated how environmental conditions encountered during the migration could be used as a cue to adjust migration speed and timing to optimize arrival date and reproductive success in a changing environment. In this analysis, I used temperature as a proxy of environmental conditions encountered along the migration. Chapters 1 to 3 present the results of this thesis in details.

Chapter 1 describes temporal changes in the relationships between individual components of the reproductive success (total clutch laid, nesting success, egg survival, hatch success, prefledging survival and postfledging survival) and laying date. These reproductive components comprise the reproductive season occurring in the High Arctic and the subsequent survival of young up to 1-year old. This chapter also provides insights on temporal changes in intra-seasonal variations of laying date from the earliest to the latest breeders in the population.

Chapter 2 integrates the results from the different reproductive components analyzed in chapter 1 to estimate the temporal changes in overall reproductive success in relation to laying date. This information was used to identify temporal changes in the date of the highest reproductive success compared to the median laying date of the population. Using a hypothetical clutch size over the range of 2 to 6 eggs, this chapter also evaluates how the consequences of breeding decisions (i.e. laying date) on the expected reproductive success changed over the course of this study.

Chapter 3 investigates how temperature encountered by geese at various migratory stopovers in spring can help them to anticipate conditions further north and adjust their migration speed and arrival time on the breeding ground. This chapter also examines if temperature experienced at various stopover during the spring migration can have a carry-over effect on laying date in the Arctic in addition to temperature encountered at arrival on the breeding site.

Figure 1 Trophic match **(a)** and mismatch **(b)** between offspring hatching time (blue solid line; population mean represented by the dashed line) and food availability. Seasonal variation in food abundance (e.g. insects) is represented by the purple line and seasonal variation in nutritive quality of plants is represented by the green line. Shading area represents the peak in either food abundance or quality. Arrows represent the advancement of the peak in food abundance or food quality in warm years, leading to a trophic mismatch with the offspring hatching time.



Chapter 1. Consequences of a changing environment on the breeding phenology and reproductive success components in a long-distance migratory bird

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1.1 Résumé

Les oiseaux migrateurs ont une fenêtre de temps limitée pour se reproduire, particulièrement dans l'Arctique, où les individus nichant plus tôt ont le meilleur succès reproducteur. Nous avons évalué les changements temporels (1991-2015) des composantes du succès reproducteur en lien avec le moment de la reproduction chez les grandes oies des neiges (*Chen caerulescens atlantica*). Cette espèce se reproduit dans l'Arctique canadien, une région ayant connu une forte tendance au réchauffement. Nous avons testé l'effet de la date de ponte ou d'éclosion, de l'année et leur interaction sur six composantes reproductives : taille de ponte totale, succès de nidification, survie des œufs, succès d'éclosion, survie pré- et post-envol. Sur une période de 25 ans, la date de ponte moyenne a peu changé, même si elle a avancé de 1.8 jour chez les oies se reproduisant tôt en saison et a été retardée de 3 jours chez les individus se reproduisant tard en saison. De même, le nombre d'œufs dans les nids initiés tôt en saison a diminué de 0.6 œuf, tandis que pour les nids tardifs, il a augmenté de 0.3 œuf. Le succès des nids initiés tôt et tard dans la saison a été inférieur à celui des nids initiés près de la moyenne de la population et a augmenté de façon constante au fil du temps. La proportion d'œufs survivant à la prédation partielle et la survie post-envol ont diminué avec la date de ponte mais le patron n'a pas changé au fil du temps. En revanche, la survie pré-envol n'était pas affectée au départ par la date de ponte, mais a diminué pour les nids initiés tard dans la saison vers la fin de l'étude. Dans l'ensemble, les nids initiés près de la moyenne de la population ont montré peu de changement temporel pour la plupart des composantes du succès reproducteur et semblent moins affectés par les changements environnementaux que les nids initiés tôt et tard en saison.

Mots clés : *Chen caerulescens atlantica*, survie des oisons, grande oie des neiges, date de ponte, moment de la reproduction

1.2 Abstract

Migratory birds have a narrow time window to breed, especially in the Arctic, where early nesting typically yields the highest reproductive success. We assessed temporal changes (1991–2015) in reproductive success components in relation to timing of breeding in greater snow geese (*Chen caerulescens atlantica*). This species breeds in the Canadian Arctic, a region that has experienced a strong warming trend. We tested the effect of laying or hatching date, year and their interaction on six reproductive components: Total clutch laid, nesting success, egg survival, hatching success, prefledging, and postfledging survival. Over 25 years, mean laying date changed little, even though it advanced 1.8 days in early breeders and was delayed 3 days in late breeders. Likewise, the number of eggs in nests initiated early in the season decreased by 0.6 egg, whereas in late nests it increased by 0.3 egg. Success of nests initiated early and late in the season was lower than nests initiated near the population mean, and consistently increased over time. The proportion of eggs surviving to partial predation and postfledging survival decreased with laying date but the pattern did not change over time. In contrast, prefledging survival was not affected by laying date initially but declined in nests initiated late in the season toward the end of the study period. Overall, nests initiated close to the population mean showed little temporal change for most components of reproductive success and seem to be less affected by environmental change than nests initiated early and late in the season.

Keywords: *Chen caerulescens atlantica*, gosling survival, greater snow goose, laying date, timing of breeding

1.3 Introduction

Time is a major constraint on the reproductive success of migratory birds, particularly in highly seasonal environments (Perrins 1970, Verhulst and Nilsson 2008). In those environments, optimal reproductive conditions usually deteriorate over the season and exhibit high inter-annual variability (Meltofte et al. 2007). Typically, early breeders have a larger clutch size and achieve a higher reproductive success (i.e. number of surviving young) than late breeders (Lepage et al. 2000, Naef-Daenzer et al. 2001, Weiser et al. 2018), partly due to a seasonal decline in offspring value (Lepage et al. 1999, Bêty et al. 2003, Descamps et al. 2011). Migratory birds that evolved in seasonal environments should adjust their annual reproductive phenology to local weather and food availability to maximize reproductive success (Bêty et al. 2003, Meltofte et al. 2007, Descamps et al. 2011). At the same time, some aspects of their annual routine, such as migration, are regulated by endocrine mechanisms usually triggered by photoperiod, which may limit their ability to adjust to local conditions (Gwinner 1996, Visser et al. 2004).

Climate change may disrupt ecological processes and species interactions in seasonal environments, including phenology (Visser et al. 2004, Post et al. 2009). Species responses to climate warming are variable, but phenological adjustments have often been documented (Høye et al. 2007, Post et al. 2009, Ovaskainen et al. 2013, Dunn and Møller 2014). Many bird populations have advanced their laying date in response to warmer spring temperatures, although their response is often insufficient to match the magnitude of climatic warming (Visser et al. 2004). Migratory birds breeding in the Arctic may be especially vulnerable to those changes because climate warming is more pronounced at high latitudes than at their stopovers or wintering grounds located at lower latitudes (Clausen and Clausen 2013). The predicted rate of temperature change in those environments may exceed the natural variability experienced by migratory birds as well as their capacity to adjust (Lameris et al. 2018). Failure of individuals to adequately adjust their phenology to those changes may lessen their reproductive success and ultimately reduce their population size (Both et al. 2006, Møller et al. 2008, Ross et al. 2017). Late breeders generally have the lowest reproductive success and could be the most affected by warming temperatures (Cooke et al. 1984, Lepage et al. 2000, Weiser et al. 2018).

From the egg-laying to young surviving at 1 year of age, reproductive success can be decomposed into several successive components (Etterson et al. 2011). Each component will contribute differently to overall reproductive success (Lepage et al. 2000, Öberg et al. 2014), and can be uniquely influenced by climatic conditions (Dickey et al. 2008). For instance, early in the reproductive season warm temperature can enhance food availability for egg-laying females, increase clutch size (Winkel and Hudde 1997, Dunn and Møller 2014), and reduce embryo mortality (Arnold 1993). In contrast, warm and sunny conditions can decrease water availability for incubating females, modifying their behavior during incubation recesses and increasing egg predation risk (Lecomte et al. 2009). Warm spring temperatures can also accelerate plant phenology and seasonal decline in plant nutrient content (Doiron et al. 2014), thereby causing a mismatch between the peak food quality and the hatching date of young herbivores, reducing subsequent juvenile growth and survival (Brook et al. 2015, Doiron et al. 2015, Lameris et al. 2018).

As climate warming accelerates, it is critical to identify and predict its effects, especially on migratory birds breeding at high latitudes (Both and te Marvelde, 2007, Miller-Rushing et al. 2008, Both et al. 2010). Although phenological adjustments in response to warming have been documented in some populations (Høye et al. 2007, Gunnarsson and Tómasson 2011, Ovaskainen et al. 2013, Lameris et al. 2018), others have apparently been unresponsive to those changes (Miller-Rushing et al. 2008, Møller et al. 2008, Dunn and Møller 2014, Ross et al. 2017). The greater snow goose (*Chen caerulescens atlantica*), a long-distance migrant breeding in the High Arctic, is a prominent example of a species with constant mean laying date despite a warming trend on its breeding ground (Gauthier et al. 2013). Studies on this species documented a strong seasonal decline in reproductive success (Lepage et al. 2000, Bêty et al. 2004). This, combined with climate warming and the lack of long-term changes in laying date, creates a strong potential for trophic mismatch and negative effects on reproduction (Doiron et al. 2015).

In this study, we assessed temporal variations in reproductive success components in the greater snow goose in relation to timing of breeding. First, we examined temporal changes in nesting synchrony and shape of the laying date distribution. Second, we investigated changes over time in the seasonal patterns of reproductive success components previously reported in this population (Lepage et al. 2000). Research conducted over the past 25 years had documented the influence of several local and regional environmental factors on various reproductive components in this population. We used this knowledge to generate a series of predictions regarding expected changes in the seasonal patterns of reproductive success components over time in response to climate warming (Table 1.1).

1.4 Methods

1.4.1. Study species and study area

The greater snow goose is a migratory waterfowl that winters in the East Coast of the United States and breeds across the Eastern Canadian High Arctic during the summer. Females rely on a mixed capital/income breeding strategy, as a large proportion of nutrients used for egg-production come from arctic food sources (Gauthier et al. 2003). Females initiate a single nest per year soon after snowmelt with a high degree of synchrony among individuals and do not renest after a failure (Lepage et al. 2000). Predation by artic foxes (*Vulpes lagopus*) and avian predators is the main cause of egg losses and nesting failure (Bêty et al. 2001). Goslings are precocial and leave the nest 24 hr after hatch. Young and adults are herbivorous, feeding mostly grasses and sedges (Manseau and Gauthier 1993). Geese are hunted in spring and fall during the stopover in southern Canada, and in winter in the United States.

Our study site is located on the south plain of Bylot Island, Canada (73°N, 80°W), where ca. 20,000 pairs breed each year (Reed et al. 2002). The landscape is composed of low hills with gentle slopes and lowlands dominated by mesic tundra. Wetlands associated with ponds and tundra polygons are also abundant in lowlands (Massé et al. 2001). Common plants in wetlands are grasses (*Dupontia fisheri*), sedges (*Eriophorum scheuchzeri*, *Carex aquatilis*) and mosses. Most birds nest in a main colony located in the central portion of the south plain but some individuals also nest in a disperse fashion across the island. After hatching, goose families disperse up to 30 km from the main nesting colony to brood-rearing areas with a high density of wetlands (Mainguy et al. 2006).

1.4.2. Field methods

The reproductive activity of this population has been studied annually since 1989. For this study, we used data for the period 1991–2015, when monitoring has been most complete. Intensive nest searches were conducted throughout the laying and incubation periods to ensure that both early and late nests were found. We monitored several hundred nests each year (range: 130–493) but sampling schemes used to find nests varied among years (Annex S1.1). In monitored nests, we marked each egg with a felt-tip pen and recorded number of eggs and nest stage (laying or incubation). Nests were revisited once or twice during incubation to record the number of eggs still present, at hatch when goslings were web-tagged and shortly after hatch to determine that goslings had left the nest. For monitored nests that could not be revisited at hatch, the presence of membranes was used as an indicator of a successful hatching during a subsequent visit. For each nest, laying date was estimated as the date when the first egg was laid, based on the number of eggs present and stage (i.e. laying or incubation) at which it was found (Lepage et al. 1999, Annex S1.2). Hatching date of a brood was the date when at least half of the goslings hatched. Relative laying date and relative hatch date (henceforth referred to as "relative dates") were estimated for each nest as a deviation from the annual median date.

To estimate prefledging and postfledging survival of young, we captured families of parents with their young in mass banding drives. Several hundred birds were captured at a time, when adults were molting and flightless and goslings were ~35-day-old, about 1 week before fledging (see Menu et al. 2001 for details). All birds (adults and young) were banded with a metal band and some adult females received a neck collar. All goslings were sexed by cloacal examination and about half of them were weighed and measured (culmen, tarsus, ninth primary wing feather, and head length). Previously banded birds and web-tagged goslings were noted as recaptures. All applicable institutional and/or national guidelines for the care and use of geese were followed. Field protocols were approved by the Animal Care Committee of Université Laval. We also obtained information on banded birds shot and reported by hunters to the Bird Banding Laboratory of the U.S. Geological Service.

1.4.3. Reproductive success components

Reproductive success was decomposed into six successive steps (hereafter called "components") from egg- laying until young reach 1 year of age (Figure 1.1; Rockwell et al. 1993, Lepage et al. 2000). Since geese use different areas through time, we could not follow the same individuals across the six components; thus, data come from three different samples: Monitored nests, web-tagged goslings, and banded birds. The first component, total clutch laid (TCL), was defined as the maximum number of eggs found after the start of incubation in a nest that was visited at least twice. Following Lepage et al. (2000), we only retained data from nests with 2–7 eggs, as larger clutches result from nest parasitism and 1 egg clutches are likely due to partial predation (2.5% of the nests were excluded). Nests from neck-collared females were excluded due to a possible negative effect of the collar on clutch size (Reed et al. 2005). Nesting success (NS) was the probability that at least one egg hatched in a nest. Among successful nests, egg survival (ES) was the proportion of eggs surviving to partial predation until hatch and was calculated as ES = CSH/TCL, where CSH = clutch size at hatch. Hatching success (HS) was the proportion of surviving eggs that hatched (i.e. egg viability) and was calculated as HS = GLN/CSH, where GLN = number of goslings leaving a nest.

Prefledging survival (S1) was calculated using the sample of web-tagged goslings. Because of the absence of a third capture event after banding, it was impossible to use conventional capture-recapture methods to estimate survival probability. Instead, prefledging survival was estimated for individual broods as the proportion of web-tagged goslings recaptured in broods where at least one gosling was recaptured at banding ($S1 = N_{\mathrm{recaptured}}/N_{\mathrm{marked}}$). This method could be used because young stay with their parents throughout the summer, brood-mixing and adoption are uncommon (Williams 1994) and web-tag loss is low (<5%). However, this method underestimates survival since broods in which all young die cannot be detected even if their parents are recaptured because adults are not marked. We thus assumed that seasonal variation in partial versus total brood loss were similar. Finally, postfledging survival (S2), the probability of a juvenile surviving from fledging until 1 year of age, was estimated by standard capture–recapture methods using the sample of banded goslings.

1.4.4. Statistical analyses

Prior to our main statistical analyses, we verified that the nesting data obtained with different sampling schemes could be combined, which was the case as we found negligible differences in phenological parameters among them (Annex S1.3, Tables S1.1 and S1.2). In all subsequent analyses, year was used as continuous variable because we were interested in temporal trends, with the first year of the study (1991) set as year 0.

In a first analysis, we investigated temporal changes in laying date distribution using quantile regression (see Cade and Noon 2003), a robust statistical technique that allows modeling the explanatory variable at different quantiles τ (where $0 < \tau < 1$) of the response variable. Unlike standard linear regression, quantile regression examines relations at different locations of the response variable distribution. It assigns higher weights to the observations below the percentile of interest than to the rest of the distribution, minimizing the sum of their absolute residuals. This statistical approach is suitable when the extremes of a distribution change at a different rate than at the mean and has been used to detect changes in arrival dates of migratory birds (Gordo et al. 2013). Using the R package "quantreg" (Koenker 2016), we tested for a linear or quadratic (x^2) effect of year on relative laying date at $\tau = 0.05, 0.10, 0.25, 0.75, 0.90$, and 0.95. Model selection was based on AIC and 95% confidence intervals (CI) were obtained by bootstrap methods.

In the second part of our study, we built a set of candidate models to examine seasonal and temporal effects on each of the six reproductive components. Explanatory variables included relative date to account for the seasonal pattern, year to look for linear changes over time, year^2 to test for possible quadratic effects, and the interactions relative date * year and relative date * year^2. Year and year^2 were mean-centered to mitigate collinearity issues. Relative date^2 was used as an explanatory variable when a nonlinear relationship was previously identified (Lepage et al. 2000). If the preferred model included a significant interaction, this indicated a change over time in the seasonal pattern and was represented in tridimensional graphs. Prehatch components were analyzed with respect to laying dates, whereas posthatch ones were analyzed using hatching dates.

TCL was analyzed using general linear models. Egg survival, hatching success and prefledging survival were proportions and were analyzed using quasibimonial models to account for over- and under-dispersion (Bolker 2017). Nesting success was analyzed as daily survival rate (DSR) of nests using a binary response variable (success or failure of the nest) modeled with the logistic-exposure method (Shaffer 2004). In these models, we adjusted for nest age, estimated with respect to the first day of the season each year. Nesting success was estimated as $(DSR)^{27}$, where 27 is the sum of incubation length (23 days) plus 4 days to account for the time needed to lay an average clutch of four eggs. Data analyses were conducted in R 3.2.3 (R Core Team 2015, available at https://www.R-project.org/). Model selection in all cases was based, as appropriate, on the Akaike Information Criterion (AIC) or quasi-AIC (QAIC) values and weights; models with ΔAIC < 2 were considered competitive but the most parsimonious model was preferred in those cases (Arnold 2010).

Postfledging survival (S2) combined live-recaptures and dead-recoveries (Gauthier and Lebreton 2008) in a multi-event capture–recapture model using the program E-SURGE V1.9.11 publicly available online at https://www.cefe.cnrs.fr/fr/recherche/bc/bbp/1045-desc/264-logiciels (Choquet et al. 2009a, Annex S1.4, Table S1.3). The general model included relative hatching date as individual covariate and year as group covariate, which was standardized to improve model convergence. We used age of goslings captured at banding to determine their hatching date. For nonweb-tagged goslings, we estimated their age from annual relationships relating age of web-tagged goslings recaptured at banding and their ninth primary feather length (see Lepage et al. 1998).

1.5 Results

From 1991 to 2015, a total of 7,067 goose nests were monitored, 46,096 goslings were web-tagged during hatching, and 73,220 birds were banded, including 47,084 young and 26,136 adults. A total of 2,438 web- tagged goslings were recaptured during banding.

1.5.1 Laying and hatching date

The earliest mean laying date was 6 June in 1993 and the latest was 21 June in 1992 (overall mean = 13 June; Annex S1.5, Figure S1.1). Over a 25-year period, mean laying date was delayed by 0.7 day (slope = 0.03, 95% CI: 0.01, 0.04, Annex S1.5, Figure S1.2). However, we found some contrasting temporal changes in laying date within the breeding season; while early breeders ($\tau = 0.05$ and 0.10) laid about 1.8 and 1.4 days earlier respectively over the 25-year period, late breeders ($\tau = 0.90$ and 0.95) delayed laying by up to 3 days although the trend apparently stabilized during the second half of the study (Figure 1.2; Annex S1.5, Figure S1.3 and Table S1.4).

The earliest mean hatching date was 3 July, 1993, and the latest was 17 July, 1992. Laying and hatching dates were highly correlated across years (slope = 0.85, 95% CI: 0.83, 0.87). We found no temporal trend in the mean hatching date (slope = −0.01, 95% CI: -0.03, 0). The average hatching date, 9 July, was the same for monitored nests, nests where goslings were web-tagged, as well as for individual goslings recaptured at banding.

1.5.2 Prehatch nesting components

TCL averaged 3.80 eggs, and varied from 3.22 eggs in 1999 to 4.44 eggs in 1993. The best-supported model for TCL included both the interactions laying date * year and laying date * year^2 (Annex S1.6, Tables S1.5a and S1.6; other candidate models performed poorly, ΔAIC > 3.7). The seasonal decline in TCL was steep in early years of the study period, from an average of 6.2 eggs for nests initiated at Day −10 to 1.7 at Day +10 (Figure 1.3a; Annex S1.7, Figure S1.6). This seasonal decline has weakened over time as in the most recent years, nests initiated at Day −10 averaged 5.6 eggs compared to 2.0 at Day +10.

Daily survival rate (DSR) of nests varied annually from 0.925 in 1999 to 0.997 in 1993, which yielded nesting success rates ranging from 12% to 92% with an overall mean of 68%.

The preferred model included a significant interaction laying date^2 * year^2, followed by a competitive model (ΔAIC = 2.0) with the additional nonsignificant interaction laying date^2*year (Annex S1.6, Tables S1.5b and S1.6; other candidate models performed poorly, ΔAIC >13). Nesting success was much higher for nests initiated near the median laying date than those earlier or later, and showed a general increase over time. At the beginning of the study period, nests initiated on Day −10 or +10 had a mean success of 2% compared to 66% for those initiated at Day 0; at the end of the study period, success had increased to 22% for nests initiated on Day −10 or +10 compared to 84% for nests initiated at Day 0 (Figure 1.3b; Annex S1.7, Figure S1.7).

Egg survival averaged 89%, and varied annually from 69% in 1999 to 96% in 2005. Although our best- supported model included an interaction laying date * year^2 (Annex S1.6, Table S1.5c), this interaction and the variable year^2 were nonsignificant (year^2: slope = 1.30E−03, 95% CI: −2.84E−04, 2.91E−03; interaction = −4.52E−04, 95% CI: −1.09E−03, 1.86E−04). We thus based our interpretation on the fourth-ranked model (ΔQAIC = 1.5), which was the most parsimonious model and only included the effects of laying date and year (Annex S1.6, Table S1.6). We found a slight seasonal decline in egg survival, from about 92% for nests initiated in Day −10 to 87% for nests initiated in Day +10, and a weak decline in egg survival over time (Figure 1.3c; Annex S1.7, Figure S1.8).

Hatching success varied annually from 85% in 1999 to >99% in 2012 and 2015, with an overall mean of 95%. Our best-supported model included laying date, year and year^2, and our third model (ΔQAIC = 1.4) an interaction laying date * year, but these effects were nonsignificant (laying date: slope = 3.00E−02, 95% CI: −9.09E−03, 6.93E−02; interaction: slope = 2.44E−03, 95% CI: −4.62E−03, 9.49E−03). We thus based our interpretation on the second best model, (ΔQAIC = 1.0) which included the effects of year and year^2 (Annex S1.6, Tables S1.5d and S1.6). Hatching success increased from 94% at the beginning of the study period to 99% at the end (Annex S1.7, Figure S1.9).

1.5.3 Posthatch survival

Prefledging survival varied from 49% in 1991 to 72% in 2000, with an overall average of 61%. The best- supported model included a significant interaction between relative date and year^2, although the null model was a close competitor (ΔQAIC = 1.1, Annex S1.6, Tables S1.5e and S1.6). The seasonal decline in prefledging survival was absent at the beginning of the study period, but gradually appeared over time and was steep at the end (Figure 1.3d; Annex S1.7, Figure S1.10). During early years of the study period, prefledging survival was 54% for goslings hatched on Day −5 compared to 64% for those hatched on Day +8 whereas during the last years of the study period, it decreased from 70% on Days −5 to 37% on Day +8.

Postfledging survival ranged from 70% in 1991 to 12% in 2015. The best-supported model included a nonsignificant interaction between relative hatching date and year (slope = 0.02, 95% CI: −0.04, 0.08). We thus based our interpretation on the second-ranked model (ΔQAIC = 0.6; Annex S1.6, Table S1.5f), which included additive effects of relative hatching date and year (Table S1.6). Across years, postfledging survival declined seasonally from an average of 75% for goslings hatched on Day −10 to 13% for goslings hatched on Day +10 and decreased slightly over the years (Figure 1.3e; Annex S1.7, Figure S1.11).

1.6 Discussion

The seasonal patterns found in most reproductive success components of greater snow geese in early years of the study period are consistent with those reported by Lepage et al. (2000) for the years 1991–1997. However, our analyses reveal that seasonal patterns followed different trends for various components over 25 years, particularly TCL, nesting success and prefledging survival. Furthermore, trends in reproductive phenology diverged between early breeders, which nested progressively earlier, and late breeders, which nested progressively later. While many studies on long-distance migratory birds report temporal trends in laying date or reproductive success components at the population level, few studies have examined changes of seasonal patterns over time. The temporal trend of each reproductive component and its magnitude show how they are uniquely influenced by environmental changes within seasons and over time.

1.6.1 Laying date and TCL

In greater snow geese, timing of snow melt and spring temperature on the breeding ground have a strong influence on laying date (Dickey et al. 2008, Gauthier et al. 2013). Despite a warming trend in spring temperatures and earlier snowmelt on Bylot Island (Gauthier et al. 2013), we found a slight delay of 0.7 day in mean laying date over 25 years. However, our detailed analyses reveal some contrasting changes in both the upper and lower tails of the distribution. The advancement of laying date by up to 1.8 days over time in early breeders suggests that they were able to take advantage of improved feeding conditions due to earlier snowmelt. This is possible because early breeders at our study site have a longer prelaying period (Bêty et al. 2003) and rely more on local resources for egg production than late breeders (Gauthier et al. 2003). Other studies also found individual adjustments in early breeders that laid earlier despite nonsignificant changes at the population mean (Ahola et al. 2009, Goodenough et al. 2011, Jónsson et al. 2017). In contrast, laying date of late breeders was extended by up to 3 days over time. This is surprising because these individuals should experience a strong pressure to breed early because delaying nesting entails a cost for both parents and offspring (Lepage et al. 2000, Doiron et al. 2015). A possible explanation is that in recent years a high proportion of late breeders are birds that did not previously breed. These inexperienced birds may now attempt to breed because of improved feeding conditions due to earlier snowmelt, but at a cost of delayed nesting. Overall, our results highlight the need to look for trends in different segments of the population and not only at the mean population.

Contrary to our prediction, seasonal decline in TCL became weaker over time. The biggest change in TCL was found in early breeders, as TCL decreased on average by 0.6 egg over 25 years. This reduction may be a strategic adjustment to partially compensate negative effects of trophic mismatch on young survival by advancing hatching date (Doiron et al. 2015), thereby preserving the reproductive value of already laid eggs (Bêty et al. 2003, Weiser et al. 2018). However, it is unclear if such adjustment may be enough to cope with current environmental changes. Larger changes in laying date or TCL may also be constrained by the timing of other life-cycle events such as molt, which have to be completed before the onset of fall migration (Marmillot et al. 2016). A food supplementation experiment in great and blue tits (*Parus major* and *Cyanistes caeruleus*) reported a similar pattern of advancing laying date and TCL reduction (Harrison et al. 2010) and TCL decreased in early breeders in a wild population of great tits (Ahola et al. 2009). In contrast, other studies reported that species advancing their laying date also increased TCL, although these changes were small (Dunn and Møller 2014).

TCL in late breeders showed a modest increase, also contrary to our expectation. Late breeders usually arrive late and need time to regain body condition in order to produce eggs (Bêty et al. 2003). Improved feeding conditions in spring due to earlier snowmelt may allow them to regain body condition faster and invest more endogenous reserves in egg production, increasing TCL. However, an increase in TCL in late breeders may have a high energetic and reproductive cost with a low chance of success. Alternatively, this increase in TCL could be partly a statistical artifact due to the inclusion in the same analysis of early breeders, which showed a moderate decrease in TCL.

1.6.2 Nesting success, egg survival and hatching success

Nesting success and egg survival are two components driven by predation (Bêty et al. 2002), but can also be indirectly influenced by environmental changes affecting parental behavior (Table 1.1, Poussart et al. 2001, Lecomte et al. 2009). As reported in other arctic goose species (Pieron and Rohwer 2010, Kellett and Alisauskas 2011), we found a much lower success in early and late nests than in those initiated at the population mean, a pattern maintained throughout our study. Synchronous nesting reduces nest failure via predator-swamping and can provide indirect benefits due to the nest defense and vigilance of neighbors (Bêty et al. 2002). In contrast, early and late breeders do not benefit from the protection offered by high goose densities, leading to high predation rates, especially by arctic foxes (Bêty et al. 2001). However, we found a general increase in nesting success and less pronounced seasonal effects over time, which is contrary to our expectation based on the mechanism (Table 1.1) proposed by Lecomte et al. (2009). Improved feeding condition in recent years due to earlier snowmelt may allow birds to begin incubation with larger endogenous reserves, thereby increasing nest attentiveness. High attentiveness can lead to higher nesting success because most predation occurs when females are off the nest during incubation recesses (Bêty et al. 2002). Early snowmelt may also offer more high-quality nesting sites with reduced predation risk (Madsen et al. 2007). Alternatively, a change in the predator community could explain the temporal increase in nesting success. However, we have no evidence that the abundance of predator or of their main prey, lemmings, changed over time at our study site (Gauthier et al. 2013, Ehrich et al. 2019).

