Effets reportés de multiples perturbations rencontrées en migration sur la reproduction de la grande oie des neiges

Mémoire

Thierry Grandmont

Maîtrise en biologie - avec mémoire
Maître ès sciences (M. Sc.)

Québec, Canada

Effets reportés de multiples perturbations rencontrées en migration sur la reproduction de la grande oie des neiges

Mémoire

Thierry Grandmont

Sous la direction de :

Pierre Legagneux, directeur de recherche

Joël Bêty, codirecteur de recherche

Résumé

Les organismes vivants font continuellement face à différentes perturbations. Les effets découlant de celles-ci peuvent se manifester dans l'immédiat, ou encore se manifester plus tard au cours du cycle annuel de l'individu. Ces effets prenant origine de l'expérience passée d'un individu se nomment les effets reportés. Avec les changements globaux causés par l'humain, les perturbations et les effets reportés en découlant, sont amenés à augmenter en fréquence et en amplitude. L'objectif de ce mémoire est d'investiguer, chez une espèce migratrice longévive, la grande oie des neiges (*Anser caerulescens atlanticus*), les mécanismes sous-jacents aux effets reportés observés sur la reproduction résultant de deux types de perturbations rencontrées en migration. Dans un premier temps, nous avons simulé une perturbation aiguë en migration et avons observé les conséquences sur les décisions de reproduction des individus. Par la suite, nous avons comparé la phénologie de migration et de reproduction des oies au cours des 26 dernières années et avons testé l'effet de différents facteurs environnementaux sur ces paramètres phénologiques. Nos résultats indiquent que les oies sont capables de pallier les effets des deux types de perturbation en migration en modulant leurs décisions de migration et de reproduction selon les conditions environnementales qu'elles rencontrent. Ce mémoire révèle différents mécanismes qu'utilise une espèce longévive pour répondre à de multiples perturbations environnementales.

Abstract

Living organisms constantly face different perturbations. The effects occurring from those perturbations can manifest themselves immediately, or only surface later in the individual's life cycle. These effects originating from the past experiences of an individual are called carry-over effects. With global changes brought by humans, perturbations and their effects, are believed to become more intense and frequent. The objective of this thesis is to investigate, on a long-lived migratory species, the greater snow goose (*Anser caerulescens atlanticus*), the mechanisms underlying the carry-over effects on the reproduction of two types of perturbation encountered in migration. Firstly, we simulated an acute perturbation in migration and observed the consequences on the individuals' reproductive decisions. Secondly, we compared the migration and reproduction phenology of snow geese over the last 26 years and tested for the effect of different environmental factors on these phenology parameters. Our results indicate that geese are able to mitigate the effects of both types of perturbation in migration by modulating their migration and reproduction decisions with the environmental conditions they encounter. This thesis reveals different mechanisms a long-lived species uses to respond to multiple environmental perturbations.

Table des matières

Liste des figures

Figure 2.1 Tracked female greater snow goose's migration and reproduction phenology parameters over the three periods of the study (1997-1999, 2006-2008, 2019-2022): (A) departure date from the spring staging area, (B) migration duration (arrival - departure dates), (C) arrival date on the breeding grounds, (D) prelaying duration (lay date - arrival dates), and (E) laying date. Error bars show 95% confidence intervals.

Figure 2.2 Relationships between migration and reproductive phenology in tracked female greater snow geese. For all 6 scatterplots, each dot represents a specific individual for a given year. Regression lines (dotted lines represent non-significant relationships) and 95% confidence interval are presented. Relationships between departure and arrival and dates (A), arrival dates vs. migration duration (B), prelaying vs. migration durations (C), prelaying duration vs. arrival date (D), laying vs. arrival dates (E) and laying date vs prelaying duration (F). Note that in three years of low reproductive success (1999, 2007, and 2022), no radio-tracked females were found nesting.

Figure 2.3 Temperature and snowmelt conditions across the study. (A) shows the yearly average of temperatures for April and May in Quebec City and Montreal, (B) shows yearly average of Pond Inlet June temperatures, and (C) shows days of 50% snow cover at Bylot Island's research station. The first, second and third period of the study are colored in red, green, and blue respectively. Non-significant trends for the 26 years of data are represented with the dotted black line and 95% confidence intervals are shown.

Figure 2.4 Wind assistance across the study. (A) shows the yearly average of wind assistances from mid-May to mid-June in the northern section of snow geese's migratory route, between the tip of Nunavik and Bylot Island, (B) shows the yearly average of wind assistances from mid-May to mid-June in the southern section of snow geese's migratory route, between the St. Lawrence Valley and the tip of Nunavik. The first, second, and third period of the study are colored in red, green, and blue respectively. Non-significant trends for the 26 years of data are represented with the dotted black line and 95% confidence intervals are shown.