Interestingly, the steep decline in nesting success of early and late-nesting birds due to reduced predator-swamping effect may be a constraint limiting laying date adjustment in response to environmental changes in this population. For instance, even if feeding conditions improve in spring due to earlier snow-melt, the high predation risk to which early nesting birds are exposed may be sufficient to prevent them from advancing their laying date. Thus, in addition to bottom-up effects (e.g. food availability), a top-down factor, predation, has the potential to influence timing of breeding by maintaining a selection pressure for synchronous nesting.

We detected for the first time in this population a weak seasonal decline in egg survival. However, this seasonal decline did not become steeper as predicted although overall egg survival declined across years. While egg predation from foxes usually results in total nest failure, avian predators often remove a single egg at a time, thereby accounting for most of partial egg losses in active nests (Lecomte et al. 2008). Early in the season, nests at the egg-laying stage may be visually less conspicuous for avian predators, for instance due to lack of down at the nest, contributing to higher egg survival. In contrast, reduced nest density at the end of the nesting season or lower nest attentiveness by females may increase predation risk by avian predators. We have no evidence of temporal change in the abundance of avian predators at our study site (Gauthier et al. 2013).

We found a temporal increase of hatching success, consistent with the positive effect of warm temperature previously reported on this component (Van Oudenhove et al. 2014). Nonetheless, the lack of seasonal decline in hatching success suggests that females may be able to buffer variation in environmental conditions by maintaining a suitable microenvironment inside the nest through their incubation behavior (see review in Deeming 2002).

1.6.3 Posthatch survival

Previous studies in this population reported a seasonal decline in gosling growth and survival (Lepage et al. 1998, 2000). We detected a seasonal decline in prefledging survival only near the end of the study period, possibly because we were not able to apply conventional capture–recapture methods to our dataset as in Lepage et al. (2000). Low survival of late-hatched gosling is driven by a seasonal decline in food quality and gradual food depletion (Lindholm et al. 1994, Doiron et al. 2014). Early-hatched goslings have access to the most nutritious food on the brood-rearing areas, whereas late-hatched individuals have to invest more time and energy to acquire enough nutrients, which reduces their growth (Lepage et al. 1998, Doiron et al. 2015). The progressive increase in the steepness of the seasonal decline in prefledging survival is in line with our findings that the frequency distribution of laying dates has extended toward late-breeding, with some birds nesting progressively later. This increases the trophic mismatch between the peak nutritive quality of plants, which tends to occur earlier in the season with advancing snowmelt, and the period of high energy demand of late-hatched goslings, reducing their growth (Brook et al. 2015, Doiron et al. 2015).

Early-hatched goslings had a higher postfledging survival than late-hatched ones, as previously reported in this goose population and in several others (Lepage et al. 2000, Menu et al. 2005, Cooch 2010). Although this seasonal pattern remained the same throughout our study, overall survival tended to decline over time. The seasonal decline can be explained by the poor growth of late-hatched goslings, due to the low nutrient content in the food and the lack of time to complete their growth before the onset of fall migration (Lepage et al. 1998, Doiron et al. 2015). Unlike prefledging survival, the seasonal decline was detected throughout the study years, possibly due to the large sample size analyzed, which covered the full hatching period. The temporal decline in postfledging survival regardless of hatching date may be because trophic mismatch has increased over time, affecting all goslings alike. Alternatively, this may be due to increasing density-dependent effects, as reported in another high-density goose population (Williams et al. 1993). Surprisingly, late-hatched goslings were not disproportionally affected by trophic mismatch as the seasonal decline did not become steeper over time, as observed in prefledging survival. A possible explanation is that among late-hatched goslings, the ones that had the poorest growth died before late summer, hence they were absent from the sample of birds banded near fledging.

1.6.4 Study limitations

Our study has a few limitations that may introduce some unknown biases in our analyses. First, because it is impossible to follow the complete reproductive event of the same individual from egg-laying until young surviving at 1 year of age, we had to use different samples of individuals for different reproductive stages (nesting, brood and first year survival). Since we are not tracking the same individuals at all reproductive stages, we cannot account for factors like female age, which is known to affect reproductive performance (Rockwell et al. 1993, Verhulst and Nilsson 2008). Moreover, our inability to assess total brood loss limited our analysis of prefledging survival to partial brood loss of web-tagged goslings. However, the seasonal pattern of total brood loss may differ from that of partial brood loss, thus introducing biases in our prefledging survival analysis. Furthermore, the samples analyzed did not measure the survival of the earliest goslings (because we did not recapture goslings hatched before Day −5) and may partly explain the absence of seasonal decline in survival at the beginning of the study period when it was presumably weak. Another limitation is that individuals may occasionally skip breeding (Souchay et al. 2014) and become unobservable in those years. Since our analyses are based on the subsample of the population that breeds every year, this may not be a random sample (e.g. see Bêty et al. 2004).

1.7 Conclusion

Despite a warming climate with earlier snowmelt at our study site, it is surprising that breeding phenology of snow geese showed little changes. Average laying date did not advance during the study period as we could have expected, although we detected changes in some segments of the population, as early breeders are now nesting slightly earlier and late breeders later. Interestingly, various reproductive success components were affected differently by environmental changes. While some apparently improved over time (e.g. nesting success), others tended to decrease (clutch size, posthatch survival). Overall, nests initiated close to the population mean showed little temporal change for most components of reproductive success unlike those initiated early or late in the season. For instance, temporal changes in seasonal patterns of posthatch survival suggest that trophic mismatch may have worsened over time, and that in recent years late-hatched goslings may be the most affected, especially before fledging. The reduction in clutch size detected in early breeders over time may be a strategic adjustment to advance hatching date and mitigate the impact of environmental changes on gosling survival and reproductive success (Bêty et al. 2003, Weiser et al. 2018). However, given that laying date did not change for the bulk of the population, it appears unlikely that an adjustment of clutch size alone will be sufficient to prevent an overall decline in reproductive success of this population in face of a changing climate.

1.8 Acknowledgments

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The authors declare that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

1.9 Annex S1: Supplementary material

Table 1.1 Mechanisms and expected changes in seasonal variation of reproductive success components of the greater snow goose.

Component	Expected change over time	Mechanism
Total clutch size (TCL)	The seasonal decline will become steeper due to a decrease in TCL in late nesters.	Earlier spring and warmer temperature advance the peak food quality and increase trophic mismatch for goslings, which favors a reduction in TCL in late-laying females to advance hatching date[1,2].
Nesting success, egg survival	The seasonal decline after the population mean will become steeper due to a decrease success in late nesters.	Warmer temperatures reduce water availability for late nesting females and increase predation risk and nest failure[3, 4, 5].
Hatching success	A general increase.	Warmer temperatures reduce embryo mortality[3, 6].
Prefledging and postfledging survival	The seasonal decline will become steeper due to a decrease in survival of late-hatched goslings.	Earlier spring and warmer temperature advance the peak food quality and increase trophic mismatch with goslings, reducing their survival[2, 7].

[1] Bêty et al. 2003, [2] Doiron et al. 2015, [3] Poussart et al. 2001, [4] Lecomte et al. 2009, [5] Dickey et al. 2008, [6] Oudenhove et al. 2014, [7] Menu et al. 2005.

Figure 1.1 Reproductive success components of greater snow geese from egg-laying until birds reach 1-year of age. The lines under the figure refer to the three datasets used to estimate the reproductive components (monitored nests, web-tagged goslings and banded birds). NS, nesting success; ES, egg survival; HS, hatching success; S1, prefledging survival; S2, postfledging survival.

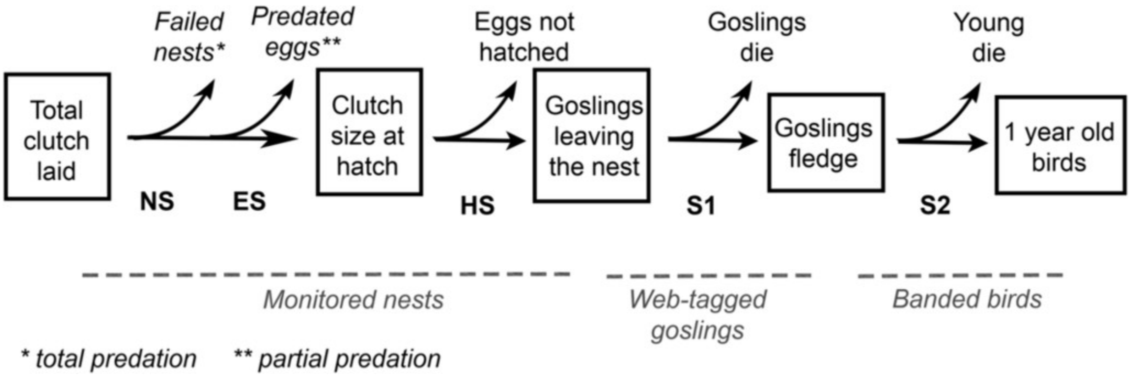


Figure 1.2 Scatterplot and regression lines between relative laying date (0 = population median) and study year (year 0 = 1991) for various quantiles (τ) of the laying date data distribution of greater snow geese. Early breeders (τ ≤ 0.25) are represented by dashed lines and late breeders (τ ≥ 0.75) are represented by solid lines. Gray dots represent observed relative laying date. All lines are significant (see Annex S1.5, Table S1.4).

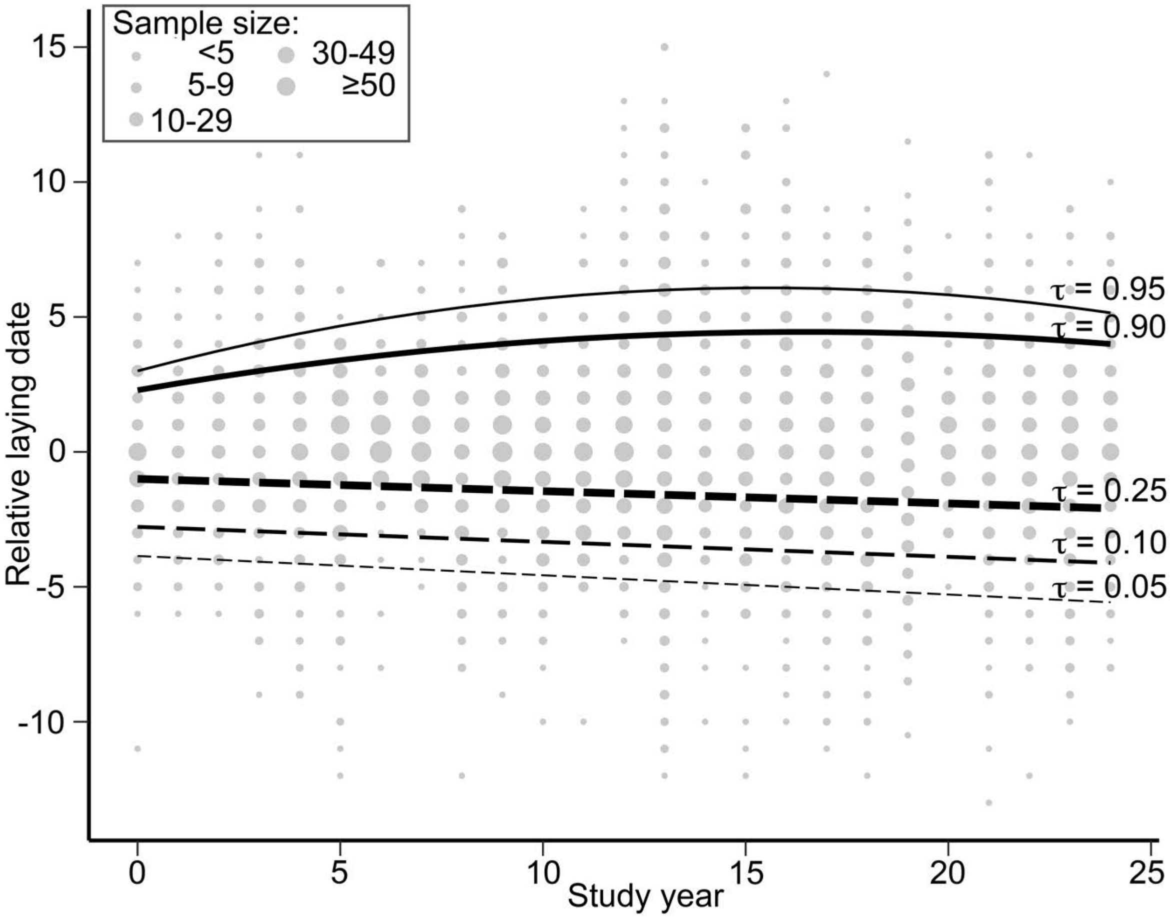
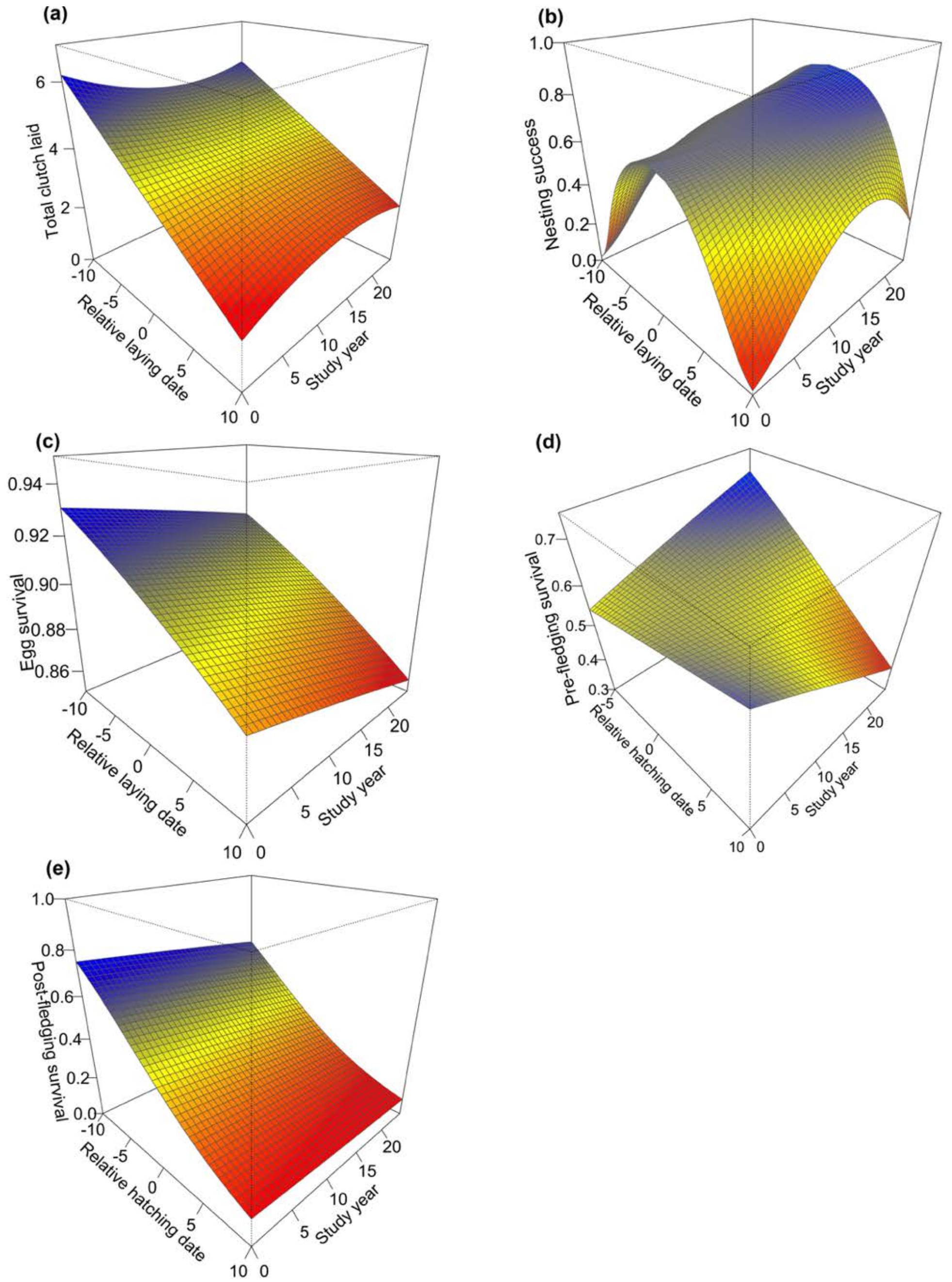


Figure 1.3 Reproductive success components **(a)** total clutch laid, **(b)** nesting success, **(c)** egg survival, **(d)** prefledging survival, **(e)** postfledging survival as a function of study year and relative date (from Day -10 to +10 in relation to population median) of greater snow geese from 1991 to 2015. Study year is presented as a continuous variable, where 1991 is year = 0. The surface represents the interpolation of predicted values for each relative day across the study years. Blue indicates the highest values in the component, and red the lowest values. Nesting success surface was estimated from daily survival rate of nests (DSR, with nest age fixed at the mean value).



Chapter 2. Temporal changes in reproductive success and optimal breeding decisions in a long-distance migratory bird

In preparation:

Reséndiz-Infante C and Gauthier G. **Temporal changes in reproductive success and optimal breeding decisions in a long-distance migratory bird.**

2.1 Résumé

Plusieurs migrateurs de longues distances ne réussissent pas à ajuster leur phénologie de reproduction aux conditions changeantes sur leurs aires de reproduction causées par le réchauffement climatique. Par conséquent, la période d'éclosion des jeunes peut ne plus coïncider avec la période où la disponibilité de nourriture est la plus élevée, ce qui affecte de façon négative la croissance et la survie des jeunes. Nous avons étudié les changements saisonniers du succès de reproduction de la grande oie des neiges (*Chen caerulescens atlantica*), un migrateur arctique de longue distance, sur une période de 25 ans. Notre hypothèse était que l'augmentation de l'asynchronie entre l'éclosion des jeunes et le pic de la qualité de la nourriture causé par le réchauffement climatique a augmenté le déclin saisonnier du succès reproducteur. Nous nous attendions également à ce que la date d'initiation optimale à laquelle le succès reproducteur est maximal se soit éloignée graduellement de la moyenne populationnelle. Nous avons constaté que pendant une période de 25 ans, le succès reproducteur a augmenté chez les couples nichant tôt en saison et diminué légèrement chez ceux nichant tardivement. Ainsi, tel que prévu, le déclin saisonnier dans le succès reproducteur s'est accentué avec le temps. La différence entre la date d'initiation associée au succès reproducteur le plus élevé et la date d'initiation médiane de la population a augmenté avec le temps, ce qui suggère une augmentation dans le différentiel de sélection pour ce trait. Toutefois, la date d'initiation moyenne de la population n'a pas été devancé, possiblement dû aux contraintes rencontrées pendant la migration. La taille de ponte observée était plus faible que la taille de ponte donnant le succès reproducteur le plus élevé et ce, pour la majorité des dates d'initiation. Cependant, la taille de ponte pourrait quand même être optimale au niveau individuel si le temps supplémentaire requis pour acquérir les nutriments nécessaires pour pondre des œufs additionnels est compensé par une réduction plus grande du succès reproducteur causé par une date d'initiation retardée. Néanmoins, la phénologie de nidification des oies des neiges ne pourra probablement pas répondre à une vitesse suffisante pour s'ajuster aux changements environnementaux causés par le réchauffement des températures dans les années à venir.

Mots clés : *Chen caerulescens atlantica*, grande oie des neiges, phénologie de reproduction, taille de ponte, date de ponte

2.2 Abstract

Many long-distance migrants have failed to adjust their breeding phenology to changing conditions encountered on their breeding ground due to climate warming. Consequently, the hatching period of young may no longer match the period of peak food availability, with negative consequences for offspring growth and survival. We studied seasonal changes in reproductive success of the greater snow goose (*Chen caerulescens atlantica*), a long-distance arctic migrant, over a 25-year period. We hypothesized that increasing mismatch between the timing of gosling hatch and peak food quality induced by climate warming has increased the seasonal decline in reproductive success. We also expected that the optimal laying date yielding the highest reproductive success has moved away from the population mean over time. We found that reproductive success increased in early breeders and decreased slightly in late breeders over 25 years. Consequently, the seasonal decline in reproductive success became steeper over time as expected. The difference between the laying date yielding the highest reproductive success and the median laying date of the population increased over time, suggesting an increase in the selection differential for that trait. However, the mean laying date of the population did not advance, possibly due to constraint encountered during the migration. The observed clutch size was lower than the clutch size yielding the highest reproductive success for most laying dates. However, at the individual level clutch size could still be optimal if the additional time required to acquire nutrients to lay extra eggs is compensated by a greater reduction in reproductive success due to a delayed laying date. Nonetheless, the breeding phenology of snow geese is unlikely to respond at the speed required to match environmental changes induced by warming temperatures in the years to come.

Keywords: *Chen caerulescens atlantica*, greater snow goose, breeding phenology, clutch size, laying date

2.3 Introduction

Animals living in seasonal environments should optimize the timing of breeding to maximize their reproductive success, which is typically highest when offspring are born during the peak in food availability (Siikamäki 1998, Post et al. 2003, Both and Visser 2005, Visser et al. 2006, Reed et al. 2013). Accordingly, the two most critical decisions in breeding birds are when to start laying eggs and how many eggs to lay (clutch size), two decisions that are linked (Rowe et al. 1994, Bêty et al. 2003). Birds can adjust both to reach an optimal combination that yields the maximum reproductive success possible. In long-distance migrants, weather encountered during migration and on the breeding grounds can have a strong influence on these decisions because it can affect body condition and feeding opportunities upon arrival (Drent et al. 2006, Both et al. 2010). Individual quality also plays a role in breeding decisions because high-quality individuals often arrive early at the breeding areas (Verhulst and Nilsson 2008). Early arriving birds usually show better body condition, start nesting earlier, lay larger clutches and ultimately have a higher reproductive success than those arriving later (Bêty et al. 2003). In seasonal environments, delaying nest initiation due to a late arrival or poor body condition entails a cost in terms of the reproductive value of eggs (Rowe et al. 1994, Bêty et al. 2003, Descamps et al. 2011). Nonetheless, breeding too early also entails potential costs. For instance, individuals laying very early may face more severe and unpredictable environmental conditions or higher egg predation risk due to reduced synchrony with the bulk of the colony, which attenuates the predator-swamping effect (Lepage et al. 2000, Jean-Gagnon et al. 2018).

Climate warming may disrupt the optimal combinations of arrival time and prebreeding body condition that maximize reproductive success of long-distance migrants breeding in seasonal environments (Penteriani et al. 2014). Species at different trophic levels are likely to respond at different rates to climate warming. Processes occurring at low trophic levels, such as onset of vegetation growth or insect outburst, typically advance the fastest in response to warming, which may result in trophic mismatches between offspring hatch and peak food availability (Both et al. 2006, 2009). Phenotypic plasticity is a mechanism that can allow migratory birds to cope with phenological changes induced by climate warming (Charmantier et al. 2008, Gienapp et al. 2008). Birds can adjust the timing of breeding or clutch size, but often not enough to fully match the energetic needs of their offspring with phenological changes occurring at lower trophic levels (Visser et al. 1998, Both and Visser 2001, Both et al. 2009).

The consequences of trophic mismatch are exacerbated in arctic-nesting geese because their breeding cycle is relatively long, they breed in highly seasonal environments where the summer is short and they are exposed to rapid climate warming. In this environment, the time window to achieve optimal reproductive success is narrow, leaving few opportunities for individuals to adjust timing of breeding to changing environmental conditions (Gauthier et al. 2013). In greater snow geese, early breeders have a higher reproductive success than late breeders because they lay more eggs that hatch early and their goslings have access to more nutritious plants for a rapid growth (Lepage et al. 1998, 2000). Birds arriving late on the breeding ground or in poor body condition have to delay laying in order to regain condition; however, a delay in egg laying reduces reproductive success due to late hatching. Therefore, females may trade off a reduction in clutch size for an advance in hatching date to minimize the fitness cost of delayed laying (Bêty et al. 2003).

Prior research documented strong seasonal effects on several components of reproductive success in greater snow geese, from egg-laying until young survive to 1 year of age (Lepage et al. 2000). Despite a strong warming trend on their breeding ground on Bylot Island (Canada), the laying date changed little in this population over the past 3 decades, thereby increasing the potential for a trophic mismatch (Gauthier et al. 2013, Reséndiz-Infante et al. 2020). We previously showed that seasonal patterns of some reproductive success components (clutch size, nesting success, pre- and postfledging survival) followed different and sometimes opposite trends over 25 years in this population (Reséndiz-Infante et al. 2020). In this study, we integrated all the components, from egg laying until offspring survive to one year, to estimate the observed reproductive success and investigated seasonal changes over time. We also studied seasonal changes over time in expected reproductive success for different clutch size laid at different dates. We hypothesized that increasing trophic mismatch between the timing of gosling hatch and of peak food quality induced by climate warming

(Doiron et al. 2015) has reduced reproductive success of nests initiated late in the season. We also expected that the optimal laying date yielding the highest reproductive success has moved away from the population mean over time, and that optimal egg-laying decisions at different clutch sizes have changed over time due to individual adjustments.

2.4 Methods

2.4.1 Study species and study area

The greater snow goose overwinters on the East Coast of the United States and migrates to their breeding grounds in the Eastern Canadian High-Arctic, with a major stopover in Southern Quebec (Gauthier et al. 2005). Though it is a mixed capital/income breeder, egg production depends largely on Arctic food resources available before and during laying (Gauthier et al. 2003). A single clutch is laid per year, and predation is the main cause of nesting failure (Bêty et al. 2001). Young and adults are strictly herbivorous, feeding predominantly on leaves, grasses and sedges.

We studied the snow goose population of the south plain of Bylot Island, Nunavut, Canada (72˚53.49' N, 79˚54.38'W) where ca. 20,000 pairs breed (Reed et al. 2002). Typical landforms on the south plain include low hills generally with gentle slopes and large flat areas; mesic tundra dominates the landscape, but wetlands associated with ponds and tundra polygons are very common (Massé et al. 2001). Most geese nest in a main colony located in the central portion of the south plain, but some individuals also nest in a dispersed fashion across the area (Mainguy et al. 2006, see Reséndiz-Infante et al. 2020 for details).

2.4.2 Field methods

Goose reproduction has been monitored annually on Bylot Island since 1989. In this study, we used data collected during the reproductive seasons 1991–2015. We found a sample of nests during egg-laying and early incubation and monitored them until hatch (range: 130–493 nests annually). Within 24-h after hatch, we marked goslings with web-tags before they left the nest. Right before fledging, we captured family groups (parents with their young) in mass banding drives and each bird received a metal leg-band (see Menu et al. 2001 for details). Recaptures of leg-banded adults in previous years and web-tagged goslings at hatch were recorded. We also obtained bands-recovery data reported by hunters to the Bird Banding Laboratory of the U.S. Geological Service (see Reséndiz-Infante et al. 2020 for more details on methods).

2.4.3 Reproductive success components

Laying date was the date on which the first egg was laid in a nest. We back-calculated laying date according to the nest stage at the first visit (egg-laying, incubation or at hatch), using three different methods (see Reséndiz-Infante et al. 2020). We defined hatching date of a brood as the date on which at least half of the clutch hatched. To adjust for inter-annual environmental variability, we centered individual values on the annual median laying and hatching dates of the population (i.e. relative day with respect to the annual population median set equal to 0). Hereafter, centered dates are referred as relative laying and hatching dates.

We decomposed reproduction into several successive components from egg-laying until young surviving to one-year of age (Reséndiz-Infante et al. 2020). Total clutch laid (TCL) was the maximum number of eggs found in a nest after the start of incubation. We excluded observations of nests where TCL was 1 egg, most likely a consequence of partial predation, and >7 eggs, considered a result of intraspecific brood parasitism (Lepage et al. 2000). Nesting success (NS) was the probability of at least one egg hatching in a nest. Egg survival (ES) was the proportion of eggs surviving to hatch time in successful nests and was calculated as $\mathrm{ES} = \mathrm{CSH}/\mathrm{TCL}$, where CSH = clutch size at hatch. Hatching success was the proportion of eggs that hatch in a successful nest and was calculated as $\mathrm{HS} = \mathrm{GLN}/\mathrm{CSH}$, where GLN = number of goslings leaving a nest.

We estimated prefledging survival (S1) from goslings web-tagged at hatch that survived over the brood-rearing period and were recaptured at banding time. We could not use conventional capture-recapture methods here because we had a single recapture event. S1 was thus estimated for individual broods where at least one gosling was recaptured as $\mathrm{N}_{\mathrm{recaptured}}/\mathrm{N}_{\mathrm{marked}}$. However, this approach underestimates survival because broods in which all young die (total brood loss) cannot be detected even if their parents are recaptured because parents are not marked. We corrected S1 estimates for total brood loss as described in Annex S2.1. Finally, postfledging survival (S2) was the probability of a juvenile surviving from fledging until one year of age and was estimated by applying standard capture-recapture methods to the dataset of banded birds. Because of the use of different areas by geese through time, we could not follow the same individuals from the egg-laying stage until one year of age, and thus data used for estimating reproductive components come from three different samples: monitored nests, web-tagged goslings and banded birds (see Reséndiz-Infante et al. 2020 for details).

2.4.4 Data analyses

2.4.4.1 Observed reproductive success

We estimated reproductive success (RS) by the product of all individual components defined above. We calculated observed reproductive success for each relative laying date (*d*) of the season (i.e. laying dates from Day -10 to +10) and each study year using the equation from Rockwell et al. (1993) and Lepage et al. (2000).

$$E(RS)_d = TCL_d \times NS_d \times ES_d \times HS_d \times S1_{d'} \times S2_{d'} \qquad \text{Eq (1)}$$

In Equation (1) we used predicted values from the seasonal and annual effects found on each of these reproductive components modeled by Reséndiz-Infante et al. (2020; Annex S2.2, Table S2.1). Confidence intervals (95%) were computed using 10,000 Monte Carlo simulations. In each simulation, we randomly sampled a value from the distribution of predicted values for each reproductive component to obtain the sampling variance used to calculate standard errors and confidence intervals.

Because posthatch components S1 and S2 were analyzed using relative hatching dates, we adjusted the hatching date to its corresponding laying date (d') to match the response variable used in the prehatch components. We know that a clutch size larger than the mean will delay hatching by 1 day for each additional egg laid, and conversely hatching will be advanced by 1 day for each egg removed. Therefore, the modal clutch size of 4 eggs was subtracted from the observed clutch size for each day of the season (TCL_d) and this value added to d to estimate the hatching date d' corresponding to laying date d as suggested by Lepage et al. (2000; Equation 2).

$$d' = d + (\overline{TCL_d} - 4) \qquad \text{Eq (2)}$$

2.4.4.2 Expected reproductive success

We evaluated the consequences of individual breeding decisions (laying date and clutch size) on reproductive success according to our model. Expected reproductive success was calculated for a bird laying a given clutch size over the range of 2 to 7 eggs on relative dates ranging from -10 to +10 across the 25-year study period. We estimated the expected offspring survival at the nest (OS; Equation 3), which is the probability of producing a gosling leaving the nest, for each day of the season and year with the following equation:

$$E(OS)_d = NS_d \times ES_d \times HS_d \qquad \text{Eq (3)}$$

Expected reproductive success for different hypothetical clutch size *C* (from 2 to 7 eggs; Equation 4) and laying date of the season (from -10 to +10) were calculated as the product of expected offspring survival at the nest (OS) and posthatch components:

$$E(RS)d = C \times OS_d \times S1_{d''} \times S2_{d''} \qquad \text{Eq (4)}$$

For the same reason as for the calculation of observed reproductive success, relative laying date of posthatch components was adjusted (d") when combined with prehatch components depending of the value of *C* using the Equation (5).

$$d'' = d + (C - 4) \qquad \text{Eq (5)}$$

2.5 Results

2.5.1 Seasonal pattern of reproductive success

At the beginning of the study period, the earliest breeders (nests initiated at Day -10) had a low reproductive success of 0.03 young. Success increased rapidly with laying date to peak at 0.52 young on Day -4 and declined steadily after that to 0.45 at Day 0 and <0.01 at Day +10 (Figure 2.1; Annex S2.3, Figure S2.1). Success of the earliest nests as well as the maximum success increased over time to reach 0.26 and 0.74 young, respectively, after 25 years, but the seasonal decline became steeper over time. At the end of the study period, reproductive success declined from 0.74 young on Day -6 to 0.42 at Day 0 and 0.01 at Day +10.

At the beginning of the study period, the maximum reproductive success was achieved for birds laying on Day -4 and gradually advanced to Day -8 after 10 years; however, after 17 years, maximum success started to move back and was at Day -6 at the end (Figure 2.2). Overall, the difference between the date of the maximum reproductive success and the median laying date of the population increased over 25-years (slope = -0.11, 95% CI: -0.18, -0.05, $R^2 = 0.33$).

2.5.2 Clutch size, laying date and expected reproductive success

The expected reproductive success of birds laying a hypothetical clutch size of 2 to 7 eggs (Annex S2.3, Figures S2.2 and S2.3) showed seasonal and annual patterns of variation generally similar to the observed reproductive success (Figure 2.1). We superimposed on the same graph the seasonal variation in expected reproductive success of birds laying a clutch size of 2 to 6 eggs at the beginning, half way and at the end of the study period (Figure 2.3). Difference in expected reproductive success among various clutch sizes decreased in larger clutches and the seasonal decline in success was steeper in larger clutches than in smaller. Consequently, all lines tended to converge for birds laying on Day +5 or later, especially at the beginning and the end of the study period. For almost all laying dates, the observed clutch size was lower than the clutch size yielding the highest reproductive success according to our model. For early laying birds (Day -7 to -3 in 1991, -7 to -6 in 2003 and -8 to -7 in 2015), observed clutch size was only one egg less than the clutch size yielding the highest success. However, for progressively later laying dates, this difference was two eggs and even sometimes three eggs.

2.6 Discussion

The general pattern of seasonal variation in the reproductive success of greater snow geese was maintained over a 25-year period, with the highest success achieved for birds laying before the population median. The maximum reproductive success increased over time and the date at which it was achieved advanced by about 2 days although the median egg-laying date did not change in the population (Reséndiz-Infante et al. 2020). Consequently, the seasonal decrease in reproductive success became steeper over time. Our analysis also suggests that the clutch size laid by geese was lower than the clutch size yielding the maximum reproductive success for most laying dates throughout the study period.

2.6.1 Change in seasonal pattern of reproductive success

Even though egg-laying is highly synchronized in greater snow geese (87% of the nests initiated over 11 days on average), reproductive success shows strong seasonal variations. Reproductive success was highest in early-nesting birds, mainly from Day -6 to -4, suggesting a clear advantage for birds to lay early. However, laying too early also entails a cost as the reproductive success of the earliest breeders was low. The poor success of the earliest nests is driven mostly by the nesting success component (Reséndiz-Infante et al. 2020), as they suffer high predation by arctic foxes (*Vulpes lagopus*), the main cause of nest failure (Bêty et al. 2003). The earliest nests do not benefit from the predator-swamping effect provided by high goose densities (Findlay and Cooke 1982, Bêty et al. 2001).

Reproductive success of birds laying before the population median, which includes those with the highest success, showed a temporal increase. We found previously that nesting success increased over time in this population, suggesting a reduction of breeding failure due to predation (Reséndiz-Infante et al. 2020). Better feeding conditions in spring due to climate warming may have increased the body condition of early nesting birds, thereby improving nest attendance of incubating females and reducing predation risk. Another factor may be the temporal increase in prefledging survival of early nesting birds found in this population (Reséndiz-Infante et al. 2020). Food plays a key role in gosling growth (Lepage et al. 1998, Doiron et al. 2015) and subsequent survival (Sedinger and Chelgren 2007, Sedinger and

Nicolai 2011). Contrary to late-hatched goslings, feeding conditions of those early hatched may have been maintained or improved due to warmer summers, because they still hatch close to the peak in food quality.

Reproductive success of birds laying at the population median or after changed little contrary to those laying earlier. This is somewhat surprising considering that prefledging survival of late-hatched goslings tended to decrease over time (Reséndiz-Infante et al. 2020), possibly because the mismatch between hatching date and the peak in plant nutritive quality increased (Doiron et al. 2015). Recent evidence shows that black brant goslings (*Branta bernicla nigricans*) can respond to decreasing food availability with behavioral adjustments (reduced resting periods and increased search time for food; Lohman et al. 2019), which could buffer the negative effects of trophic mismatch. The general increase in nesting success over time in our population also may have partly offset the negative effect of reduced prefledging survival on overall reproductive success of late-nesting birds.

The laying date that achieved the highest reproductive success advanced over time in the first half of the study period but levelled off in the second half. At the beginning of the study period, birds laying on Day -4 had the highest reproductive success, as found by Lepage et al. (2000), but in recent years this occurred on Day -6. This suggests a strong selection pressure for birds to lay earlier. Climate warming has disrupted trophic interactions in seasonal environments and has increased the selection differential for early breeding in several wild populations (Visser et al. 1998, Gienapp et al. 2006, Charmantier et al. 2008). Our results suggest that this also applies to our population, probably because warming has pushed the peak in nutritive quality of plants for goslings earlier in the season, thereby advancing the date when maximum reproductive success is achieved. Despite this apparent temporal increase in the selection pressure for early laying, average laying date did not advance in our population (Reséndiz-Infante et al. 2020). Interestingly, a finer analysis revealed that laying date of the earliest breeders advanced by 2 days, suggesting a possible adjustment for some components of the population, perhaps the highest quality individuals.

The absence of a general response of the population to an apparent increase in the selection differential for early laying may be due to other phenological constraints such as the arrival date of birds on the breeding ground (Both and Visser 2001). Departure of geese from the wintering grounds is largely driven by photoperiod, a non-environmental cue, although movement through successive stopovers may be influenced by timing of food availability (van Wijk et al. 2012). A slower rate of warming at lower latitudes may prevent geese from adjusting their migration schedule and arrival time to conditions prevailing on their arctic breeding ground. Considering that birds need to recover body condition for egg formation after their arrival (Gauthier et al. 2003), this may impose a minimum delay between arrival and laying, which limits the ability of most individuals to advance laying date. Our results suggest that warming may have created a selection pressure that favors early breeders in this population due to a trophic mismatch (Doiron et al. 2015) and could have contributed indirectly to increased success by reducing vulnerability of nests to predation. The opposite is true for late breeders, which may explain why the seasonal decline in breeding success became steeper in our population over time.

2.6.2 Clutch size, laying date and reproductive success

The strong decline in reproductive success in seasonal environments can be explained by the condition-dependent optimization model of Rowe et al. (1994), which predicts the optimal combination of clutch size and laying date in relation to arrival time and body condition of individuals. This model is based on a trade-off between clutch size and laying date as a strategy to maximize individual fitness. In our study population, Lepage et al. (2000) found that the observed clutch size matched the clutch size that yielded the maximum reproductive success for most laying dates in the earlier years of the study period, in accordance with Rowe et al. (1994) model. Therefore, females were apparently trading-off an additional egg for earlier laying to achieve the maximum possible reproductive success, thereby leading to a strong seasonal decline in clutch size at the population level.

Our analysis, which uses the same approach but over a much longer time period (25 years instead of 7 years), differs from that of Lepage et al. (2000) as the observed clutch size was lower than the one yielding the highest reproductive success for various laying dates. This analysis, however, overlooks an important aspect of Rowe et al. (1994) model, which is the time required to acquire enough nutrients to lay an additional egg. In greater snow geese, nutrients invested in egg-production come from a combination of body reserves accumulated during migration and from feeding at arrival on breeding ground, during prelaying (Gauthier et al. 2003). In order to lay an additional egg to increase its reproductive success (Figure 2.3), a bird will need time to accumulate enough nutrients to form this additional egg. It is thus possible that the time required to acquire those nutrients could cause a delay in the start of egg-laying that results in a greater reduction in reproductive success than the one gained by laying the extra egg. For instance, at the beginning of the study period, a female having sufficient nutrient reserves to lay 5 eggs on Day -4 (i.e. the observed mean clutch size for that date) would need time to acquire more nutrients to produce an extra egg, which would delay laying. If the feeding time required to acquire these nutrients is ≥ 2 days, then the reproductive success associated with this 6-egg clutch will actually be lower than the one expected by laying 5 eggs on Day -4 (Figure 2.3a). In this example, laying a smaller clutch size at an earlier date (i.e. 5 eggs on Day -4) still could be the optimal solution for that individual in terms of reproductive success. Therefore, females arriving on the breeding ground may face a conflict between laying as early as possible to avoid a mismatch between hatching date of their offspring and the peak in plant nutritive quality and delaying laying to gain additional nutrients to form extra eggs (Bêty et al. 2003). The solution to this conflict would depend on female individual body condition at arrival and the rate of nutrient gain, information that was not available in our study.

2.6.3 Limitations of the study

In this study, we were unable to monitor the same individuals from egg-laying to young surviving at one year of age. Therefore, we had to combine independent samples collected at various time periods to obtain the overall reproductive success, which may reduce some of the individual variability. For the same reason, we do not have information on some factors known to influence reproductive success at the individual level such as female age (Rockwell et al. 1993, Verhulst and Nilson 2008). This also limits our ability to conduct genetic analysis at individual level in this population.

Geese are known to skip breeding in some years (Souchay et al. 2014) making it possible that our data, which are based only on individuals that actually attempted to breed, may not be a totally random sample of the population. Including the decision of breeding or not breeding could affect the seasonal variation in reproductive success (e.g. Bêty et al. 2004) It is also possible that early breeders are not the same every year and that laying date may depend on reproductive success in the previous year (Souchay et al. 2014).

2.7 Conclusion

Long-distance arctic migrants like geese are under a strong pressure to lay early in the season to maximize their reproductive success. Our analysis suggests that, over a 25-year period, reproductive success of early breeders increased slightly and the laying date that maximizes success became progressively earlier as climate warmed. However, mean laying date of the population did not advance, possibly due to constraints encountered during migration, which resulted in an apparent increase in the selection differential for that trait. Nonetheless, our results may still be consistent with the hypothesis that geese are maximizing their reproductive success at the individual level by trading off additional egg in their clutch for an earlier laying date, as predicted by the Rowe et al. (1994) model, but this would depend on the time required to acquire nutrients to lay extra eggs.

2.8 Annex S2: Supplementary material

Annex S2.1 Estimation of total brood loss

Annex S2.2 Seasonal and annual effects detected on individual reproductive success components

Annex S2.3 Supplementary results

Figure 2.1 Observed reproductive success of greater snow geese for each study year and relative date (from Day -10 to 10) from 1991 to 2015. Day 0 is the median laying date of the population. Study year is presented as a continuous variable, where 1991 is year 0. The surface represents the interpolation of reproductive success values for each relative day across the study years. Blue indicates the highest values in the component, and red the lowest values. Confidence intervals for each relative laying date are presented for year 0 and are similar across years. See also contour plot in Annex S2.3, Figure S2.1.

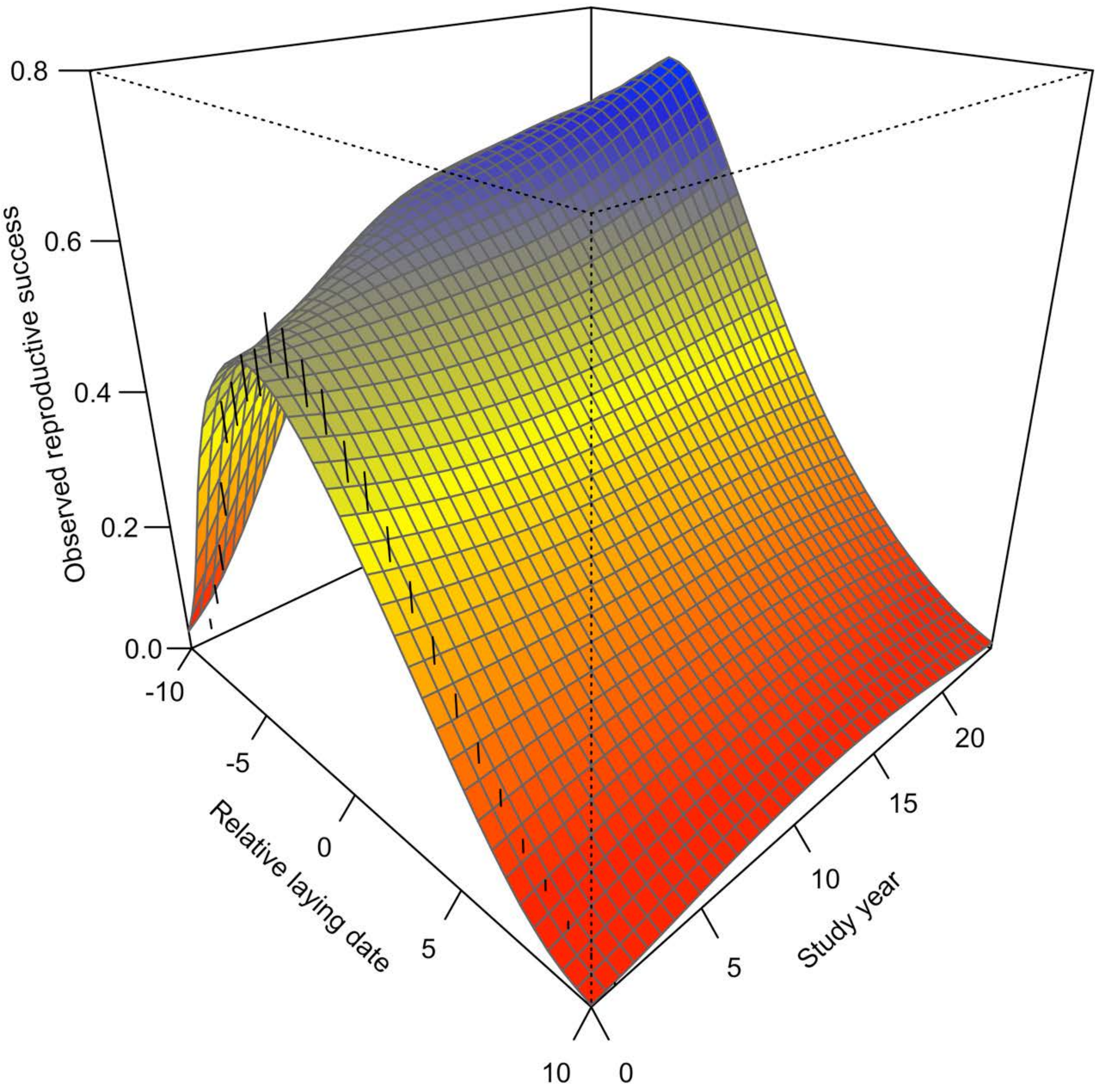


Figure 2.2 Difference in laying date yielding the maximum reproductive success and the median laying date of the population from 1991 to 2015. Black solid line indicates the temporal trend.

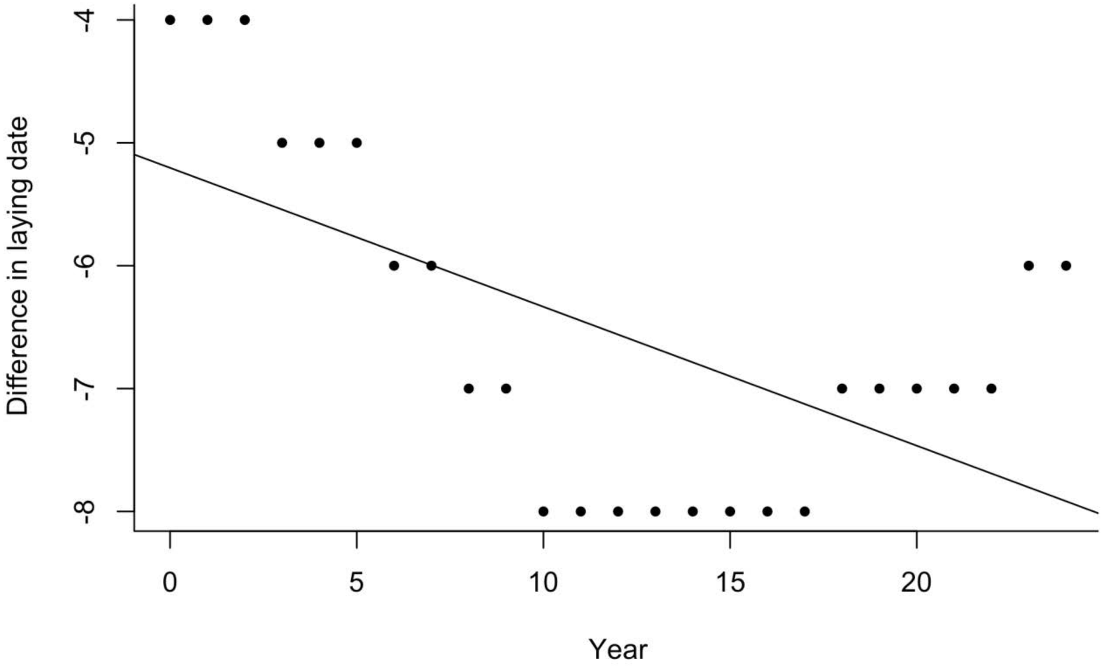
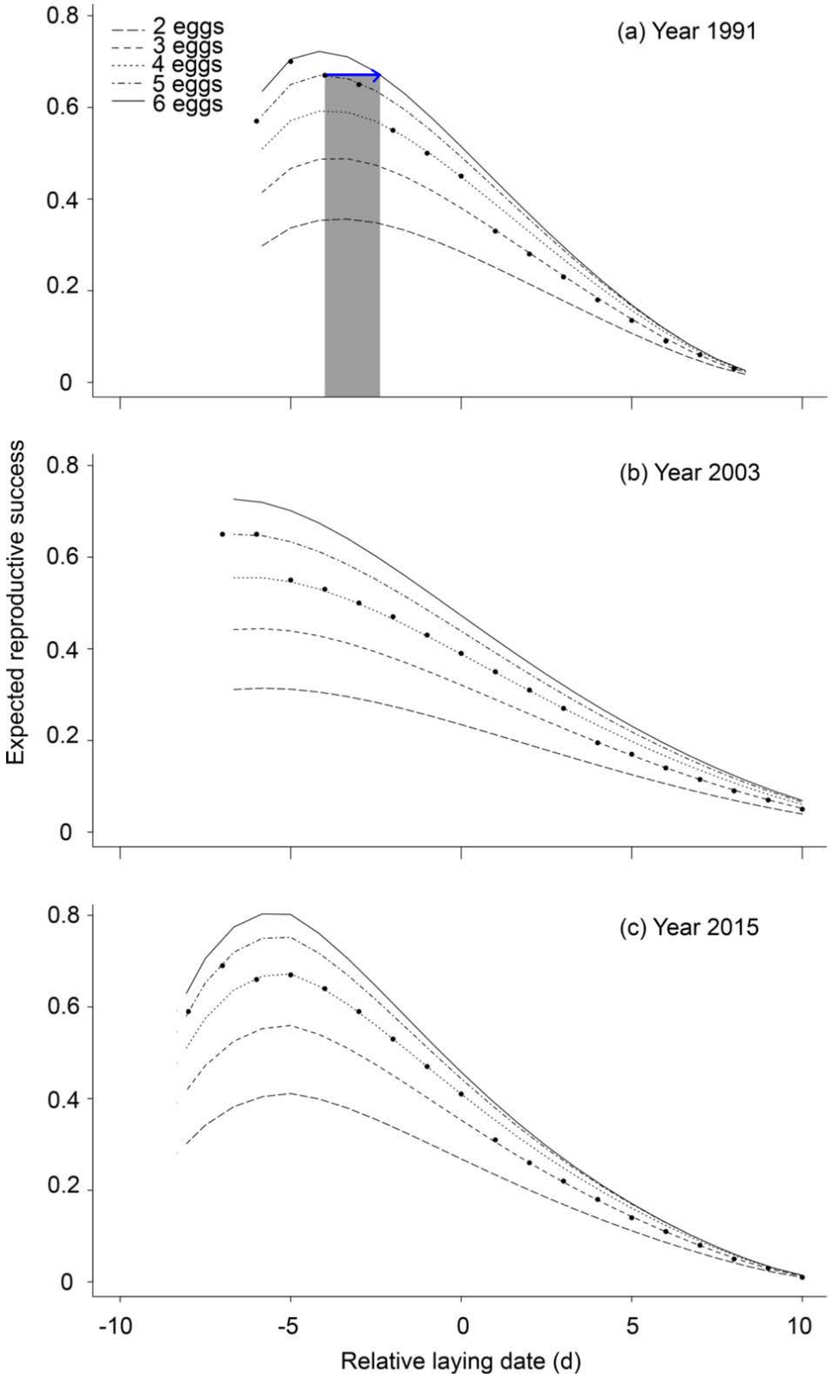


Figure 2.3 Expected reproductive success of greater snow geese in relation to relative laying date for birds laying a hypothetical clutch size of 2 to 6 eggs at the beginning (a), half-way (b) and at the end (c) of the study period. Dots represent mean observed clutch size for each laying dates in those years. On panel (a), the blue arrow and associated gray shading represents the maximum number of days that a bird about to lay 5 eggs on Day -4 could delay laying in order to acquire enough nutrient to lay an extra egg and achieve a higher reproductive success (see text for details).



Chapter 3. Can spring migrants anticipate conditions at sites further north from those encountered along the way? The case of the greater snow goose

In preparation:

Reséndiz-Infante C and Gauthier G. **Can spring migrants anticipate conditions at sites further north from those encountered along the way? The case of the greater snow goose.**

3.1 Résumé

La phénologie de reproduction de nombreux migrateurs de longue distance se reproduisant à de hautes latitudes reste insensible ou ne réagit peu au réchauffement climatique. Afin de permettre l'ajustement de la vitesse de migration et de la date d'arrivée sur le site de reproduction, les signaux environnementaux rencontrés pendant la migration doivent être reliés aux conditions prévalant sur le site de reproduction. En outre, l'hétérogénéité du réchauffement climatique aux différentes latitudes peut également entraver la capacité des oiseaux à ajuster leur vitesse de migration de façon adéquate. Nous avons examiné dans quelle mesure les températures rencontrées sur les haltes migratoires étaient de bons prédicteurs de la température dans les haltes subséquentes et au site de reproduction de la grande oie des neiges (*Chen caerulescens atlantica*), une espèce arctique dont la phénologie de reproduction a peu changé au cours des trois dernières décennies. Nous avons également examiné les tendances de la température à diverses haltes migratoires utilisées par les oies sur une période de 40 ans. Nous avons constaté que le réchauffement était plus marqué dans les haltes migratoires et les aires de reproduction arctique que dans celles plus au sud. La température moyenne et le taux de changement de la température observés dans les haltes migratoires au sud, où cette espèce accumule la plus grande partie de ses réserves endogènes, étaient faiblement corrélés à la température prévalant dans les haltes migratoires plus au nord et sur le site de reproduction situé 3 000 km plus au nord. Les corrélations entre la température aux haltes migratoires et le site de reproduction diminuaient également avec l'augmentation de la distance entre les sites. Enfin, la date de ponte était fortement liée à la température à l'arrivée sur le site de reproduction et pendant la période précédant la ponte, mais pas à la température rencontrée aux haltes migratoires. Les températures rencontrées le long de la route migratoire sont donc un mauvais prédicteur des conditions prévalant sur le site de reproduction au cours d'une année donnée, sauf lorsque les oies s'approchent suffisamment du site de reproduction. Il peut s'agir d'une contrainte majeure qui empêche les oies d'ajuster leur phénologie migratoire aux conditions de leur aire de reproduction et qui peut expliquer pourquoi leur phénologie reproductive n'a pas changé malgré une forte tendance au réchauffement sur l'aire de reproduction.

Mots clés : *Chen caerulescens atlantica*, migrateurs de longue distance, température, haltes migratoires, réchauffement climatique

3.2 Abstract

The breeding phenology of many long-distance migrants breeding at high latitudes remains unresponsive or respond only slightly to climate warming. In order to adjust migration speed and arrival time on the breeding ground, environmental cues encountered during the migration must be related to conditions prevailing at the breeding site. In addition, heterogeneity in climate warming across latitudes may further hamper the ability of birds to adjust their migration speed adequately. We examined to what extent temperature encountered at staging areas were a good predictor of temperature at subsequent staging areas and at the breeding site in greater snow geese (*Chen caerulescens atlantica*), an arctic species that showed little change in its breeding phenology over the past 3 decades. We also examined temperature trends at various staging areas used by geese over a 40-year period. We found that warming was stronger in the arctic staging areas and breeding site than at southern staging areas. The mean temperature and the rate of temperature change encountered at southern staging areas, where this species accumulates most of its body reserves, were weakly correlated to temperature prevailing at more northern staging areas and the breeding site located 3,000 km further north. Correlations in temperature between staging areas and the breeding site also decreased with increasing distance between sites. Lastly, laying date was strongly related to temperature at arrival and during prelaying on the breeding ground but not to temperature encountered on staging areas during migration. Temperatures encountered along the migratory route are thus a poor predictor of conditions prevailing at the breeding site in any given year except when geese are getting very close to the breeding site. This may be a major constraint preventing geese of adjusting their migratory schedule to conditions on their breeding ground and may explain why their reproductive phenology did not change despite a warming trend at their breeding site.