Figure 2.5 Migration duration (A), arrival dates on the breeding grounds (B) and laying dates (C) measured for tracked female greater snow geese are presented in relationship with scaled mean Wind assistance for each year (with specific regression lines and confidence intervals). Wind assistance was compiled for the 22 days prior individual arrival dates. Note that in three years of low reproductive success (1999, 2007, and 2022), no radio-tracked females were found nesting. 95% confidence intervals are shown.

Figure 2.S1 Comparison between the mean of daily wind assistance for the specific migration duration of individuals and the mean of daily wind assistance for 22 days before the arrival of individuals on the breeding grounds. Both indices consider migration duration to be the time in days spent between Île-aux-Oies, QC and Bylot Island, Nunavut. A period of 22 days represents the mean migration duration of all individuals with known arrival date and departure date (n = 16). Adjusted $R^2 = 0.85$.

Figure 2.S2 Comparison between the mean of daily wind assistance for the specific migration duration of individuals and the mean of wind assistance associated with GPS location for individuals tracked during their spring migration. For the mean migration duration wind assistance, migration duration is considered to be the time spent traveling between Île-aux-Oies, QC and Bylot Island, Nunavut. For the GPS track mean wind assistance, GPS coordinates selected during spring migration are those between those same two locations. Adjusted $R^2 = 0.93$.

Figure 2.S3 Comparison between the mean of daily wind assistance for 22 days before the arrival of individuals on the breeding grounds and the mean of wind assistance associated with GPS location for individuals tracked during their spring migration. Both indices consider migration duration to be the time spent or the distance traveled between Île-aux-Oies, QC and Bylot Island, Nunavut. 22 days represent the mean migration duration of all individuals with arrival date and departure date in this study. Adjusted $R^2 = 0.92$.

Liste des tableaux

Liste des abréviations, sigles, acronymes

COE : Effets reportés / Carry-Over Effects

GLMM : Modèle linéaire mixte généralisé / Generalized Linear Mixed Model

NAO : Oscillation Atlantique Nord / North Atlantic Oscillation

VHF : Très haute fréquence d’ondes électromagnétiques / Very High Frequency electromagnetic waves

GPS : Système de positionnement global / Global Positioning System

WA : Assistance des vents / Wind Assistance

MODIS : Imagerie spectroradiomètre à résolution modérée / Moderate Resolution Imaging Spectroradiometer

Pourquoi alors un oison ne dirait-il pas : « Tous les éléments de l'univers sont faits à mon intention : la Terre me sert à marcher, le Soleil à m'éclairer, les étoiles à me fournir leur influence ; je tire profit des vents, j'en tire aussi des eaux ; il n'est rien que la voûte céleste ne regarde aussi favorablement que moi ; je suis l'enfant chéri de la Nature. N'est-ce pas l'homme qui me nourrit, qui me loge, qui me sert? »

Montaigne, M. 1595. Les essais livre II

Remerciements

Je trouve aussi difficile d’accepter d’associer un seul nom à ce mémoire que de réussir à remercier tous les gens qui y ont contribué, de manière ou d’une autre. Tellement de sacrifices, de temps et d'efforts ont été investis par une multitude de personnes, autant dans la réalisation de ce projet que dans le support qu’on m’a apporté. La moindre des choses que je puisse faire maintenant est de vous remercier adéquatement.

Pierrot, je n’aurais pu tomber sur un meilleur superviseur. Je suis éternellement reconnaissant de tous les efforts que tu as faits pour m’aider et me guider dans la réalisation de ce projet. Ton dévouement à m’offrir ce dont j’avais besoin m’aura permis de m’épanouir dans ce processus. Entre autres, avec les cinq mois de terrains qui se sont fait annuler devant nos yeux, tu as su m’offrir les opportunités pour combler l’amoureux de terrain que je suis. Enfin, par ton attitude, par ton énergie, ma foi débordante, par ces nombreux appels qui commencent toujours par une niaiserie, tu m’as continuellement rappelé qu’au final, on est là pour avoir du *fun*.