Keywords: *Chen caerulescens atlantica*, long distance migrant, temperature, staging areas, climate warming

3.3 Introduction

Migrating animals often travel over long distances to exploit seasonal resource pulses occurring at high latitudes during the summer (Alerstam et al. 2003, Shaffer et al. 2006). In birds, environmental conditions encountered during spring migration can influence timing of breeding and reproductive success due to carry-over effects (Studds and Marra 2005, Legagneux et al. 2012, Harrison et al. 2013). Bird migration requires a considerable amount of energy and most long-distance migrants have to make multiple stops along the route in order to rest and replenish energy stores (Shaffer et al. 2006). Staging areas typically provide birds with abundant and high quality food resources, but their timing and availability depend on inter-annual fluctuation in environmental conditions (Tøttrup et al. 2008).

Departure time of long-distance migrants from wintering grounds is mainly triggered by the photoperiod, a fixed cue independent from environmental conditions (Gwinner, 1996, Bauer et al. 2008). As migrating birds approach their breeding grounds, they should fine-tune their movements using environmental cues such as temperature and food availability to cope with inter-annual variation in conditions (Marra et al. 2005; Tøttrup et al. 2008). Although many weather-related factors influence migration speed, temperature remains one of the most important (Bauer et al. 2008, Tøttrup et al. 2010, Ovaskainen et al. 2013, Haest et al. 2018). Temperature is a key determinant of biological processes such as the onset of plant growth or insect emergence and thus influences refueling opportunities at stopovers. It was proposed that herbivorous birds moving northwards in spring surf on a “green wave” as they continuously encounter nutritious young plants at successive stopovers due to the staggered onset of vegetation growth with latitude (Drent et al. 1978, Shariatinajafabadi et al. 2014, Kölzsch et al. 2015, but see Wang et al. 2019). Birds should time their migratory movements in order to benefit from optimal feeding conditions because individuals arriving too early or too late at a staging areas may face reduced feeding opportunities.

Arrival time on the breeding ground has a strong influence on timing of breeding and reproductive success of migratory birds (Saino et al. 2003). This is especially true in arctic ecosystems due to the short breeding season and narrow peak of food availability in summer.

Arriving at the optimal time depends on the capacity of birds to anticipate environmental conditions at the breeding ground using available information along the flyway (Marra et al. 2005). Because seasonality increases with latitude, environmental cues such as temperature and food availability are likely to become more reliable to anticipate conditions further north as birds approach their breeding grounds (Bauer et al. 2008). As birds advance in their migration, potential adjustments in migration speed will be increasingly constrained by staging duration and departure time from previous stopovers (Nilsson et al. 2013; Schmaljohann and Both 2017). Therefore, temperature and feeding conditions encountered at successive staging areas and upon arrival in the Arctic may both influence the timing of breeding.

Migrating birds have experienced climate warming across much of the northern hemisphere in recent decades, but the rate of warming has been faster at higher than lower latitudes (IPCC 2014, Francis et al. 2017). Uneven rates of climate warming along the flyway may create a mismatch between conditions encountered at successive staging areas (Both and te Marvelde 2007). For herbivores, this means that their migration schedule may no longer be in phase with the 'green wave', leading to a mismatch between feeding requirements of migrants and vegetation availability at staging areas. This may have important consequences on their body condition and future reproduction.

The greater snow goose (*Chen caerulescens atlantica*) is a long-distance migrant that must accumulate large fat stores at spring stopovers for migration and subsequent reproduction. Despite a warming trend on the breeding ground, its mean laying date has remained constant over the last three decades (Gauthier et al. 2013, Reséndiz-Infante et al. 2020), leading to potential mismatch between hatching of goslings and the timing of peak food availability (Doiron et al. 2015). We examined some factors that could explain the lack of response of the breeding phenology of this goose population to warming temperature. First, we determined to what extent warming trends differ among spring staging areas and the breeding ground, which could limit the ability of migrating geese to adjust their breeding phenology. Secondly, we hypothesized that conditions encountered at their temperate staging areas could be a poor predictor of conditions prevailing at their arctic staging and breeding sites, which would prevent birds from adjusting their migration schedule and arrival time to conditions on the breeding ground. To test this idea, we examined if mean temperature or its rate of change encountered at any given stopover during the migration were correlated to temperature at subsequent stopovers and ultimately at arrival on the breeding ground in the same year. We expected these correlations to be weak, especially between temperate and arctic staging areas, because birds move across different air masses. Lastly, previous studies had shown that laying date in this population was strongly related to temperature prevailing during the prelaying and laying period on the breeding ground (Dickey et al. 2008). We tested if laying date could also be affected by temperature encountered at various stopovers during spring migration.

3.4 Methods

3.4.1 Study species and study areas

The greater snow goose winters along the Atlantic coast of the United States (Gauthier et al. 2005). At the end of the winter, in late March, they migrate to the St. Lawrence valley in southern Quebec where they stage for 6 to 8 weeks (Figure 3.1, Béchet et al. 2003). During that period, they gradually move downriver and northeastward. Geese accumulate most of their body reserves for the subsequent migration to the Arctic and reproduction while staging along the St. Lawrence River (Gauthier et al. 1992). In these areas, geese feed on waste corn, new growth in hayfields and in coastal marsh plants (bulrush, *Schoenoplectus americanus* and cordgrass, *Spartina alterniflora*, Gauthier et al. 2005).

Greater snow geese breed across the eastern Canadian Arctic Archipelago, north of ca. 68˚N (Gauthier et al. 2005). The largest colony is located on Bylot Island (73˚N, 80˚W), where the breeding ecology of the population has been studied for the past 30 years (Gauthier et al. 2013, Reséndiz-Infante et al. 2020). Geese depart from the St. Lawrence valley for the Arctic in mid to late May, rather synchronously every year (Bêty et al. 2003). Migration from the St. Lawrence valley to the Bylot Island colony, a distance of ca. 3,000 km, lasts 1 to 2 weeks (Gauthier et al. 1992, Bêty et al. 2003). Geese are known to stop in two regions in between. A first area is along river valleys throughout a large portion of Nunavik (LeHenaff et al. 1995), a low Arctic region dominated by low shrubs, mainly dwarf birch (*Betula nana*) and willows (*Salix* spp). A second area is located further north in low-lying coastal areas of north Foxe Basin and further inland on Baffin Island (Matt Evans, pers. comm.), an area where some birds also breed. Duration of stopovers at these two arctic sites is likely variable among individuals and years and it is unknown if all birds stop at both sites or if one may be overflown. Average distances traveled by geese between these staging areas are 1,470 km from the St. Lawrence valley to Nunavik, 1,300 km from Nunavik to Baffin Island and 400 km from Baffin Island to the breeding colony of Bylot Island (distance based on centroid of area used at each site).

In late May, when geese arrive in these northern areas, most of the ground is still covered by snow and feeding opportunities may be limited. Upon arrival on Bylot Island, geese concentrate on the few snow-fee patches located on south-facing slopes where they can feed prior to laying (Gauthier 1993). Egg production relies on a combination of nutrient stores accumulated by females at southern staging areas and food acquired locally in the Arctic during the prelaying period (Gauthier et al. 2003). Reproductive success is strongly related to the timing of breeding, being highest in early breeders (Lepage et al. 2000).

3.4.2 Definition of stopover areas

Areas used by geese during their stopover in the St. Lawrence valley are well known. We delimited this stopover based on the citizen science database eBird (Sullivan et al. 2009) and on scientific studies (Reed et al. 1998, Béchet et al. 2003, Gauthier et al. 2005). Although geese gradually move downriver along the St. Lawrence valley as spring progresses, the area was considered as a single stopover because the whole area is used by geese during spring and temperatures are highly correlated among different sites within this area. Stopover areas in Nunavik and on Baffin Island were delimited using: (1) locations of birds (n = 54) marked on Bylot Island with satellite transmitters and tracked from 2007 to 2011 (Joël Bêty, unpubl. data), (2) data from aerial surveys conducted in 2006 during environmental assessment studies for industrial projects in Nunavut (Matt Evans, pers. comm.) and (3) the literature (LeHenaff et al. 1995). In these two regions, stopovers were defined as the area where groups of radio tracked geese (n > 2 birds) were observed to stay >2 days. Although not all radio-tracked birds migrated to the breeding colony of Bylot Island, data on areas used by these birds during the spring migration was still adequate to coarsely delimit stopover areas suitable for migrating snow geese. Polygons for the three stopover areas were refined according to known goose habitat preferences using vegetation and elevation digital layers in shapefile format obtained from Natural Resources Canada (http://geogratis.gc.ca/geogratis/en/search). Finally, the breeding area for this study was defined as the south plain of Bylot Island where a large snow goose colony is located. See Figure 3.1 for the delimitation of the stopovers and breeding area used in this study.

3.4.3 Data

We obtained daily temperature data from 1979 to 2018 for each of the delimited stopover areas and the breeding area on Bylot Island from the high-resolution North American Regional Reanalysis (NARR, pixel=32 km) produced by the National Centers for Environmental Prediction (Mesinger et al. 2006). Temperature data from weather stations are very scarce for the arctic regions. Reanalysis methods integrate remote sensing data with observational ground data into multidimensional datasets that provide a continuous spatial and temporal time series of temperature. We nonetheless validated temperature data from the reanalysis with observational data from weather stations at a few sites (Annex S3.1, Table S3.1).

We extracted temperature data for the period when the bulk of the geese were most likely to be present at each stopover and for the period of arrival and prelaying on the breeding ground. These periods were 1 April to 15 May in the St. Lawrence valley, 10 to 31 May in Nunavik, 20 May to 5 June on Baffin Island and 30 May to 15 June on Bylot Island. Because of the lengthy period that geese stage in the St. Lawrence valley, we also used a shorter sub-period similar in length to other sites, from 1–15 May, which corresponds to the end of the staging there. There was some overlap between successive periods due to inter-individual differences in the time that geese arrive and depart at each site. Daily mean temperatures were extracted from reanalysis data to create subsets for each of these areas and periods. Datasets and digital layers were processed in ArcGIS 10.4 and R 3.2.3 (R Core Team 2015, available at https://www.R-project.org/). Data on laying dates of the population breeding on Bylot Island were collected from 1991 to 2018 (for details see Reséndiz-Infante, 2020)

3.4.4 Statistical analyses

We first examined temperature trends over the period 1979–2018 during spring migration. We calculated average annual temperature for each area and time period defined above based on daily values. A preliminary analysis revealed the presence of autocorrelation in most time series. Because of that, we first fitted auto-regressive integrated moving average (ARIMA) models for each period and study site (methodological details are provided in Annex S3.2) to extract temporal trends.

In a second analysis, we measured the degree of correlation in mean temperature between areas and periods in the same year for the time period 1979 to 2018. We used the residuals from the models selected in the ARIMA analyses to conduct the correlation analyses among sites. We first correlated mean temperature in the St. Lawrence valley (both periods, i.e. 1 April–15 May or 1–15 May) to mean temperatures in Nunavik, Baffin Island and Bylot Island for the same time periods and for later periods (10–31 May, 20 May–5 June, and 30 May–15 June). In the next analysis we correlated Nunavik mean temperatures for the period 10–31 May to Baffin Island and Bylot Island mean temperatures during the same period and during 20 May–5 June, and 30 May–15 June. Finally, we correlated Baffin Island mean temperatures for the period 20 May–5 June to those on Bylot Island during the same period and during 30 May–15 June. We also calculated the annual rate of change in temperature at each site. Using daily temperature data, we conducted linear regression analyses for each year, site and time period. The slope of these annual relationships were correlated to the slopes from another area for the same or the subsequent period following the same logic as for mean temperature (see above).

Finally, we examined the influence of temperature encountered by geese at various stopovers and at arrival on the breeding ground on laying dates with regression analysis for the period 1991–2018. To do so, we built a set of models using different combinations of stopover areas along with the breeding area. No multicollinearity issues were found, besides correlation coefficients among variables entered in this analysis were low ($r \leq 0.37$; see results). Model selection and model averaging was based on AIC using the R package AICmodavg (Mazerolle 2019).

3.5 Results

Over the period 1979–2018, temperature between 1 April and 15 May increased by 0.5°C in the St. Lawrence Valley (slope = 0.013°C/yr; Figure 3.2 and Annex S3.3, Table S3.2), 2.1°C in Nunavik (slope = 0.053°C/yr), 3.4°C in Baffin Island (slope = 0.085°C/yr), and 2.6°C at the breeding ground (slope = 0.065°C/yr). During the staging of geese in the Arctic, temperature warmed by 1.6°C in Nunavik between 10 and 31 May (slope = 0.039°C/yr) and 1.1°C in Baffin Island between 20 May and 5 June (slope = 0.028°C/yr). Finally, at Bylot Island, temperature warmed by 0.85°C between 30 May and 15 June (slope = 0.021°C/yr).

In the second analysis, we first examined if temperature at the various staging areas and at arrival on the breeding ground were correlated for the same time periods (Figure 3.3). Mean temperature during the whole staging period along the St. Lawrence valley was moderately correlated to mean temperature in Nunavik at the same time but weakly with sites further north. However, when restricting the analysis to the last two weeks of staging in the St. Lawrence (1-15 May), the correlation with Nunavik weakened and disappeared with sites further further north. Mean temperature between Nunavik, Baffin Island and Bylot Island were correlated, with the strongest correlation found between the last two sites, which were the closest ones.

Next, we examined how temperature encountered at each staging sites was a good predictor of temperature encountered by geese at the next time period in areas further north. In all cases, correlations were weaker than in the previous analysis (Figure 3.4). Mean temperature along the St. Lawrence was correlated with mean temperature at the next time period in Nunavik but not with areas further north; all correlation coefficients were weak and non-significant when restricting the analysis to the last two weeks of staging in the St. Lawrence (Figures 3.4a, b). Mean temperature in Nunavik was moderately correlated with temperature at the next time period on Baffin Island but not with the arrival time on Bylot Island (Figure 3.4c). Finally, mean temperature on Baffin Island was moderately correlated to temperature at arrival time on Bylot Island.

Analyses based on rate of change of temperature revealed the same pattern as with mean temperature except that most correlations were weaker and almost all were non-significant, either for the same or the next time periods between sites (Annex S3.3, Figures S3.1 and S3.2). The only strong correlation was between Baffin and Bylot Islands for the same time period, but it disappeared when comparing successive periods.

In our analysis of the effect of temperature encountered by geese at staging sites on laying date, there were five competitive models (ΔAIC<2) with various effects (Annex S3.4, Table S3.3). All these models retained an effect of temperature on Bylot Island at arrival, but three models including the top one also retained an effect of temperature at the Baffin Island staging site. The multi-model inference on the 5 models with ΔAIC< 2 showed that laying date was negatively related to temperature at arrival on Bylot Island (model-averaged estimate = -1.34, 95% CI: -2.04, -0.65; Annex S3.4, Table S3.4). However, laying date was not significantly related to temperature encountered by geese on Baffin Island despite a negative trend (model-averaged estimate = -0.63, 95% CI: -1.39, 0.13). Repeating the analysis using temperature only during the last part of the staging period along the St. Lawrence (1-15 May) instead of the full period yielded the same results (Annex S3.4, Tables S3.5 and S3.6).

3.6 Discussion

We used a 40-year temperature dataset to determine if conditions along the migratory route could be used by greater snow geese to anticipate those at sites further north. We found that all sites used by geese in spring experienced recent warming trends but that they were generally more intense in the Arctic than at temperate staging areas. Mean temperature and rate of change in daily temperature at spring staging areas were weakly related to those at the next staging area, and generally not related to those at more distant areas or at the breeding site. Therefore, geese would only be able to vaguely predict conditions to be expected at their next stopover at best. Lastly, the largest influence on laying date was from the temperature prevailing at arrival at the breeding site on Bylot Island.

3.6.1 Warming and other changes along the migration route

As expected, warming trends along the spring migratory route were heterogeneous across latitudes and time periods, and warming was generally stronger at northern latitudes than at lower latitudes in the temperate region. The weakest warming trend occurred in the St. Lawrence valley, the most southern staging area. In the latter region, greater snow geese accumulate most of their body reserves for spring migration and subsequent reproduction (Gauthier et al. 1992). Over the last 40 years, departure dates of geese from the St. Lawrence Valley for the Arctic did not change as most geese depart between 15 and 23 May (Gauthier et al. 1992, Bêty et al. 2003, P. Legagneux unpubl. data). Due to human-made modifications along the St. Lawrence valley, geese have switched their feeding behavior from predominantly marsh plants (bulrush, cordgrass) to one dominated by agricultural plants (waste corn, new growth in hayfields; Gauthier et al. 2005). Nowadays, geese tend to depart in better condition for the Arctic than in the past (Gauthier et al. 2005). Since 1999, a spring hunt combined with efforts from farmers to scare geese away from croplands has increased disturbance of birds along the St. Lawrence estuary. This has changed their distribution, habitat use and temporarily reduced their body condition (Béchet et al. 2003, 2004, Féret et al. 2003). In contrast to the temperate region, the arctic staging areas used by geese in Nunavik and on Baffin Island have not been directly affected by human activities but have experienced a strong warming trend and an increase in primary productivity (Berner et al. submitted). During the short period when geese are present in spring, these arctic staging areas have warmed by at least 1 to 2 °C, enough to potentially advance snowmelt and improve feeding conditions for geese.

Considering all these changes along the migratory route, we could have expected an advance in departure date of geese for the Arctic to escape human disturbance at low latitudes and benefit from climate warming effects at northern latitudes. However, this apparently did not occur (Gauthier et al. 1992, Bêty et al. 2003, P. Legagneux unpubl. data). Our analysis suggests that the weak warming trend experienced by geese on their temperate staging areas may be one of the factors preventing them from departing earlier for the Arctic. Similar to geese, purple martins (*Progne subis,* Fraser et al. 2013) and pied flycatchers (*Ficedula hypoleuca*) have experienced uneven warming across their migratory routes (Ahola et al. 2004, Both and te Marvelde 2007), which may limit their ability to conditions prevailing at the breeding site. Finally, the positive warming trends found in most of the spring staging areas where geese stop may have improved their feeding conditions, especially for early migrants which often face the harshest weather conditions (Tøttrup et al. 2010), thus enhancing their body condition. Improved body stores in early migrants may in turn be an important factor that allow them to breed early (Reséndiz-Infante et al. 2020).

3.6.2 Predicting future conditions from those encountered at the current location

Not surprisingly, distance was an important factor in explaining the strength of correlations in temperature between paired sites during the same period. Indeed, temperature between north central Baffin Island and Bylot Island, two sites ca. 400 km apart, where highly correlated whereas temperature between the St. Lawrence valley and Nunavik or Nunavik and north central Baffin Island, each separated by ca. 1,500 km, were weakly related. Considering that the St. Lawrence valley is in a temperate climate zone whereas Nunavik and North Baffin Island are in the Arctic, we could have expected a greater correlation between the two sites within the same climate zone than between sites in different zones (temperate vs Arctic) but this was not the case. The gradual decay of correlations in temperature with distance means that temperatures encountered by geese while staging in the temperate St. Lawrence valley do not provide much information on conditions prevailing in the Arctic and especially at their breeding site, which is experiencing a faster warming rate than at lower latitudes. Therefore, an early spring at a southern staging site does not imply an early spring also at a distant northern site. The same applies for geese that have entered the Arctic climate zone and are staging in Nunavik.

In order to adjust their migration schedule based on conditions encountered along the route, local conditions experienced by geese must provide reliable information on conditions to be expected at the next staging site in the coming days/weeks. However, we found that the predictive power of future conditions was low, either when using mean temperature or its rate of change within a season. This supports our prediction that conditions encountered at temperate staging areas or even low Arctic ones in spring are a weak predictor of those to be expected at or near the arctic breeding site. Without reliable environmental information, it is difficult for geese to anticipate future conditions and time their migration schedule accordingly. This lack of predictability may explain why several goose populations apparently do not surf on the green wave as previously suggested (Wang et al. 2019). Under these circumstances, photoperiod may remain the best cue to use for a good part of the migration. Other less predictable local conditions (e.g. favorable tail wind) may control departure date from staging areas within a suitable time window determined by photoperiod, like in the long-distance migrant wood thrush (*Hylocichla mustelina*, Stanley et al. 2012).

The difficulty to anticipate conditions to be encountered at upcoming staging sites based on current conditions combined with a weaker warming occurring at lower than higher latitudes, has a strong potential to lead to frequent mistimed arrival time on the breeding ground. This will limit the ability of geese of benefiting from favorable nesting conditions early in the season, especially in years with an early snow-melt. When this happens, goslings experience a trophic mismatch with the food quality peak, which advances due to early spring and results in reduced growth of goslings (Doiron et al. 2015). It is only when geese are getting close to the breeding site (i.e. Baffin Island in our case) that local conditions can be informative of conditions on the breeding ground. Based on that, geese may either overfly their last staging area to speed up migration when spring is early or stop and wait if spring is late. However, if spring is early, overflying their last staging area should result only in a minor advance in the arrival time on the breeding ground, which would prevent birds from taking full advantage of suitable feeding conditions. Prior to egg-laying, females need time to feed in order to recover body condition lost during migration (Bêty et al. 2003, Gauthier et al. 2003). This would prevent geese from laying immediately after arrival even when snow-free nesting sites are already available, thereby explaining why in early springs geese lay after the 50% snow melt date, contrary to the situation in years of late spring (Gauthier et al. 2013).

3.6.3 Laying date and temperature

The most important predictor of laying date was temperature at arrival and during prelaying on the breeding site. This is because although geese rely on a mixed capital/income breeding strategy, resources acquired on the breeding ground account for most of the energy invested in egg production (Gauthier et al. 2003). Temperature prevailing at that time will determine snow-melt, which will have a direct effect on food availability and also on nest site availability, another factor that can also affect laying (Dickey et al. 2008).

We would have expected that temperature encountered at other stopovers, and especially in the St. Lawrence valley, where accumulation of most body reserves take place in spring (Gauthier et al. 1992) would have an influence on laying date. Other studies had documented carry-over effects of environmental conditions in spring on the breeding performance in this population (Bêty et al. 2003, Legagneux et al. 2012). However, these carry-over effects appear to be more important when conditions on the breeding ground are less favorable for breeding (Legagneux et al. 2012). Thus, it is possible that geese evolved this mixed capital/income breeding strategy to cope with the high environmental variability in the Arctic. For instance, poor conditions encountered on southern staging areas in spring could be somewhat compensated by good conditions encountered at arrival on the breeding ground, or vice versa. Such situation may be frequent as our analysis showed a low correlation between temperature encountered on distant staging areas and those at arrival in the Arctic in the same year. We also found a weak trend for a positive effect of temperature encountered on the last staging area in North Baffin Island and laying date. Given the proximity between this staging site and the breeding site, egg formation may have started by at the time geese arrive in North Baffin Island, and thus feeding taking place at this site may be part of the prelaying period and influence egg formation.

3.6.4 Study limitations

In this study, we lack data at the individual level on migration chronology and subsequent reproductive performance. Detailed information on individual departure date from temperate staging areas and arrival date in the arctic breeding ground, combined with nesting success data are only available for a 2-year study in this species (Bêty et al. 2003). This is not uncommon considering that tracking migration and reproduction of long-distance migrants at the individual level require the use of expensive technology such as satellite telemetry, which considerably limits sample size or number of years of tracking (Shariatinajafabadi et al. 2014, Kölzsch et al. 2015). Some studies nonetheless showed that while migration speed and chronology often differ among individuals within populations, migratory behavior tends to be repeatable within individuals (Bêty et al. 2004, Stanley et al. 2012, Fraser et al. 2013). It is thus important to study directly the effect of warming on individual variation in timing of migration because, for instance, climatic variation affects more early migrants (Tøttrup et al. 2010). Finally, our limited knowledge of the behavior of geese at northern staging areas (Nunavik and Northern Baffin Island in our case) also prevents us of determining precisely stopover duration or to what extent geese are adjusting their migration speed (Schmaljohann and Both 2017).

3.7 Conclusion

Overall, our results show that temperature encountered along the migratory route of the greater snow goose is not a good predictor of conditions occurring at more northern staging areas or on the breeding ground. It is only when geese are getting close to their breeding site, i.e. within a few hundred kilometers, that conditions encountered are similar to those prevailing on the breeding ground but by then it may be too late to adjust migration speed to advance arrival time on the breeding ground in early spring years. Moreover, their northern staging areas and breeding ground areas are warming at a faster rate than southern staging areas, which further increases the potential for mistimed arrival on the breeding ground. This will limit the ability of this species to adjust its breeding phenology to a changing environment. However, further research needs to consider the details of spring migration at the individual level and its response to a warming climate.

3.8 Annex S3: Supplementary material

Annex S3.1 Reanalysis data validation

Annex S3.2 Description of ARIMA method

Annex S3.3 Supplementary results

Annex S3.4 Model selection

Figure 3.1 Map of the spring stopovers and the breeding grounds of the greater snow geese.

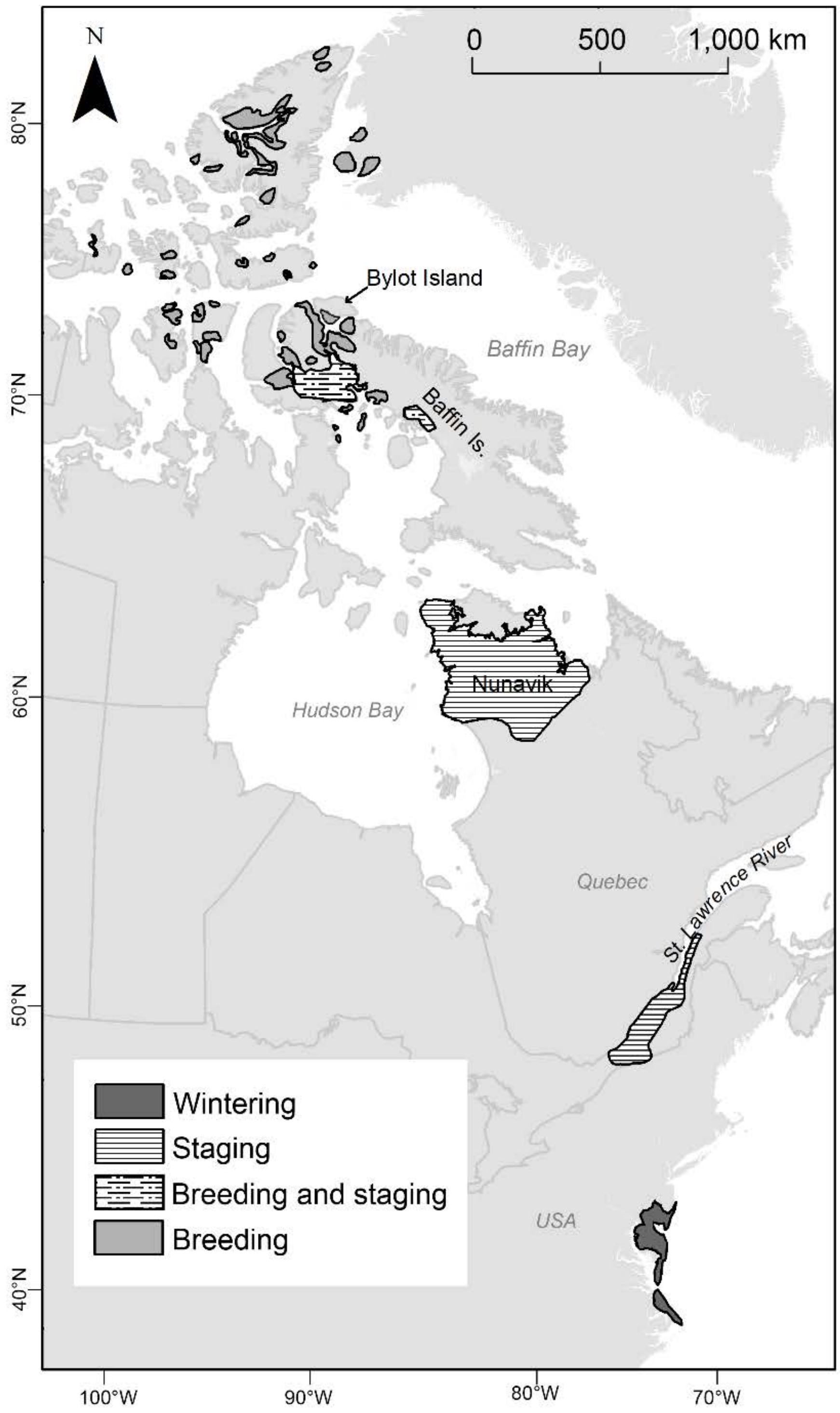


Figure 3.2 Warming trends in mean temperatures over 40 years (1979–2018) at staging areas and the breeding ground of the greater snow goose.

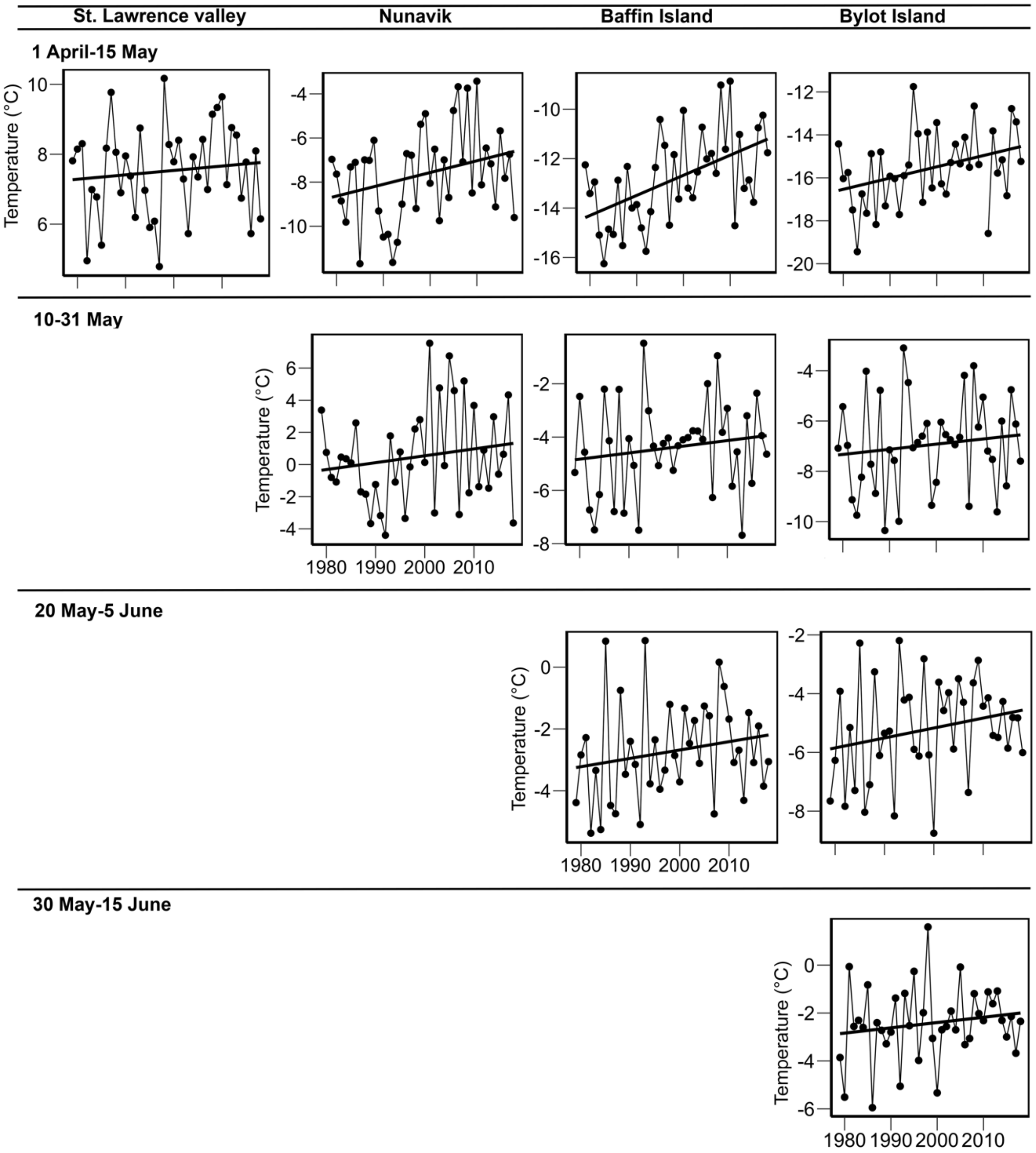


Figure 3.3 Pairwise correlations in temperature between staging areas or the breeding site (Bylot Island) of geese for the same time periods over a 40-year time span (1979–2018). For the St. Lawrence valley stopover, we used the whole staging period (1 April–15 May) and only the last two weeks (1–15 May). Temperatures are the residuals from the time series analysis of mean annual temperature based on an ARIMA (see Annex S3.3, Table S3.2). Correlation coefficients (r) and p-values are provided for each graph, df=38.

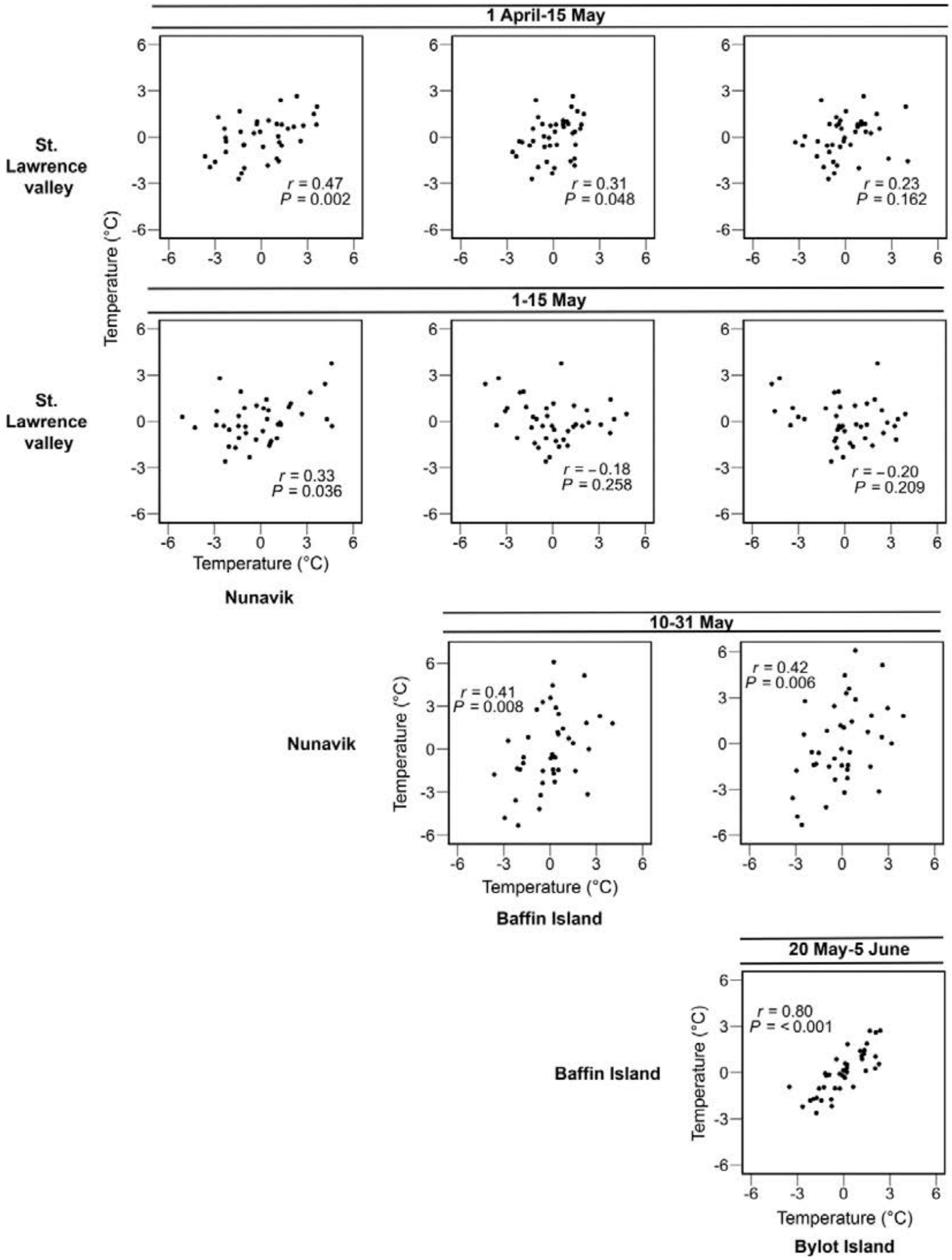
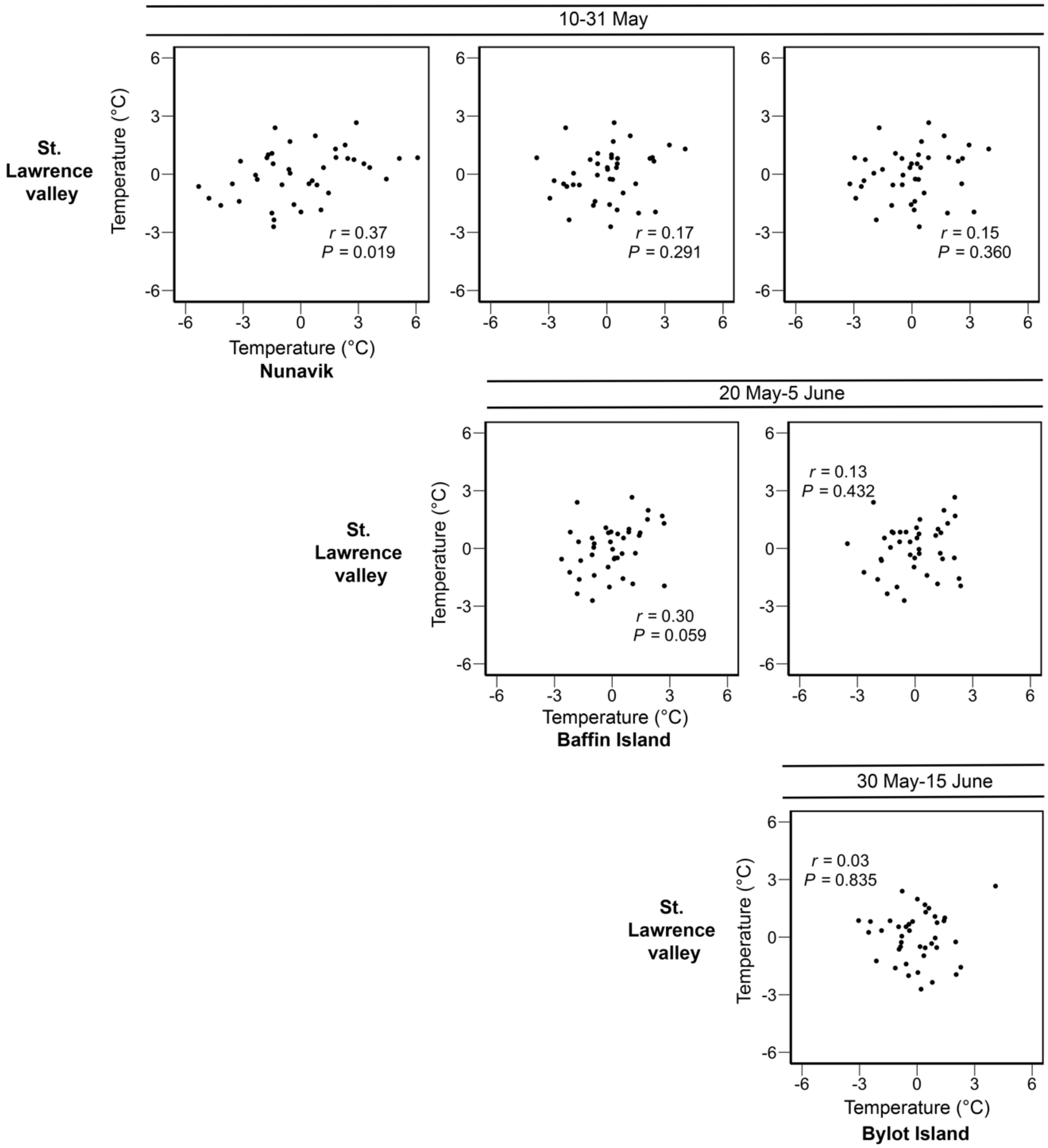
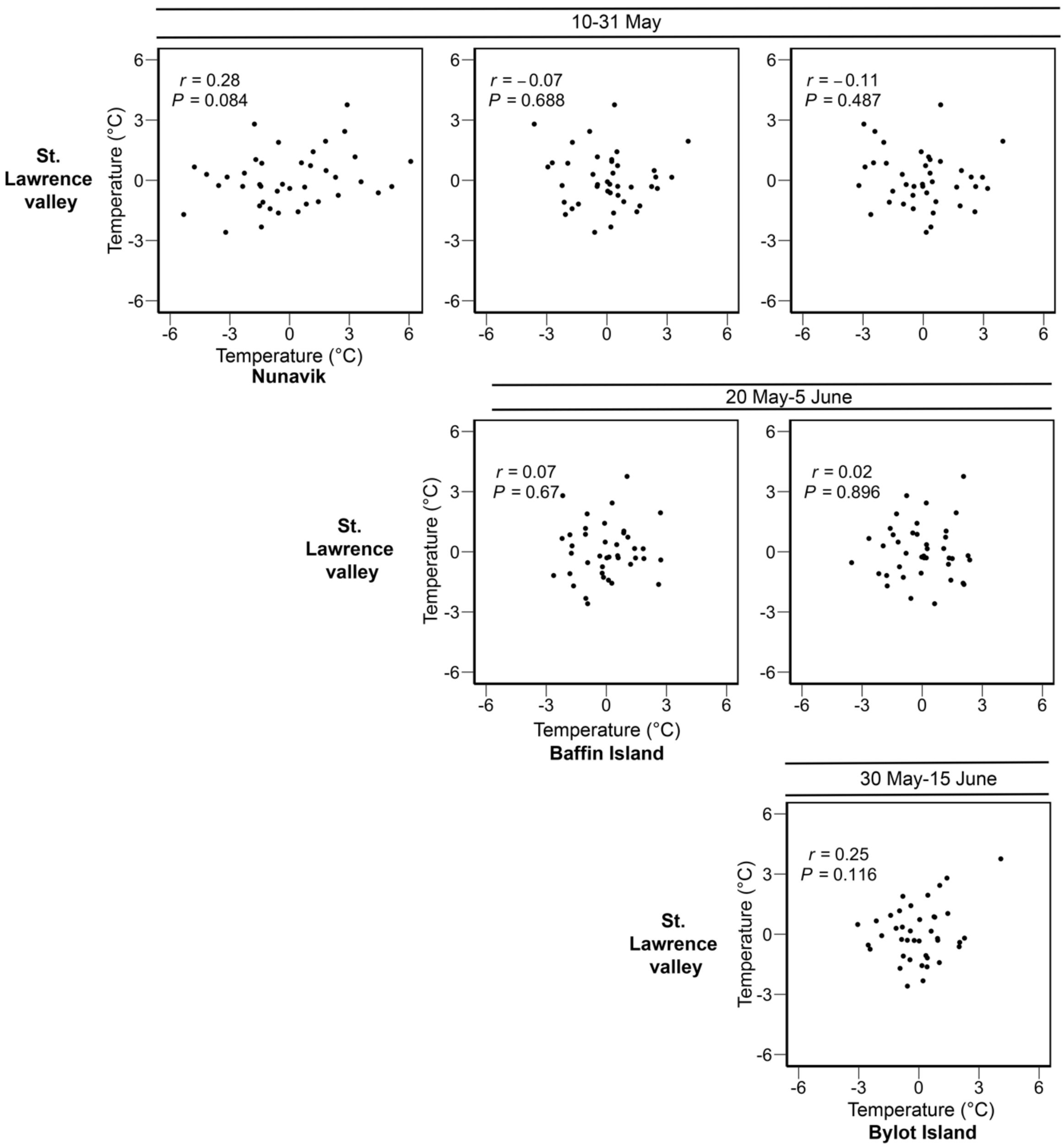


Figure 3.4 Pairwise correlations in temperature between staging areas or the breeding site (Bylot Island) of geese for subsequent time periods over a 40-year time span (1979–2018). For the St. Lawrence valley stopover, we used the whole staging period (1 April–15 May) and only the last two weeks (1–15 May). Temperatures are the residuals from the time series analysis of mean annual temperature based on an ARIMA (see Annex S3.3, Table S3.2). Correlation coefficients (r) and p-values are provided for each graph, df=38.

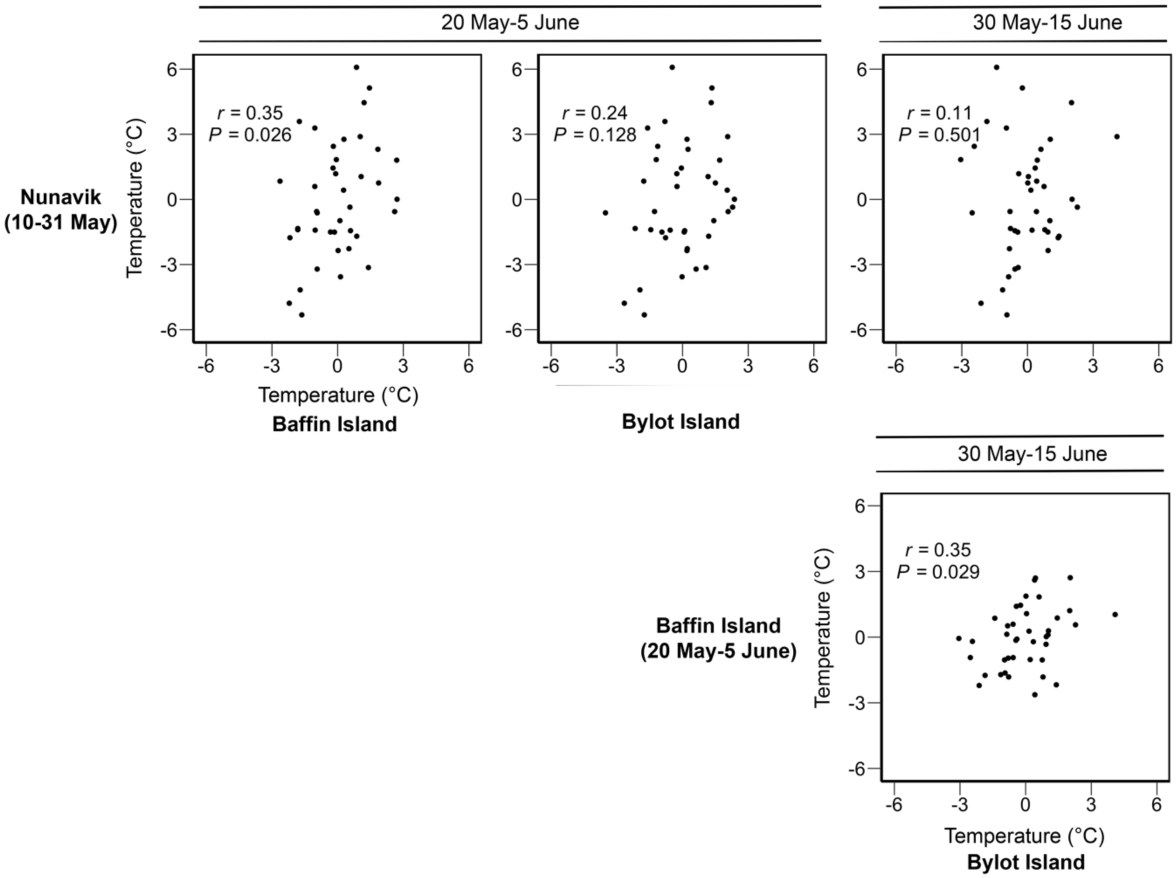
a) St. Lawrence valley (1 April–15 May)



b) St. Lawrence valley (1–15 May)



c) Arctic sites



General conclusion

Current global warming has triggered a broad range of responses in wild animal populations all over the world (Høye et al. 2007, Post et al. 2009, Ovaskainen et al. 2013, Dunn and Møller 2014). Although many bird populations have shown phenological responses to climate warming, for instance by advancing laying date, the breeding phenology of many long-distance migratory species appear to remain unchanged (Møller et al. 2008). This particular group of species seem to be constrained by their migratory schedule (Fraser et al. 2013).

Long-distance migratory birds are more vulnerable to climate warming than other groups because they travel long distances with almost no information in advance on conditions prevailing at their final destination, the breeding grounds. These birds also experience heterogeneous warming during migration, usually stronger at the breeding grounds at high latitudes, which represents an additional challenge when attempting to arrive at an optimal time on the breeding ground to maximize their reproductive success. Studying the effects and the reasons why several bird species are not adjusting their nesting phenology despite environmental changes occurring at their breeding site is essential to understand long-term consequences of climate warming in these species.

In my thesis, I studied the greater snow goose, a long-distance migrant that breeds in the High Arctic. In the last decades, this species has been exposed to rapid environmental changes during its reproductive season, but its laying date remained unchanged (Gauthier et al. 2013). To examine intra-seasonal changes in the breeding phenology of this population and their consequences for its reproductive success, I used long-term data collected on its arctic breeding ground from 1991 to 2015.

My thesis provides a long-term view of the effects of environmental change on the seasonal patterns of reproduction and ultimately on the reproductive success of individuals. While many studies have extrapolated their conclusions to the entire breeding season based on mean values, only a few have examined detailed seasonal patterns in laying date and other reproductive components such as done in my work. This is important because responses occur at the individual level and may differ between early and late breeders (see Ahola et al. 2009, Goodenough et al. 2011, Jónsson et al. 2017). I also examined the role of conditions encountered during the spring migration and upon arrival on the breeding ground in explaining the lack of response of geese in their breeding phenology. My study attempts to document the overall impact on reproductive success of changing conditions experienced by parents and their young over a 25-year period, and to disentangle positive and negative effects at various critical stages of the breeding season. Analyses such as those provided in my thesis are key to understand the vulnerability of long-distance migratory birds exposed to rapidly rising temperatures in seasonal environments.

Consequences of environmental change

In chapter 1, I studied changes in laying date as a proxy of timing of breeding. I found that early breeders nested progressively earlier and late breeders nested progressively later, whereas those near the median showed no change. However, these adjustments were < 3 days and likely not enough to match environmental change. Because of this weak response, consequences of warming temperatures experienced during the breeding season on the phenology of geese and individual components of reproductive success were of different magnitude and direction. Although the seasonal patterns were consistent with those reported by Lepage et al. (2000), environmental change over 25 years resulted in enhanced nesting success and prefledging survival and lower total clutch laid in early breeders, whereas hatching success remain unchanged across laying dates. In addition, I detected a slight seasonal decline in egg survival, which had never been reported before. Finally, survival after fledging decreased with laying date but also showed an overall decline over the course of the study period. These within-season changes highlight the importance of studying long-distance migratory populations at the individual level in order to better understand possible effects and consequences of climate change (Ahola et al. 2009, Goodenough et al. 2011, Jónsson et al. 2017).

Over the study period, some phases of the reproductive cycle of geese apparently benefitted from warming, whereas other phases were negatively affected by environmental change.

These contrasting effects of warming are principally due to improved feeding conditions early in the season due to an advance of snowmelt (Gauthier et al. 2013), which is partly offset later in the season by a trophic mismatch between the hatching time of goslings and the peak nutritive quality of plants (Brook et al. 2015, Doiron et al. 2015). As warming is increasing, these effects may intensify in the future.

Pressure for early laying

In chapter 2, I integrated the six individual components and I estimated the overall reproductive success until young reach one year of age to study the consequences of breeding decisions on the reproductive outcome. Females nesting a few days before the population median achieved the highest reproductive success of the season. Although this seasonal pattern was maintained over the study period, it became steeper over time because the highest reproductive success increased in early breeders and advanced by about 2 days with respect to the population median laying date. This, added to the marginal response of laying date to increasing environmental change, suggests an increase over time in the selection pressure for early breeding. As warming increases, gosling optimal feeding conditions, critical for their growth and survival (Sedinger and Chelgren 2007, Sedinger and Nicolai 2011), move to earlier dates in the season. This also gradually moves the highest reproductive success to earlier laying dates and increases trophic mismatch in late-hatched goslings. Lastly, the observed clutch size was lower than the clutch size yielding the highest reproductive success for most laying dates. I suggested that the time required by females to acquire nutrients for egg production at arrival may constrain their ability to advance laying date and explain the previous result. Thus, my results are still consistent with the idea that females can maximize their reproductive success by trading-off an egg (i.e. lower clutch size) for an earlier hatching (the model of Rowe et al. 1994), as previously suggested by Lepage et al. (2000).

Environmental constraints during the migration

Chapter 3 was relevant to understand factors involved in the lack of temporal change in the mean laying date of the population. First, we found heterogeneous warming along the migratory route and on the breeding ground, with stronger warming occurring at higher than lower latitudes. Second, over a 40-year period we found little correlation between temperature encountered by geese at their southern staging sites and those at more northern sites or at the breeding ground. This suggests that geese are unable to anticipate environmental conditions occurring on the breeding ground while they are at southern staging areas. The lack of reliable information on expected conditions further north is likely preventing adjustments in their migration schedule to optimize arrival time on the breeding ground, for instance by speeding up migration to benefit from early spring conditions when they occur on the breeding ground. This greatly limits their ability to advance laying date sufficiently in years of early spring, which has a strong potential to lead to a trophic mismatch and reduce reproductive success (Doiron et al. 2015).

Lastly, temperature on the breeding site had a strong influence on laying date whereas temperature encountered at staging areas during the migration had a negligible effect. Carry-over effects from poor conditions encountered during migration may be partially compensated by good conditions on the breeding ground due to the mixed capital/income breeding strategy of this population (Bêty et al. 2003, Legagneux et al. 2012). Nonetheless, my analysis showed that geese are unable to take full advantage of years with an early spring on the breeding ground by advancing laying date sufficiently due to the difficulty of anticipating upcoming breeding condition during the migration, which is exacerbated by heterogeneous warming experienced across the migration flyway.

Study limitations

A main limitation of chapters 1 and 2 of my thesis was the lack of data on the same individuals throughout the reproductive season. Detailed longitudinal data of long-distance migratory individuals like geese is difficult to obtain because of their high mobility, especially during the laying period, and after hatch as parents leave the nest with their young soon after gosling are born. This limited our capacity to extend the analyses to potential selection or adaptive processes that may occur at the individual level in response to climate warming. Some factors that play a role in reproductive performance, such as female age, were not considered in this study for the same reason. A main challenge in accomplishing chapter 3 was that temperature data from weather stations is not available in many areas used by geese. Moreover, our knowledge of the spring migration of this population between departure from the temperate staging area and arrival time on the breeding ground is still very limited. A long-term dataset of geese followed with satellite tracking devices does not exist. Although some greater snow geese were marked with satellite transmitters over a few years (2007–2011), the radio-tracking was not very successful and did not allow a complete study of the migration and reproduction at the individual level. More reliable information on arrival time and the prelaying period, which play a role in the timing of breeding (Bêty et al. 2003), would help us to better understand the causes of a lack of adjustment in the breeding phenology of geese and its consequences on reproductive success at the individual level.

The future of the greater snow goose and its research

Systematic monitoring and long-term studies are relatively recent in the Arctic. Despite the importance of this region at a global scale, our knowledge of this region and of the effects of climate change on arctic communities and ecological processes is still very limited. The long-term monitoring on Bylot Island combined with intensive research on key aspects of the biology of the greater snow goose have contributed to a better understanding of this population and its environment, making possible this thesis. It allowed me to identify changes in the breeding phenology and reproductive success of this species, and provided new insights on the ability of geese to cope with current environmental changes and their potential consequences.

Currently considered an overabundant species (Lefebvre et al. 2017), the greater snow goose may not be immediately imperiled by climate change. However, climate change poses a threat for most arctic species (Post et al. 2009, Gilg et al. 2012, Ims et al. 2013), and its negative effects should not be disregarded even for populations that currently appear healthy. Long-distance migratory species, such as the greater snow goose, face not only heterogeneous rate of warming as they move through a latitudinal gradient, but also other human-related threats. Not so long time ago, this population was quite low, with only about

25,000 individuals in the 1960s, compared to ca 800,000 birds nowadays (Lefebvre et al. 2017). It was able to recover because of the establishment of protected areas, in addition to agricultural crops that enhanced their food supply in winter and at its most important spring staging area along the St. Lawrence valley (Gauthier et al. 2005). As a game species, climate change effects should be considered in management decisions that are currently aimed at controlling its population size.

Geese play a key role in the tundra ecosystem, being the main herbivore on Bylot Island in the absence of other large herbivores such as caribou (*Rangifer tarandus*). To protect the tundra ecosystem, we should not only aim to control its population, but also study the potential negative long-term effects of climate warming. In order to understand other long-term potential impacts during the breeding season, it would be relevant to determine which factors influence migration speed and the breeding phenology of early and late breeders to adjust their timing of breeding. My results suggest that the breeding phenology of greater snow geese is strongly constrained by its migratory schedule. To confirm that, it would be useful to mark birds with satellite tracking devices to study details of the spring migratory behavior at the individual level. This could help to determine which environmental conditions contribute to slow down or speed up migration and what are the consequences for the timing of breeding and subsequent reproductive success. In doing so, we could identify and predict warming temperature effects on reproduction for the different segments of the population (i.e. earliest, early, mean, late and latest breeders). It could be also interesting to compare such data with data previously collected from radio tracked geese (2007–2011) to learn if stopover duration has changed. This would provide a better understanding of potential carry-over effects of the spring migration on arrival time, breeding phenology and ultimately reproductive success of geese in a changing climate.

A key focus of future studies should rest upon documenting the long-term effects of trophic mismatch on reproductive success and how the gap between the hatching date of goslings and the peak of food quality has changed over time. Evidence from Doiron et al. (2015) on the effects of warm spring temperatures and trophic mismatch on gosling growth leads to the question of whether trophic mismatch is increasing in parallel to current warming trends in the Arctic. The normalized difference vegetation index (NDVI) studied by Doiron et al. (2014) is a useful proxy to monitor the peak in nitrogen availability for goslings and could be used to detect how much the phenology of plant nutritive quality is moving to an earlier date in response to climate warming. As the nitrogen content of plants is expected to decrease with warming (Doiron et al. 2014), it would be important to monitor the feeding effort of goslings to detect potential changes in response to their changing food supply.

The small adjustments in laying date and clutch size in response to environmental changes found over the course of this study are likely due to phenotypic plasticity. Cooke et al. (1995) showed that the heritability of these traits in a population of lesser snow goose (*Chen caerulescens caerulescens*) is moderate for both (~0.3), which should allow geese to show some genetic response to environmental change. The inherited component of breeding decisions could thus be modified and passed to the next generation, potentially allowing for some microevolutionary changes. However, being a long-lived species, geese have a relatively long generation time of about 6 years (Gauthier and Lebreton 2004), which may slow down an optimal evolutionary response to environmental change. To better understand the future of this species, it is necessary to investigate the limits of phenotypic plasticity and potential microevolutionary changes in this species to elucidate the potential for adaptation under future warming conditions.

My study supports previous findings showing that the reproductive phenology of long-distance migratory populations breeding in seasonal environments is less responsive to climate warming than the one of residents or short-distance migrants (Møller et al. 2008). Temperatures are predicted to steadily increase in the next decades (IPCC 2014, Francis et al. 2017), but the breeding phenology of the greater snow goose is unlikely to respond to match the associated environmental changes. I showed that geese, as several other long-distance migratory species, faces a complex scenario during spring migration that may prevent them from adjusting their breeding phenology to changing conditions on their breeding grounds. As warming continues to increase, arctic vegetation is predicted to lose more nutrient content and the seasonal decline in nutritive quality should be faster (Doiron et al. 2013). Consequently, the seasonal effects on reproductive success reported in this thesis may intensify. Under this scenario, the importance of timing of breeding for successful reproduction is likely to increase in long-distance migratory birds which spend part of their life-cycle in seasonal environments (Visser et al. 2003). The range of possible individual responses to warming may reach a threshold beyond which the apparent benefits of warming on early breeders may no longer exist, reducing reproductive success even for the most productive segment of the population. Reaching such a threshold is likely to have detrimental effects for the dynamic of most populations.

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Annex S1: Supplementary material for chapter 1

Annex S1.1 Field methods used to find nests

Goose nest searches on Bylot Island were conducted using three different sampling schemes. The first one consisted of a systematic nest search within a single main plot (ca. 50 ha) located in the center of the main breeding colony and composed of a mixture of wetland and mesic habitat. All nests found in the plot were monitored in 1992 and from 1994 to 2015. This method yielded the largest number of nests in the dataset (total n = 3,660). The second sampling scheme consisted in systematic nests searches in smaller plots randomly located throughout the main goose colony in the two main habitats (wetland and mesic habitat). Plots were 1 ha in wetland and 4 ha in mesic habitat owing to the lower goose density in the latter habitat. The number of plots was variable each year, as we aimed at monitoring ~50 nests in each habitat. This monitoring took place from 1999 to 2015 and yielded 2,370 nests in the dataset. The last sampling scheme used opportunistic nest searches that were conducted on the largest brood rearing area, about 20 km north from the main nesting colony. In this area, the number of nests is low and variable from year to year and geese typically nest in a more dispersed fashion. Nest searching in this area took place from 1991 to 2015 and yielded a sample size of 1,037 nests.

Annex S1.2 Estimation of laying and hatching dates

For nests found during the laying period, we back-calculated laying date assuming that 1 egg was laid every 33 h. For nests found during incubation and with a known hatching date, we back- calculated laying date from hatching date based on its clutch size, assuming a 23-day incubation period starting at the last-laid egg. For nests found during incubation but with unknown hatching date, we used individual egg density (determined from egg measurements and weight) to estimate the number of days elapsed between laying and the first observation, and back-calculated laying date.

Incubation stage of nests found during incubation and with unknown hatching date (n = 1,795 nests in our dataset) had been estimated in the database using the egg density vs. incubation stage relationship of Lepage et al. (1999). However, this relationship had been determined on a relatively small sample size, and did not take into account if nests had been found early or late during the incubation stage. Therefore, we examined how accurately this relationship could estimate laying date. To do that, we used nests from 2003– 2013 (n = 853) where egg density was measured and for which real laying or hatching dates were also known, either because nests were found during laying or visited at hatching. We then determined the difference between real laying date or laying date inferred from hatching date and laying date estimated with egg density. To estimate the incubation stage, we added the median clutch size (i.e. 4 eggs) to the laying date and subtracted this value from the date in which the nest was found. The difference between real and estimated laying dates was regressed as a function of the incubation stage. Laying dates estimated based on the density method were adjusted by adding the correction based on the regression equation ($y = 2.50 - 0.099x$, $R^2 = 0.46$, 95% CI of slope: -0.132, -0.068; y = difference between real and estimated laying dates in days, x = incubation stage in days).

Annex S1.3. Data validation among sampling schemes used to find nests

To compare nesting data across the three sub-samples of nests (see details on sampling schemes in S1), we proceeded in two steps. We first compared nesting data between nests located in different parts of the colony (main plot in the central area vs. random plots), and then between nests within the colony and those outside the colony (i.e. nests monitored on the main brood- rearing area). We limited the analyses to years when data were available in both sub-samples to eliminate potential confounding year effect (i.e. nesting phenology could vary among years). For nests found outside the colony, we only used data from years when >20 nests were monitored. We looked for variations due to nest location and study year on laying date, hatching date and total clutch size (TCL) using a two-way ANOVA. We included TCL because this parameter is strongly affected by laying date (Bêty et al. 2003; Lepage et al. 2000). Models included the nest location (main vs. random plots or inside vs. outside the colony), study year (as a categorical variable) and an interaction between them (see Table S1.1 for sample size).

When comparing nests from the main plot with those in random plots, laying date did not differ between nest locations overall ($F_{1,4295} = 0.09$, $P = 0.76$) although it differed in some years (interaction: $F_{14,4295} = 13.5$, $P < 0.001$, Table S1.2); hatching date differed slightly between locations overall ($F_{1,2981} = 16.7$, $P < 0.001$) but these differences were not consistent across years (interaction: $F_{14,2981} = 9.89$, $P < 0.001$); finally, TCL did not differ between locations overall ($F_{1,4262} = 3.33$, $P = 0.07$) although it differed in some years (interaction: $F_{14,4262} = 1.88$, $P = 0.02$). In the second analysis (nests inside colony vs. outside), laying dates differed slightly between nest locations overall ($F_{1,4255} = 6.50$, $P = 0.01$) but these differences were not consistent across years (interaction: $F_{10,4255} = 10.0$, $P < 0.001$, Table S1.2); hatching date did not differ between locations overall ($F_{1,2911} = 0.42$, $P = 0.52$) although it differed in some years (interaction: $F_{9,2911} = 9.80$, $P < 0.001$); finally, TCL differed between locations ($F_{1,3845} = 67.6$, $P < 0.001$) but these differences were not consistent across years (interaction: $F_{9,3845} = 2.97$, $P = 0.002$). In both analyses, means were variable over time across nest location sub-samples but often followed a similar pattern (graphs not shown). Differences in phenology found between sub-samples were therefore variable among years and, overall, negligible. For example, differences in laying or hatching date were <0.45 d in all comparisons (Table S1.2). This allowed us to pool data across sampling schemes.

Table S1.1 Sample size used in each analysis.

Analysis		Laying date (n)	Hatching date (n)	Total clutch laid (n)
Main plot vs. random plots	Main plot	3,059	2,202	2,913
	Random plots	1,237	780	1,350
Inside colony[a] vs. outside	Inside colony	3,554	2,409	3,150
	Outside colony	702	503	696

[a] Main plot + random plots

Table S1.2 Mean differences found in nesting data between sub-sample of nests with their 95% CI. Numbers in bold indicate statistical significance.

Analysis	**Laying date**			**Hatching date**			**Total clutch laid**		
	Difference (d)	Low CI	High CI	Difference (d)	Low CI	High CI	Difference (eggs)	Low CI	High CI
Main plot vs. random plots	-0.03	-0.33	0.27	**0.44**	**0.11**	**0.78**	0.07	-0.01	0.14
Inside colony[a] vs. outside	-0.32	-0.68	0.03	-0.08	-0.44	0.28	**0.38**	**0.28**	**0.48**

[a] Main plot + random plots

Annex S1.4. Analysis of postfledging survival with E-SURGE

S1.4.1 Model description

The analysis combined live recaptures and dead recoveries to estimate the effect of year and relative hatching date on juvenile survival probabilities between fledging time and one year of age. We used both birds marked as young and adults to increase sample size but excluded adult females that received a neck collar from the analysis. We estimated survival probability considering two age classes, juvenile and adults (after one year, survival of individuals banded as young was constrained equal to those banded as adults). We also estimated live-recapture (*p*) and recovery (*r*) probabilities. For *p*, we considered the effects of time, age-class, banding group and sex (juvenile females, juvenile males, and adults) due to sex-biased dispersal, whereas for *r* we considered only time and age-class effects. We used in the model the states alive (A) for birds encountered alive, newly dead (ND) for birds recovered dead in any given year, and dead (D) for all years following the one when a bird was reported dead. Observable events included "caught" (i.e. when the bird was captured) and "recovered" (i.e. when the band was recovered from a dead bird by a hunter) whereas undetected birds were coded as "not encountered". Occasions started at banding time (*t*) in mid-August and were repeated at 1-year interval (*t*+1). Recoveries happened at any time in the interim and were coded as dead at the next occasion.

To create the encounter histories, we used the Headed data input format where H:H (year) stood for the encounter history for each study year, S: = 1 indicated that each row represents the encounter history of a different individual, and COV:HD identified relative hatching date (HD) as an individual covariate [xind(1)]. The term year was standardized and coded as external covariate in a txt file.

S1.4.2 E-SURGE settings

Data

Number of occasions: 26

Number of states: 3

- A: alive
- ND: newly dead
- D: dead

Number of events: 3

- 0: not encountered
- 1: caught (Individual is marked or recaptured at time t)
- 2: recovered (Individual is killed and reported by hunters between t and t+1)

Number of groups: 3

- 1=Juvenile female
- 2=Juvenile male
- 3=Adult

Number of age classes: 2

- 1=Juvenile
- 2=Adult

Parameters estimated by the model:

- *S*, Survival probability
- *p*, Recapture probability
- *r*, Recovery probability

We used shortcuts to associate the groups to the two age classes with the following formulas.

Transition:

juv = a(1).Bage(1 2)

ad = a(2).Bage(1 2)&Bage(3)

Event:

eventjuv = a(2).Bage(1 2)

eventad = a(3).Bage(1 2)&Bage(3)

GEPAT

Initial state (Individuals can only be marked alive)

$$\Pi = \begin{array}{cc} A & ND \\ \left[* \right. & \left. - \right] \end{array}$$

Transition

$$\begin{array}{c|ccc|} & A & ND & D \\ A & S & * & - \\ ND & - & - & * \\ D & - & - & * \end{array}$$

Event

$$B_t = \begin{array}{cccc} & 0 & 1 & 2 \\ A & * & p & - \\ ND & * & - & r \\ \dagger & * & - & - \end{array}$$

GEMACO

Initial state

to

Transition

The umbrella model for survival was: [i+xind(1)+t*x(1)+ xind(1).t*x(1)].juv+t.ad (xind(1) = relative hatching date covariate, x(1) = year covariate)

Event

Based on previous analyses of this dataset (Souchay et al. 2013), we tested different combinations of effects on *p* and *r* to find the best model fit (Table S1.3).

IVFV (initial values and fixed values)

Event

Beta #1 = 1

S1.4.3 Results of goodness-of-fit.

U-CARE software was used to assess the goodness-of-fit of our umbrella model to the data (Choquet et al. 2009b). Data over-dispersion was corrected using the ratio of the χ^2 statistics and the degrees of freedom, $\hat{c} = \frac{X^2}{df}$. Over-dispersion value of the dataset was 4.3 (χ^2 = 3879.6, df = 892).

S1.4.4 Results of model selection for parameters p and r

Before testing models with reduced effects on survival, we compared models with various effects on p and r using the structure of our umbrella model for survival (Table S1.3). The preferred model was the one with the full structure on p (i.e. effects of time, banding group, age and sex in juvenile) and r (i.e. time and age effects). This model had a difference in QAIC > 30 compared to the next best model. Therefore, all models with a reduced structure on survival listed in Table S6.1f below retained these effects on p and r.

Table S1.3 Effects tested on live-recapture (p) and recovery (r) probabilities to determine the best model structure on those parameters prior to survival analyses

Effects on *p*	**Effects on *r***	**GEMACO statement**
t, g, a, s	*t, a*	firste+nexte.[to(2).t.[Bage(1,2).a+Bage(3)]+to(3).t.[eventjuv+eventad]]
t, g, s	*t, a*	firste+nexte.[to(2).t.Bage(1, 2, 3)+to(3).t.[eventjuv+eventad]]
t, g	*t, a*	firste+nexte.[to(2).t.Bage(1 2, 3)+to(3).t.[eventjuv+eventad]]
t	*t, a*	firste+nexte.[to(2).t+to(3).t.[eventjuv+eventad]]
t	*t*	firste+nexte.to.t

t: time (year), *g*: banding group, *a*: age, *s*: sex (for juvenile only; coded in banding groups)

Annex S1.5 Descriptive statistics of laying and hatching date

Figure S1.1 Annual distribution of laying date and their annual mean (dashed line) from 1991 to 2015. Day of the year (DOY) represents the date in which the first egg was laid in a nest.

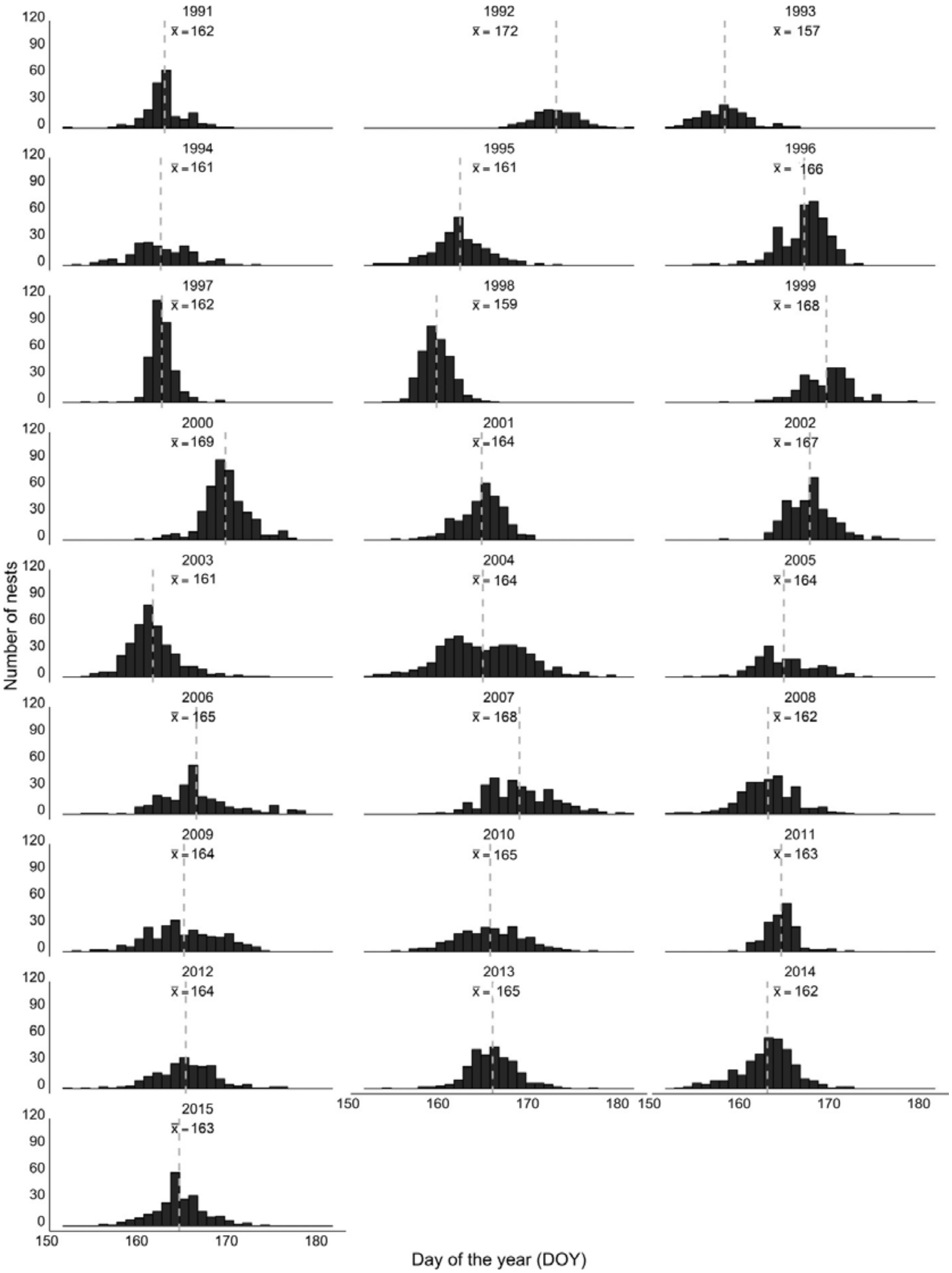


Figure S1.2 Temporal variation of the annual mean laying date expressed as day of the year (DOY) from 1991 to 2015. Black dashed line indicates the overall mean laying date of the dataset; black solid line indicates the temporal trend of mean annual laying date. Error bars represent standard errors of the mean.

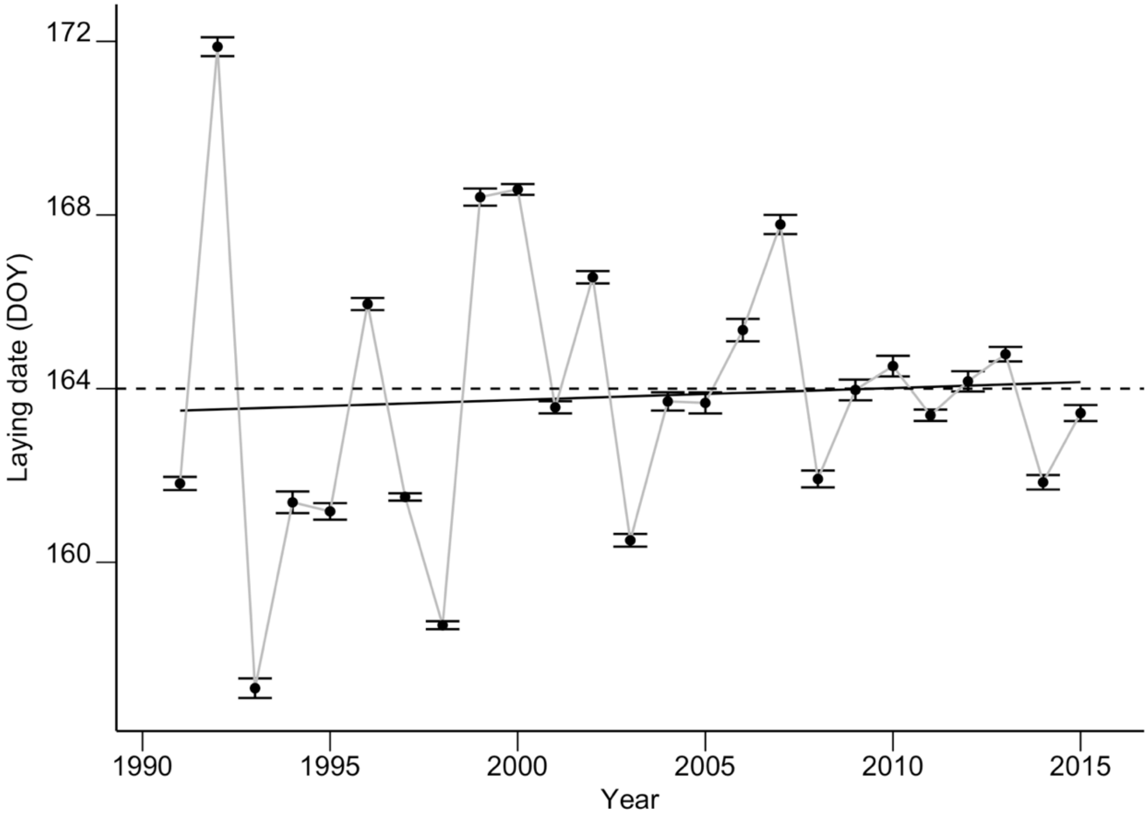


Figure S1.3 Change in slope coefficients of the relationships between relative laying date and study year for various quantile of the laying date distribution along with 95% confidence intervals. Each black dot represents the slope coefficient for the quantile analyzed, with positive value showing a trend for later nesting and a negative slope the converse. The gray solid line is the slope of the overall regression relating annual laying date and year (see Figure S1.2) and its 95% confidence interval (dashed lines).

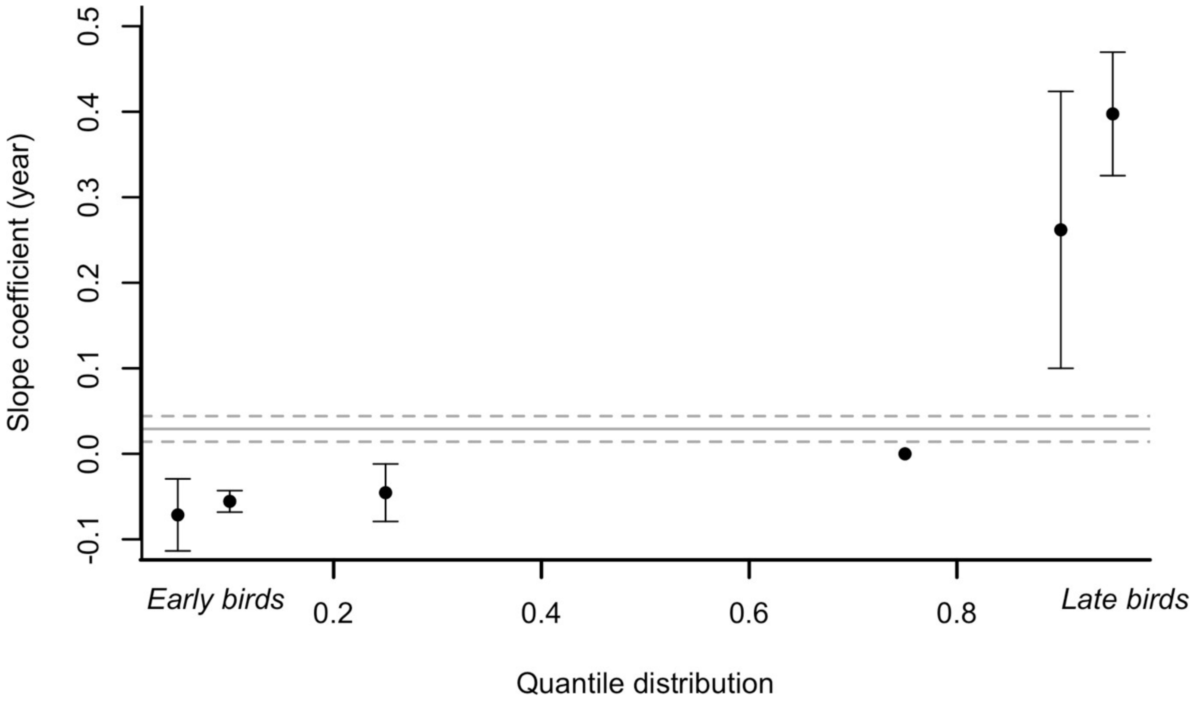


Table S1.4 Quantile regression coefficients of the laying date analysis with 95% confidence intervals.

Quantile (τ)	Parameter	Estimate	Low CI	High CI
0.95	intercept	3.00	2.54	3.46
	year	3.97E-01	3.25E-01	4.70E-01
	year^2	-1.28E-02	-1.61E-02	-9.57E-03
0.9	intercept	2.29	1.68	2.89
	year	2.62E-01	1.00E-01	4.24E-01
	year^2	-7.94E-03	-1.42E-02	-1.72E-03
0.75	intercept	2.00	2.00	2.00
	year	2.47E-17	-2.90E-18	4.64E-17
0.25	intercept	-1.00	-1.70	-0.30
	year	-4.55E-02	-7.90E-02	-1.19E-02
0.1	intercept	-2.78	-2.91	-2.64
	year	-5.56E-02	-6.81E-02	-4.30E-02
0.05	intercept	-3.86	-4.47	-3.24
	year	-7.14E-02	-1.14E-01	-2.93E-02

Annex S1.6 Model selection for each reproductive success component

Table S1.5 Model selection of the effect of relative date and year (as a continuous variable) on the individual nesting components of the greater snow goose on Bylot Island from 1991 to 2015. Dates are expressed as deviations from annual median values (relative date). Relative date refers to laying date for prehatching components (total clutch laid, daily survival rate (DSR) of nests, egg survival, hatching success) and to hatching date for posthatch components (prefledging and postfledging survival). Models ranking is based on AIC and the table presents the log-likelihood value (LL), number of estimated parameters (K), difference in AIC between the current model and the preferred one (ΔAIC), and AIC weights (w).

S1.5a Total clutch laid, TCL (n = 6,243 nests)

Rank	**Main effects**	**Interaction**	**K**	**ΔAIC**	**AIC w**	**LL**
1	laying date + year + year^2	laying date * year + laying date * year^2	7	0	0.86	-8646.28
2	laying date + year + year^2	laying date * year^2	6	3.66	0.14	-8649.12
3	laying date + year	laying date * year	5	23.63	0	-8660.10
4	laying date + year + year^2	laying date * year	6	24.86	0	-8659.71
5	laying date + year		4	26.36	0	-8662.47
6	laying date + year + year^2		5	27.53	0	-8662.05
7	laying date		3	31.41	0	-8665.99
8	year		3	1367.54	0	-9334.05
9	null model		2	1369.94	0	-9336.25

S1.5b Daily survival rate of nests[a], DSR (n = 6,990 nests)

Rank	Main effects	Interaction	K	ΔAIC	AICw	LL
1	laying $date^2$ + year + $year^2$ + nest age	laying $date^2$ * $year^2$	6	0	0.73	-5271.05
2	laying $date^2$ + year + $year^2$ + nest age	laying $date^2$ * year + laying $date^2$ * $year^2$	7	2.00	0.27	-5271.05
3	laying $date^2$ + year + $year^2$ + nest age		5	13.09	0	-5278.60
4	laying $date^2$ + year + $year^2$ + nest age	laying $date^2$ * year	6	15.00	0	-5278.55
5	laying $date^2$ + year + nest age		4	15.17	0	-5280.64
6	laying $date^2$ + year + $year^2$		4	42.89	0	-5294.50
7	laying $date^2$ + year		3	43.45	0	-5295.78
8	laying $date^2$ + year + $year^2$	laying $date^2$ * year	5	44.89	0	-5294.49
9	laying $date^2$ + year	laying $date^2$ * year	4	45.45	0	-5295.78
10	year + nest age		3	96.09	0	-5322.10
11	laying $date^2$ + nest age		3	97.51	0	-5322.81
12	laying $date^2$		2	113.25	0	-5331.67
13	nest age		2	171.08	0	-5360.59
14	year		2	171.31	0	-5360.71
15	null model		1	225.69	0	-5388.89

[a] Estimates used to determine nesting success, see details in methods section.

S1.5c Egg survival (n = 3,180 nests)

Rank	Main effects	Interaction	K	ΔQAIC	QAICw	LL
1	laying date + year + year^2	laying date * year^2	5	0	0.26	-2705.02
2	laying date + year + year^2		4	0.21	0.23	-2706.35
3	laying date + year + year^2	laying date * year + laying date * year^2	6	1.47	0.12	-2704.70
4	laying date + year		3	1.48	0.12	-2708.31
5	laying date + year + year^2	laying date * year	5	2.07	0.09	-2706.26
6	laying date + year	laying date * year	4	3.27	0.05	-2708.18
7	year + year^2		3	3.44	0.05	-2709.48
8	laying date		2	3.71	0.04	-2710.84
9	year		2	4.46	0.03	-2711.30
10	null model		1	6.14	0.01	-2713.51

S1.5d Hatching success (n = 3,089 nests)

Rank	Main effects	Interaction	K	ΔAIC	AICw	LL
1	laying date + year + year^2		4	0	0.37	-1680.04
2	year + year^2		3	1.01	0.23	-1681.54
3	laying date + year + year^2	laying date * year	5	1.39	0.19	-1679.73
4	laying date + year + year^2	laying date * year^2	5	1.89	0.15	-1679.98
5	laying date + year + year^2	laying date * year + laying date * year^2	6	3.37	0.07	-1679.72
6	laying date + year		3	48.20	0	-1705.14
7	year		2	48.84	0	-1706.46
8	laying date + year	laying date * year	4	48.84	0	-1704.46
9	null model		1	127.00	0	-1746.54
10	laying date		2	127.97	0	-1746.02

S1.5e Prefledging survival (n = 1,316 broods)

Rank	Main effects	Interaction	K	ΔQAIC	QAICw	LL
1	hatching date + year^2	hatching date * year^2	4	0	0.26	-1658.99
2	null		1	1.07	0.15	-1663.57
3	year		2	2.02	0.10	-1662.89
4	hatching date + year + year^2	hatching date * year + hatching date * year^2	6	2.40	0.08	-1657.96
5	year^2		2	2.44	0.08	-1663.16
6	hatching date		2	2.91	0.06	-1663.47
7	hatching date + year		3	3.95	0.04	-1662.84
8	hatching date + year	hatching date * year	4	4.42	0.03	-1661.85
9	hatching date + year + year^2	hatching date * year	5	5.30	0.02	-1661.13
10	hatching date + year + year^2		4	5.34	0.02	-1662.45

S1.5f Postfledging survival (n = 73,220 birds)

Rank	Effects on juvenile survival	K	Deviance	ΔQAIC	AICw
1	hatching date + year + hatching date*year	198	155709.80	0	0.52
2	hatching date + year	198	155711.60	0.60	0.38
5	hatching date	197	155731.81	3.30	0.10
3	time[a]	221	155552.66	10.11	0
4	null	175	156066.10	36.17	0
6	year	199	155871.48	39.42	0

[a] year expressed as a categorical variable

Table S1.6 Parameter estimates with 95% confidence intervals for preferred models presented in Table S1.5 along with their rank. Laying and hatching date refer to relative dates estimated as deviations from annual median values. Relative laying date was used to analyze prehatching components (total clutch laid, nesting success, egg survival, hatching success), whereas relative hatching date to analyze posthatch components (prefledging and postfledging survival).

Model	Rank	Parameter	Estimate	Low CI	High CI
TCL[a]	**1**	Intercept	3.81	3.78	3.85
		laying date	-1.33E-01	-1.43E-01	-1.22E-01
		year	-4.72E-03	-8.22E-03	-1.21E-03
		year^2	2.52E-04	-2.82E-04	7.86E-04
		laying date * year	1.47E-03	2.59E-04	2.69E-03
		laying date * year^2	-4.66E-04	-6.42E-04	-2.90E-04
DSR[b]	**1**	Intercept	4.67	4.54	4.81
		laying date^2	-7.84E-03	-1.06E-02	-4.96E-03
		year	3.69E-02	2.90E-02	4.49E-02
		year^2	2.32E-03	1.03E-03	3.62E-03
		laying date^2 * year^2	-1.02E-04	-1.51E-04	-5.16E-05
		nest age	2.68E-02	1.79E-02	3.57E-02
Egg survival[c]	**4**	Intercept	2.20	2.13	2.27
		laying date	-2.96E-02	-5.74E-02	-1.74E-03
		year	-9.56E-03	-1.93E-02	2.11E-04
Hatching success[c]	**2**	Intercept	2.58	2.45	2.72
		year	5.75E-02	4.05E-02	7.51E-02
		year^2	7.63E-03	5.09E-03	1.03E-02
Prefledging survival[c]	**1**	Intercept	0.33	0.24	0.41
		hatching date	3.16E-02	-6.73E-03	6.99E-02
		year^2	-5.87E-05	-1.51E-03	1.40E-03
		hatching date * year^2	-9.07E-04	-1.54E-03	-2.76E-04
Postfledging survival[d]	**2**	Intercept	-0.66	-0.78	-0.54
		year	-0.16	-0.30	-0.01
		hatching date	-0.15	-0.20	-0.10

[a] linear regression

[b] logistic-exposure regression

[c] quasi-binomial regression

[d] capture-recapture logistic model (with E-SURGE)

Annex S1.7 Supplementary graphs

Figure S1.4 Contour plots showing the predicted change in total clutch laid (TCL) of the greater snow goose as a function of study year and relative laying date. Contour line interval = 0.5 egg. See Figure 1.3a in main text for complementary information.

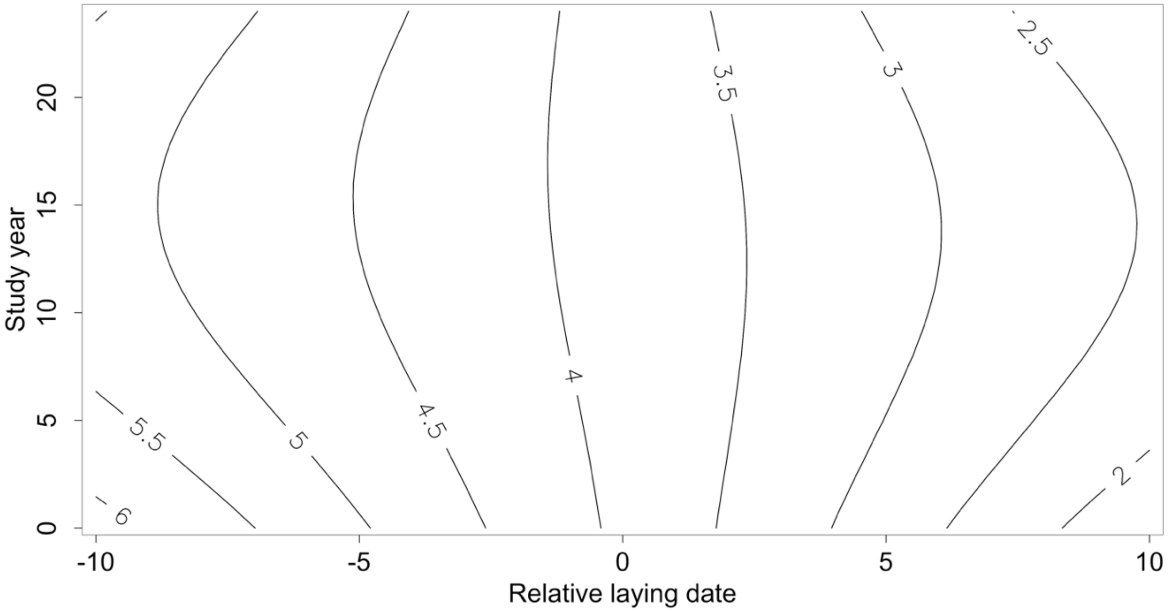


Figure S1.5 Contour plots showing the predicted change in nesting success of the greater snow goose as a function of study year and relative laying date. Contour line interval = 0.1 (proportion). See Figure 1.3b in main text for complementary information.

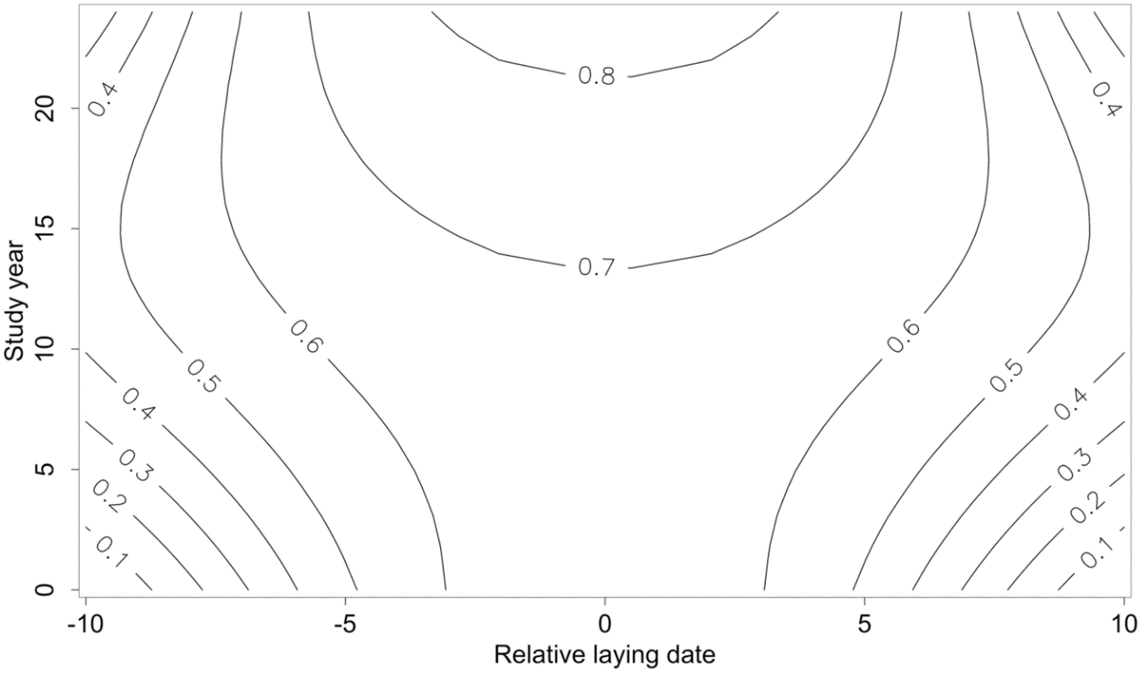


Figure S1.6 Contour plots showing the predicted change in egg survival of the greater snow goose as a function of study year and relative laying date. Contour line interval = 0.1 (proportion). See Figure 1.3c in main text for complementary information.

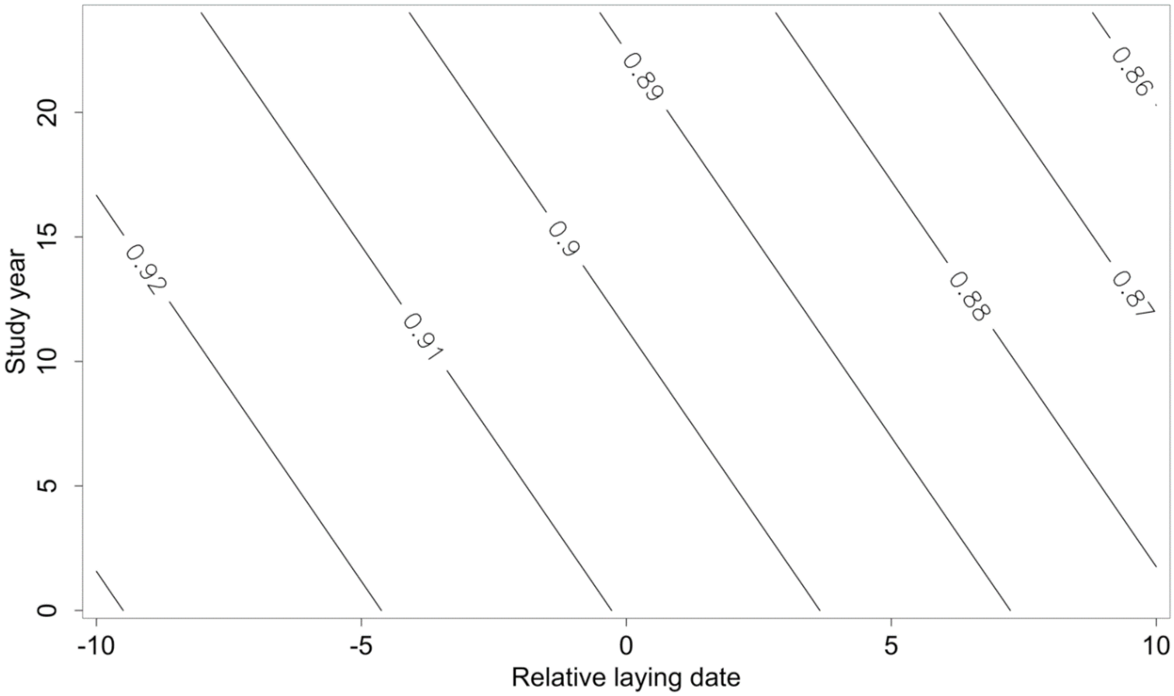


Figure S1.7 Graph showing the predicted change in hatching success of the greater snow goose as a function of study year, represented by the black solid line. The black points indicate the observed annual mean hatching success of the dataset. Error bars represent standard errors of the mean.

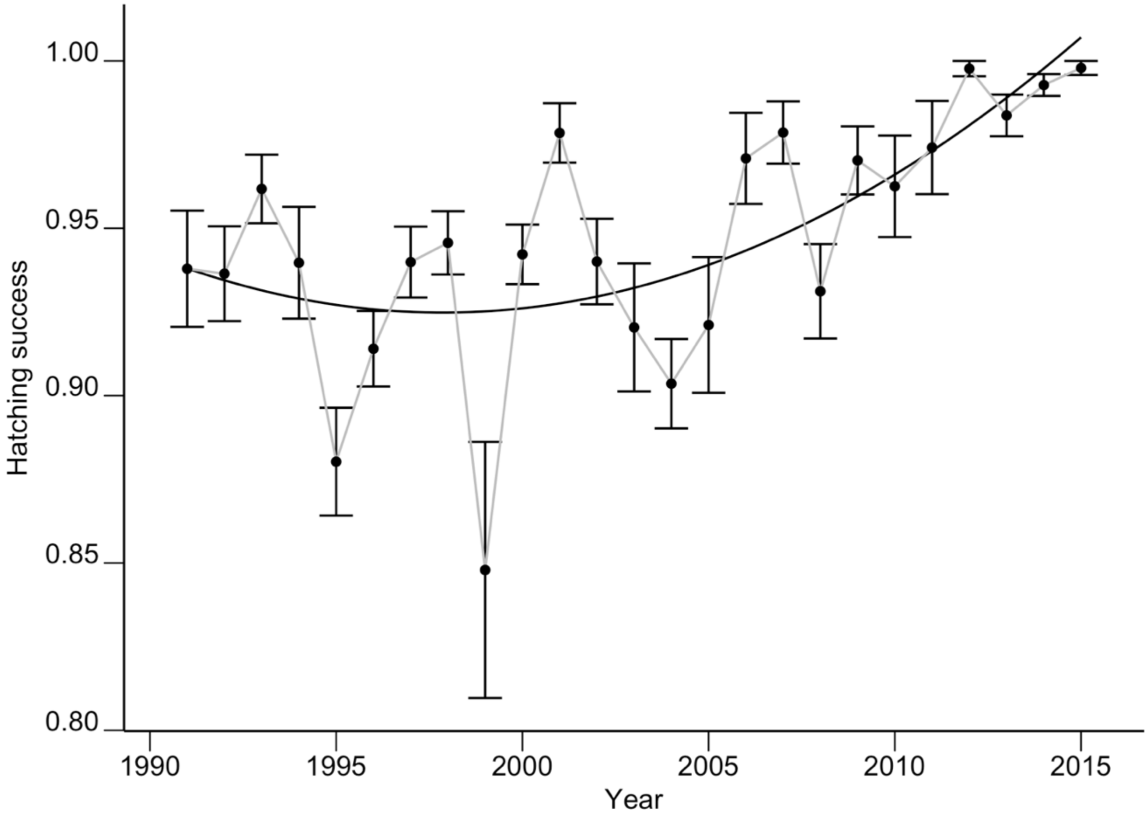


Figure S1.8 Contour plots showing the predicted change in prefledging survival of the greater snow goose as a function of study year and relative laying date. Contour line interval = 0.05 (proportion). See Figure 1.3d in main text for complementary information.

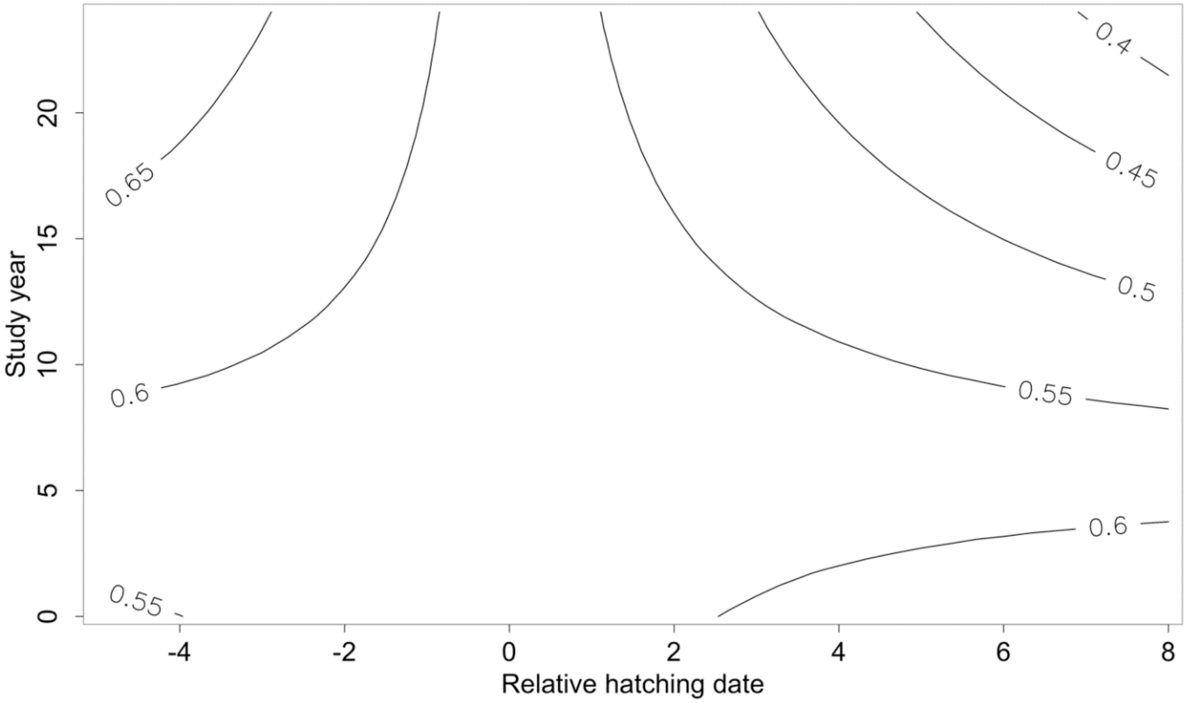
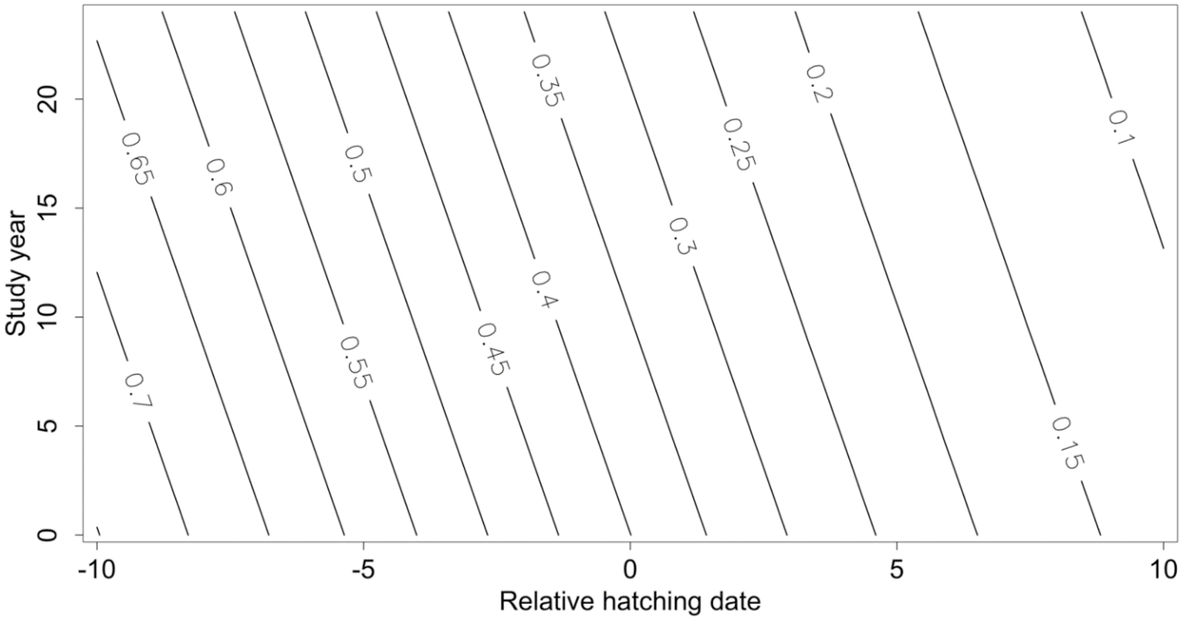


Figure S1.9 Contour plots showing the predicted change in postfledging survival of the greater snow goose as a function of study year and relative laying date. Contour line interval = 0.05. See Figure 1.3e in main text for complementary information.



Annex S2: Supplementary material for chapter 2

Annex S2.1 Estimation of total brood loss

We estimated goslings dying in broods where all young disappear, i.e. total brood loss (TBL), according to Gauthier and Brault (1998). We calculated TBL for each year using the ratio number of goslings(NG):number of adult(NA) among birds captured at banding and the average brood size (BS) at that time. We determined average brood size in free-ranging birds using spotting scopes just before the banding period on >100 broods annually. We used the formula:

$$TBL = 1 - \frac{N_G/N_A}{BS/2}$$

This estimation assumes that all young were accompanied by both parents at banding and that only successful breeders (i.e. those that hatched goslings) were caught. These assumptions could be met in our data because young are attended by both parents over the summer and brood-mixing and adoption are uncommon in snow geese (Williams 1994); thus, when young survive, parents and young are caught together. Moreover, only parents that hatched young could be captured because most non-breeders and unsuccessful nesters have completed their molt and have regained flight capabilities when goose banding occur in August (Reed et al. 2003). TBL varied among years (range: 0.01–0.41) and averaged 0.18 but showed no significant trend over time (slope = -4.42E-03, 95% CI: -1.13E-02, 2.43E-03); thus values were averaged across years. To correct prefledging survival estimates (S1) determined by the proportion of web-tagged goslings recaptured in surviving broods, we multiplied this value by the proportion of broods where at least one young survive, which was given by 1-$\overline{TBL}$.

Annex S2.2 Seasonal and annual effects detected on individual reproductive success components

Table S2.1 Effects retained in each model used to estimate individual reproductive component (from Reséndiz-Infante et al. 2020).

Component	**Selected model**
Total clutch laid	laying date + year + year^2 + laying date*year + laying date*year^2
Nesting success	laying date^2 + year + year^2 + laying date^2*year^2
Egg survival	laying date + year
Hatching success	year + year^2
Prefledging survival	hatching date + year^2 + hatching date*year^2
Postfledging survival	hatching date + year

Annex S2.3 Supplementary results

Figure S2.1 Contour plot showing the observed reproductive success of the greater snow geese as a function of relative laying date and study year. Contour interval = 0.1. See Figure 2.1 in main text for complementary information.

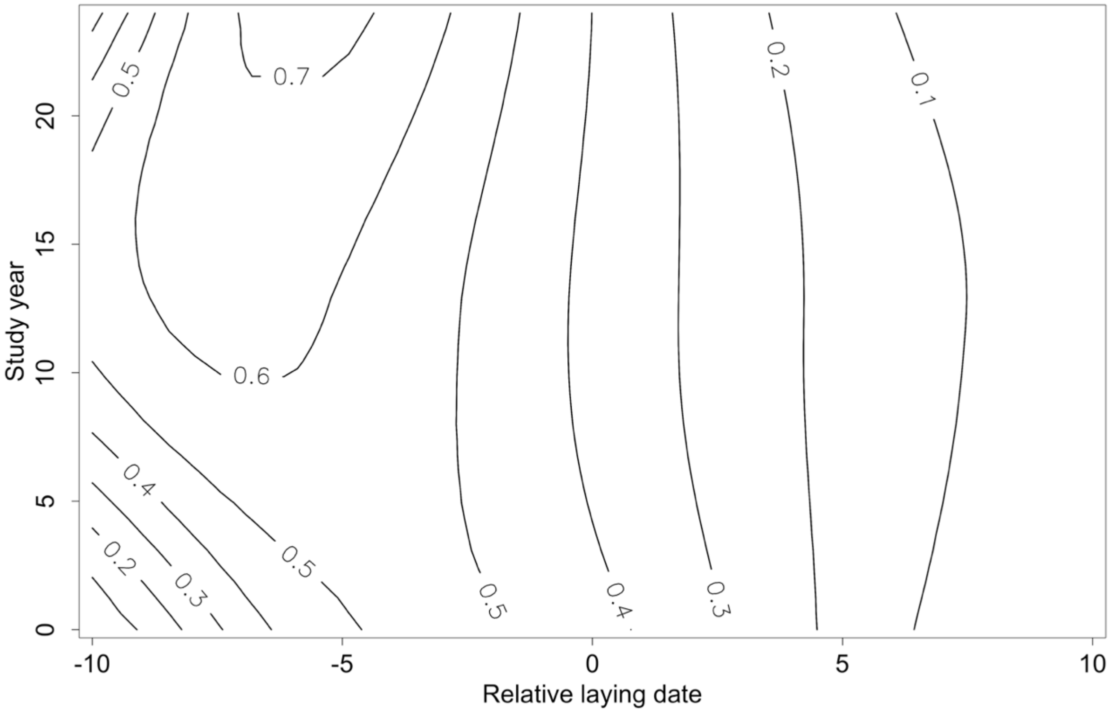


Figure S2.2 Expected reproductive success E(RS) of greater snow geese at different hypothetical clutch size (2 to 7 eggs, from (a) to (f) respectively) for each study year and relative laying date (from Day -10 to 10) from 1991 to 2015. Study year is presented as a continuous variable, where 1991 is year = 0. The surface represents the interpolation of reproductive success values for each relative day across the study years. Blue indicates the highest values in the component, and red the lowest values. Black bars represent 95% confidence intervals of year 0 (1991). See also contour plots in Figure S2.3.

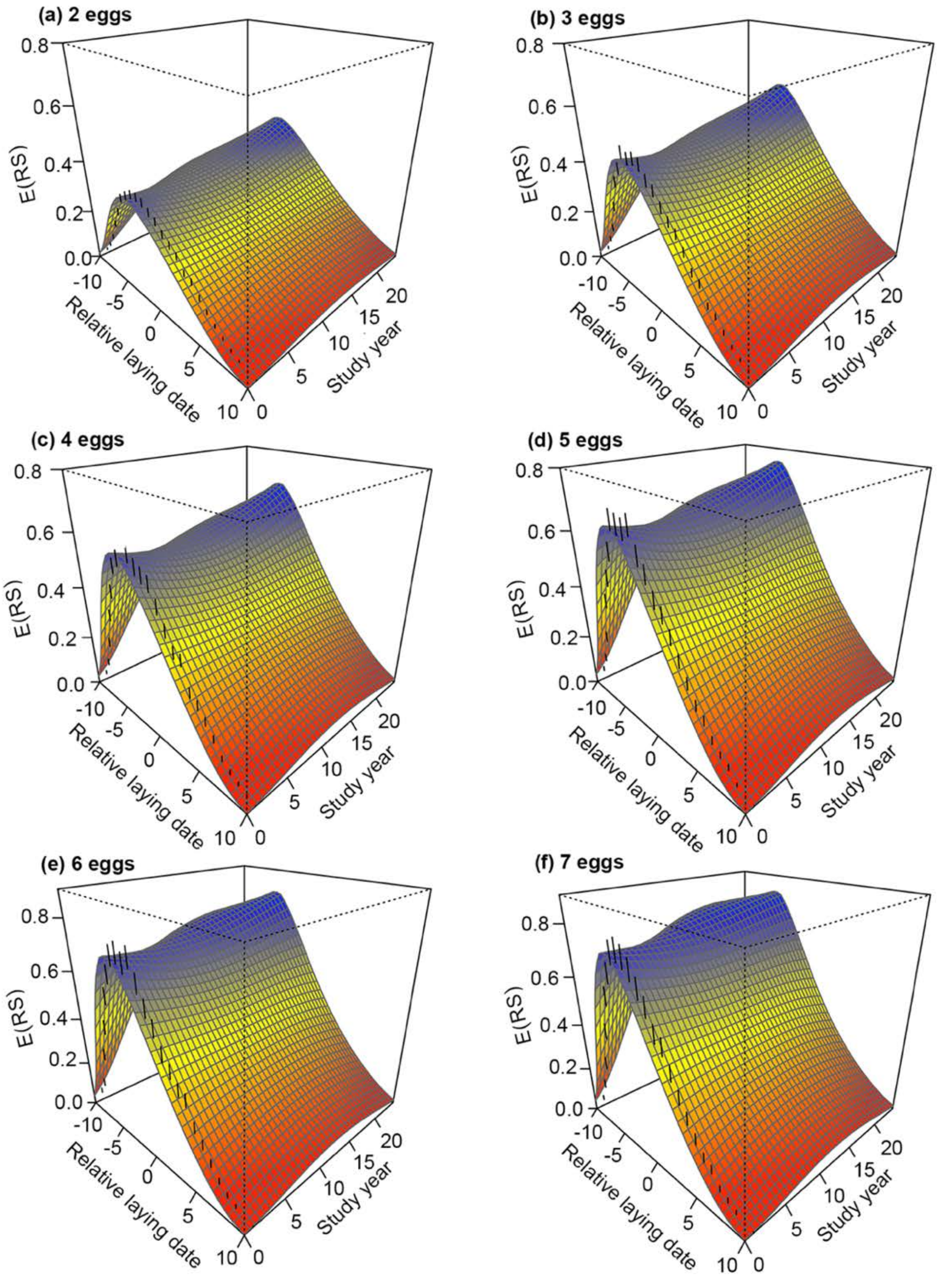
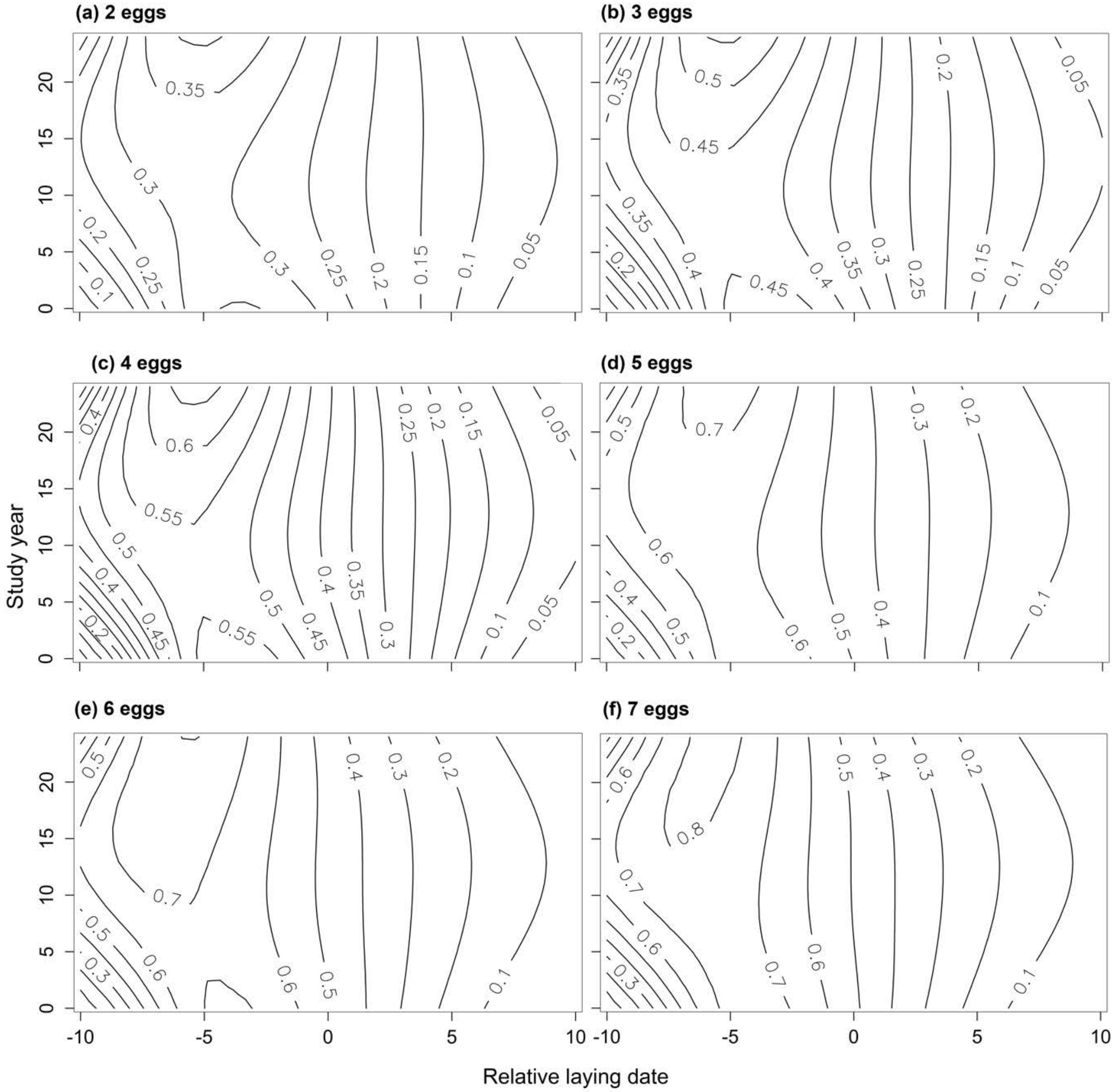


Figure S2.3 Contour plots showing the expected reproductive success E(RS) of greater snow geese at different hypothetical clutch size of 2–7 eggs, from (a) to (f) respectively, as a function of study year and relative laying date. Contour line interval = 0.05. See Figure S2.2 for complementary information.



Annex S3: Supplementary material for chapter 3

Annex S3.1 Reanalysis data validation

We correlated daily temperature data from selected weather stations in each of our stopover areas an on the breeding ground to reanalysis data from the pixel where weather stations were located. Data from weather stations were obtained from Environment Canada (http://climate.weather.gc.ca) and on Bylot Island, from a local weather station (CEN 2018). We randomly selected five years (1980, 1993, 2006, 2010 and 2014) over the 40-year span of our study.

Table S3.1 Correlation coefficient (Pearson r) between daily temperature from weather stations and reanalysis values for year 1980, 1993, 2006, 2010 and 2014. NA represent missing values, when <80% of the data were available in weather stations.

Weather station	1980	n	1993	n	2006	n	2010	n	2014	n
St. Lawrence Valley stopover area										
La Pocatière	0.84	76	0.92	76	0.89	76	0.91	74	0.94	75
Nicolet	0.91	76	0.93	76	0.94	75	0.95	76	0.96	66
Ormstown	0.93	76	0.94	76	0.94	76	0.94	76	0.95	76
Québec	0.87	76	0.89	76	0.92	76	0.94	76	0.96	76
Rimouski	0.88	76	0.85	76	0.91	76	0.91	75	0.92	63
Trois Rivières	0.89	76	0.92	76	0.94	75	0.93	76	0.95	76
St Anicet	NA	NA	0.94	76	0.94	76	0.94	76	0.96	69
Nunavik stopover area										
Rivière aux Feuilles	NA	NA	NA	NA	0.91	73	0.89	71	0.96	72
Pingualuit	NA	NA	NA	NA	NA	NA	0.94	73	0.96	74
Inukjuak	0.94	76	0.96	76	0.92	76	0.92	76	0.98	70
Baffin Island stopover area										
Hall Beach	0.95	76	0.99	46	0.95	76	NA	NA	0.94	76
Igloolik	0.94	76	0.97	76	0.95	76	0.91	74	0.91	52
Breeding area										
Pond Inlet	0.96	76	0.97	76	0.97	76	0.94	76	0.95	76
Bylot Island	NA	NA	0.96	76	0.95	76	0.93	76	0.96	76

Annex S3.2 Description of ARIMA method

ARIMA is a powerful tool to handle time series but is not commonly used in ecology (e.g. Fasola et al. 2010). ARIMA models are defined by three parameters (p, d and q), where p specifies the autoregressive order, d refers to the integrative part and the differentiation required by the data and q specifies the moving average order (Hyndman and Athanasopoulos 2018). We applied ARIMA models using the conditional sum-of-squares (CSS) method implemented in the auto.arima function of the 'forecast' package (Hyndman et al. 2019). This method computes the CSS to find the starting values followed by a maximum likelihood estimation of parameters p, d and q to find the optimal model which minimizes the Akaike Information Criterion (AIC). Goodness of fit for ARIMA models was confirmed with Ljung-Box test statistics.

Annex S3.3 Supplementary results

Table S3.2 ARIMA models for each period and study site used for warming trend analyses and to obtain residuals for correlation analyses of mean temperature between sites from 1979 to 2018. See also Figures 3.2, 3.3 and 3.4 in main text.

Staging/ breeding area	Period	ARIMA process (p,d,q)	slope	Warming trend (°C)
St. Lawrence valley	1 April–15 May	(0,0,0)	0.013	0.50
	1–15 May	(4,0,0)	0.051	2.05
Nunavik	1 April–15 May	(0,1,1)	0.053	2.13
	1–15 May	(2,0,0)	0.048	1.91
	10–31 May	(2,0,0)	0.039	1.56
Baffin Island	1 April–15 May	(1,0,3)	0.084	3.38
	1–15 May	(1,0,0)	0.046	1.84
	10–31 May	(0,0,0)	0.023	0.93
	20 May–5 June	(1,0,0)	0.028	1.13
Bylot Island	1 April–15 May	(1,0,0)	0.065	2.58
	1–15 May	(3,0,0)	0.020	0.78
	10–31 May	(0,0,0)	0.020	0.82
	20 May–5 June	(0,0,1)	0.034	1.36
	30 May–15 Jun	(0,0,1)	0.021	0.85

Figure S3.1 Pairwise correlations in rate of temperature change between staging areas or the breeding site (Bylot Island) of geese for the same time periods over a 40-year time span (1979–2018). For the St. Lawrence valley stopover, we used the whole staging period (1 April–15 May) and only the last two weeks (1–15 May). Rate of temperature change is the slope of the regression between mean daily temperature and day of the year at each staging site and on the breeding ground. Correlation coefficients (r) and p-values are provided for each graph, df=38.

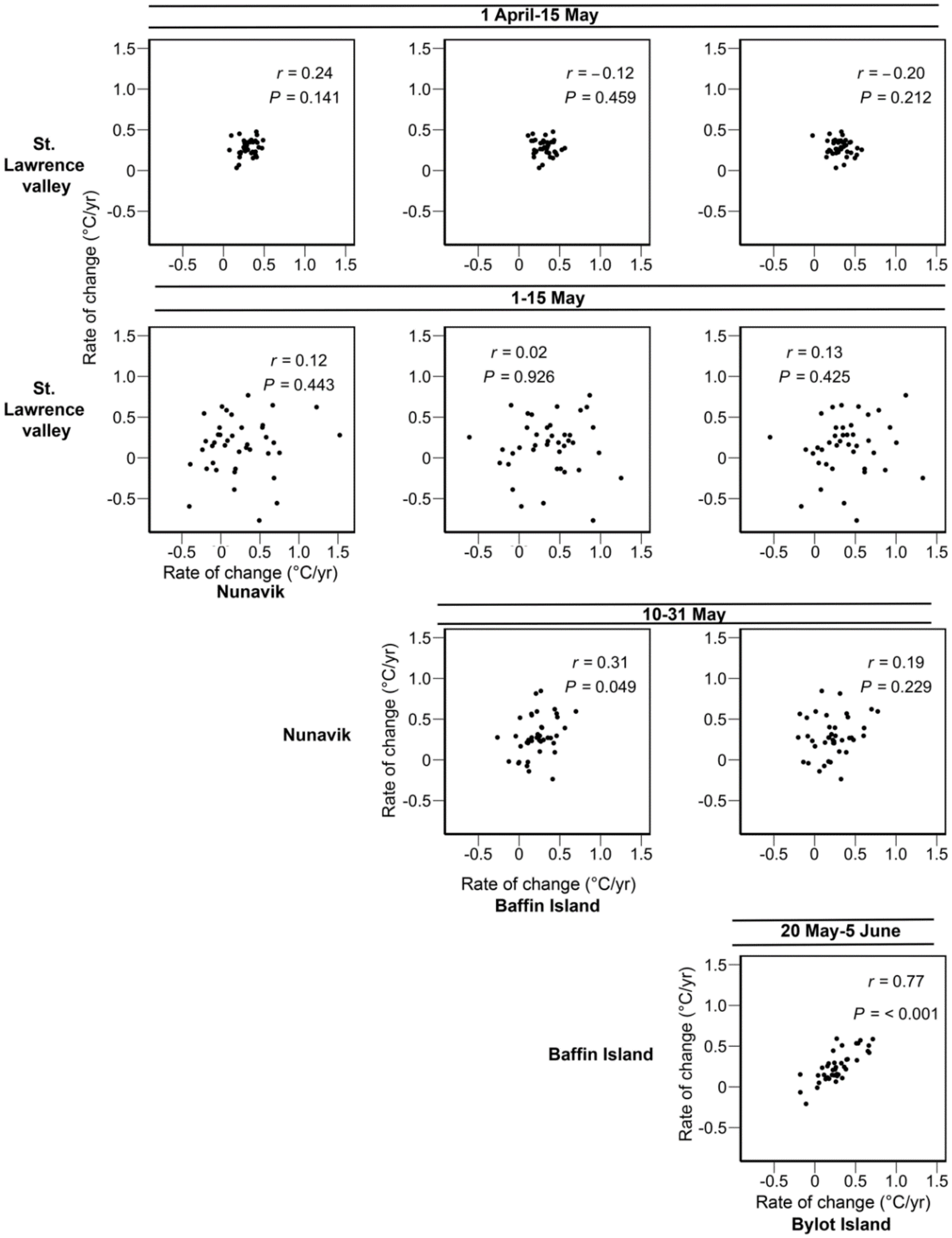
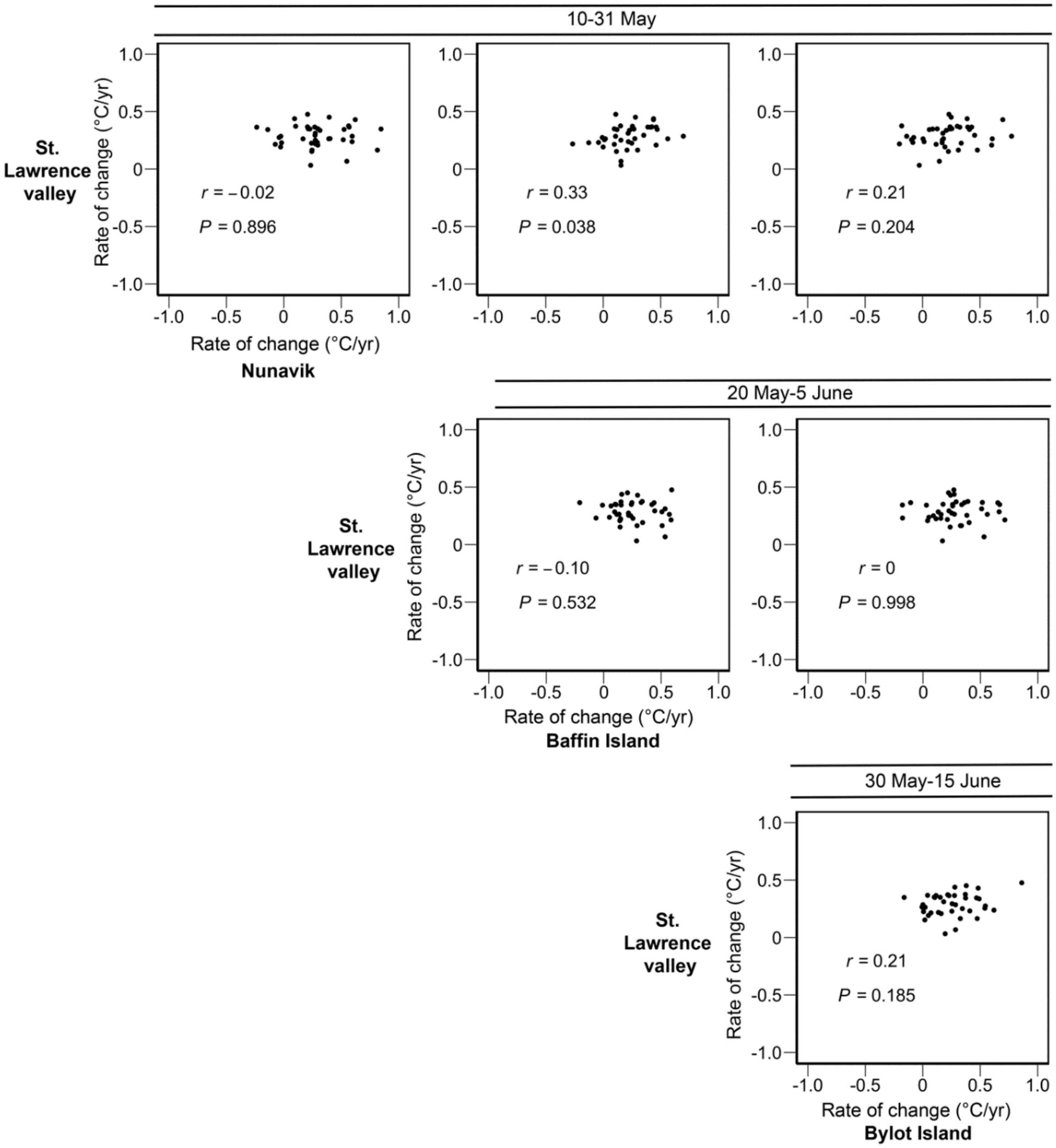
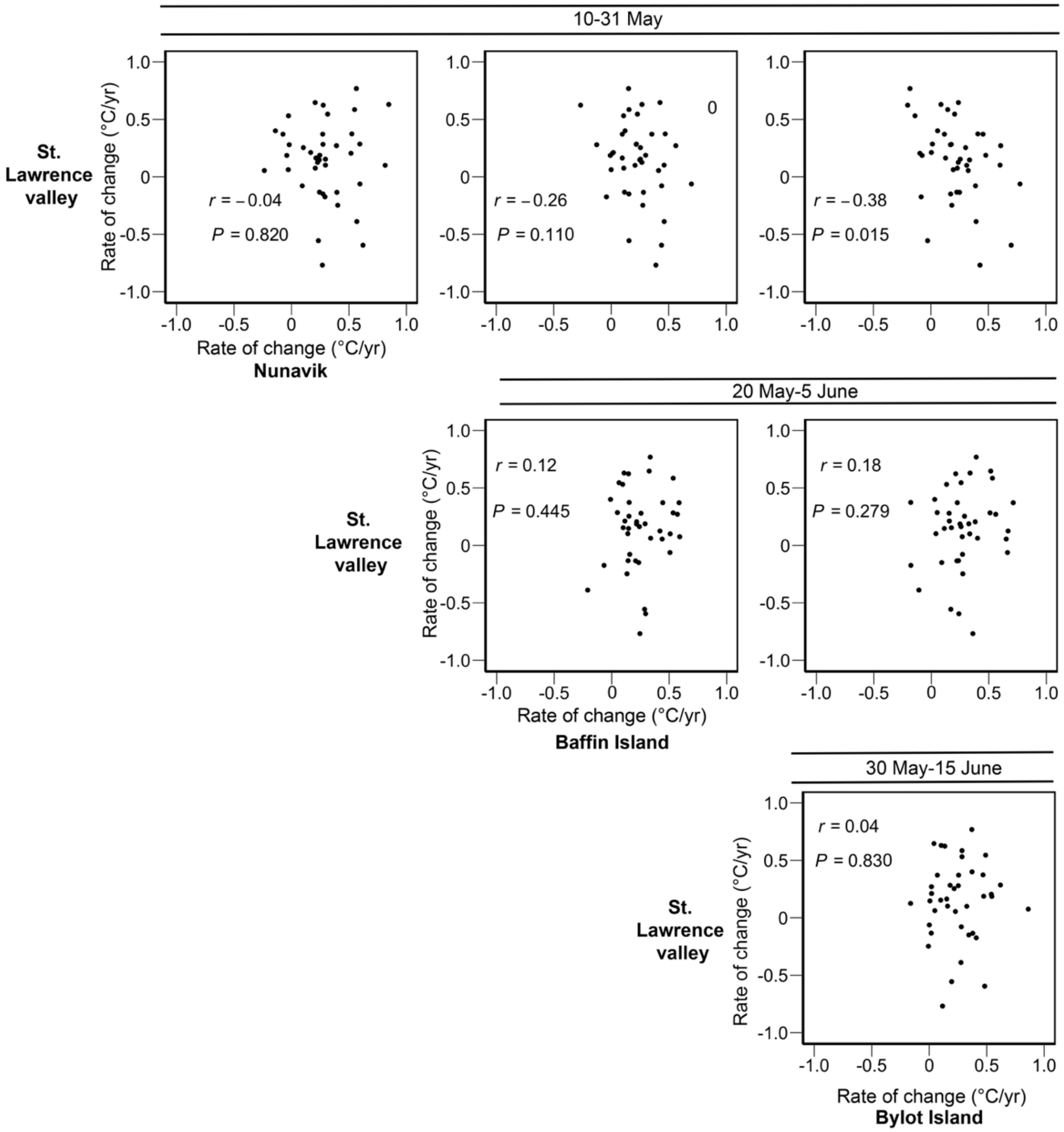


Figure S3.2 Pairwise correlations in rate of temperature change between staging areas or the breeding site (Bylot Island) of geese for subsequent time periods over a 40-year time span (1979–2018). For the St. Lawrence valley stopover, we used the whole staging period (1 April–15 May) and only the last two weeks (1–15 May). Rate of temperature change is the slope of the regression between mean daily temperature and day of the year at each staging site and on the breeding ground. Correlation coefficients (r) and p-values are provided for each graph, df=38.

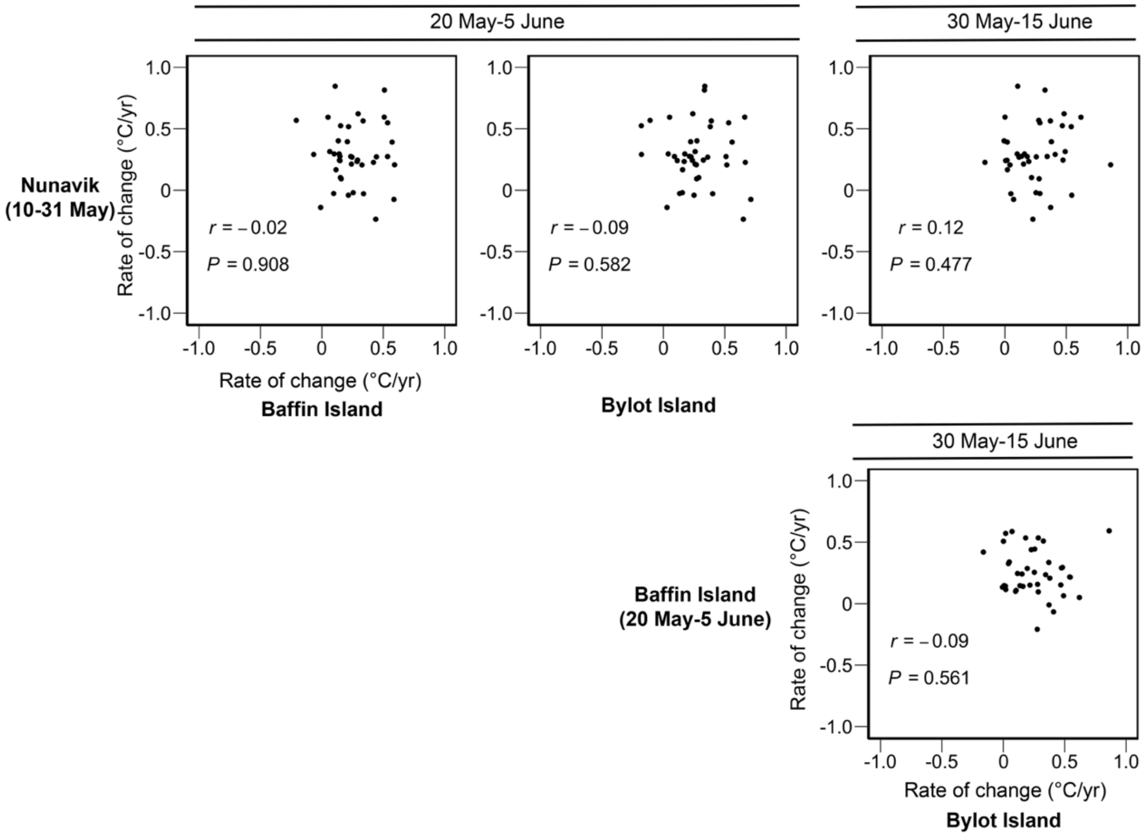
a) St. Lawrence valley (1 April–15 May)



b) St. Lawrence valley (1–15 May)



c) Arctic sites



S3.4 Model selection

Table S3.3 Model selection of the relationship between laying date of greater snow geese with temperature at different staging sites (fixed effects) when geese are present from 1991 to 2018. Time periods at each staging site: St. Lawrence valley 1 April–15 May, Nunavik 10 May–31 May, Baffin Island 20 May–5 June, Bylot Island 30 May–15 June. Number of parameters (K), difference in AIC between the top and current model (Δ AIC), AIC weights (AICw) and log-likelihood value (LL) are presented.

Rank	Fixed effects	K	ΔAIC	AICw	LL
1	Baffin Island+Bylot Island	4	0	0.26	-60.11
2	Nunavik+Bylot Island	4	0.91	0.16	-60.56
3	St. Lawrence valley+Baffin Island+Bylot Island	5	1.18	0.14	-59.70
4	Bylot Island	3	1.49	0.12	-61.85
5	Nunavik+Baffin Island+Bylot Island	5	1.51	0.12	-59.86
6	St. Lawrence valley+Nunavik+Bylot Island	5	2.48	0.07	-60.35
7	St. Lawrence valley+Nunavik+Baffin Island+Bylot Island	6	2.50	0.07	-59.36
8	St. Lawrence valley+Bylot Island	4	3.48	0.05	-61.85
9	Baffin Island	3	9.30	0	-65.76
10	St. Lawrence valley+Baffin Island	4	10.90	0	-65.56
11	Nunavik+Baffin Island	4	11.21	0	-65.71
12	St. Lawrence valley+Nunavik+Baffin Island	5	12.75	0	-65.49
13	Nunavik	3	15.91	0	-69.06
14	St. Lawrence valley+Nunavik	4	17.88	0	-69.05
15	null	2	18.32	0	-71.27
16	St. Lawrence valley	3	19.61	0	-70.92

Table S3.4 Model-averaged coefficient estimates of the effect of temperature encountered by geese at multiple sites on laying date based on the five top models (ΔAIC<2) in Table S3.3. St. Lawrence valley temperature was analyzed for the period 1 April–15 May. Values in bold indicate that the 95% confidence interval (CI) exclude 0.

Parameter	**Estimate**	**Low CI**	**High CI**
St. Lawrence valley	0.22	-0.50	0.95
Nunavik	-0.18	-0.48	0.12
Baffin Island	-0.63	-1.39	0.13
Bylot Island	**-1.34**	**-2.04**	**-0.65**

Table S3.5 Model selection of the relationship between laying date of greater snow geese with temperature at different staging sites (fixed effects) when geese are present from 1991 to 2018. Time periods at each staging site: St. Lawrence valley 1–15 May, Nunavik 10 May–31 May, Baffin Island 20 May–5 June, Bylot Island 30 May–15 June. Number of parameters (K), difference in AIC between the top and current model (Δ AIC), AIC weights (AICw) and log-likelihood value (LL) are presented.

Rank	**Fixed effects**	**K**	**ΔAIC**	**AICw**	**LL**
1	Baffin Island+Bylot Island	4	0	0.25	-60.11
2	Nunavik+Bylot Island	4	0.91	0.16	-60.56
3	St. Lawrence valley+Baffin Island+Bylot Island	5	1.21	0.14	-59.71
4	Bylot Island	3	1.49	0.12	-61.85
5	Nunavik+Baffin Island+Bylot Island	5	1.51	0.12	-59.86
6	St. Lawrence valley+Nunavik+Bylot Island	5	2.06	0.09	-60.14
7	St. Lawrence valley+Nunavik+Baffin Island+Bylot Island	6	2.59	0.07	-59.41
8	St. Lawrence valley+Bylot Island	4	2.98	0.06	-61.60
9	Baffin Island	3	9.30	0	-65.76
10	St. Lawrence valley+Baffin Island	4	11.20	0	-65.71
11	Nunavik+Baffin Island	4	11.21	0	-65.71
12	St. Lawrence valley+Nunavik+Baffin Island	5	13.09	0	-65.65
13	Nunavik	3	15.91	0	-69.06
14	St. Lawrence valley+Nunavik	4	17.90	0	-69.06
15	null	2	18.32	0	-71.27
16	St. Lawrence valley	3	20.28	0	-71.25

Table S3.6 Model-averaged coefficient estimates of the effect of temperature encountered by geese at multiple sites on laying date based on the five top models (ΔAIC<2) in Table S3.5. St. Lawrence valley temperature was analyzed for the period 1–15 May. Values in bold indicate that the 95% confidence interval (CI) exclude 0.

Parameter	**Estimate**	**Low CI**	**High CI**
St. Lawrence valley	0.17	-0.26	0.61
Nunavik	-0.18	-0.48	0.12
Baffin Island	-0.61	-1.35	0.14
Bylot Island	**-1.35**	**-2.05**	**-0.66**