Joël, merci pour ton soutien. J’ai toujours apprécié les échanges que nous avons eus sur le projet. C’était toujours signe de nouvelles idées à explorer. Plus que des conseils, tu m’as guidé, une question à la fois, vers des pistes de réflexion qui m’auront permis de progresser dans le projet. “*Teach a man to fish*” qu’ils disent…

Tout le Winneux lab, merci pour votre bon coeur et toutes vos Winneuseries. C’est un tel bonheur de partager mon quotidien avec vous. Vous expliquez, en grande partie, la tranquillité d’esprit que j’ai pu avoir au courant de cette maîtrise. Quel soulagement de vous savoir prêt et ouvert à me donner votre aide, vos conseils, vos astuces et votre bonne humeur. Ilona, Maeliss et Fred^2, je tiens à vous dire que je suis grandement reconnaissant de votre implication bien spéciale dans ce projet et dans mon cheminement.

Marie-Claude, j’ai énormément d’admiration pour toi. Si ta discipline et ton dévouement sont particulièrement admirables, c’est pour moi ton attitude envers les autres qui m’impressionne le plus. Tout en étant une des personnes les plus occupées que je connaisse, tu prends toujours le temps de te préoccuper du bien-être et de l'épanouissement des gens qui t'entourent. Que ce soit dans l'enseignement du cours d'ornitho, dans la coordination du projet crécerelle ou dans la gestion de l'Île-aux-Oies, tu t'assures toujours de partager, en toute humilité évidemment, tes connaissances, ton expérience, ton amour pour le travail bien fait et pour tout ce qui vit. Merci pour tout Marie.

Marie-Christine, je tiens à te remercier pour m'avoir aidé tout au long de ce projet, et ce depuis son commencement. Tu transmets de manière admirable tes connaissances sur l'Arctique, mais aussi sur la gestion d'un camp de recherche, d'une base de données de fou et d'une saison de baguage des oies. Par ton travail de moine, j'ai pu m'y retrouver dans cette mer d'information accumulée depuis les premières données collectées pour mon projet.

Gilles, merci pour tous tes judicieux conseils et ton immense contribution à l'ensemble du projet. Je ne suis certainement pas le premier à te dire ça dans les remerciements de son mémoire, mais tout ce projet n'existerait pas sans le travail que tu as fait et j'en suis reconnaissant.

Peter, merci de me permettre de continuer le projet que tu as commencé et pour m'avoir aidé dans le processus, c'est vraiment apprécié.

À toutes les équipes de terrain qui ont échangé sueur et éclats de rire pour une poignée de données, je vous remercie tous et toutes. Je n'ai fait qu'une seule année de terrain sur les nombreuses années de ce suivi, mais je sais comme c'est un travail demandant. Le baguage d'oies, ce n'est pas du baguage de parulines et la capture de ces magnifiques bêtes demande un effort physique considérable, une coordination hors pair et un brin de folie. C'est grâce au travail que vous avez accompli que ce mémoire voit le jour. Un merci spécial à Madeleine-Zoé pour, de ta seule présence, rendre les saisons de terrain plus agréables et drôles.

Merci à la gang de Terrebonne pour les nombreux partys fêtant mon retour, à mes amis birders de Québec pour les grosses sorties de birding à la Pointe, à la gang de la Maison bleue pour notre été incroyable, à la gang de Notre-Dame-du-Mont-Carmel pour cet été pandémique parfait.

Un merci infini pour un soutien infini. Chers parents, Manon et Jean, depuis toujours, vous vous êtes assurés de mon bien-être et m'avez encouragé dans toutes mes passions, même les plus folles comme celles qui demandent de faire six heures de route pour observer un oiseau. Je suis vraiment un enfant comblé et la personne que je suis aujourd'hui n'est que le fruit de votre dévotion et de votre amour. De la même manière, j'aimerais remercier François-Xavier et Maxence pour être les frères et sœurs parfaits que vous êtes. C'est une chance inouïe de pouvoir compter sur vous pour rire et me confier.

Finally, a special thank you to you Jillian, my partner for the (almost) entirety of my masters.' If doing a masters' project during a pandemic is difficult, it's nothing compared to maintaining a relationship. Nonetheless, being with you always felt so natural. Most importantly, you've been there on a daily basis for me, advising me into doing the right thing, and doing what's good for me. You're the one who, above all and unconditionally, reminded me to think about myself and, ultimately, made me grow. I'll never be able to thank you enough for that.

Avant-propos

Ce mémoire contient une introduction générale abordant le contexte de l'étude, deux articles rédigés en anglais et une conclusion générale discutant des limites, implications et futures avenues de l'étude. En raison de la pandémie de COVID-19, deux saisons de terrain prévues pour collecter les données pour cette étude ont été annulées. Le projet a donc dû être adapté conséquemment, demandant du temps additionnel et imposant certaines limites au projet initial.

Chapitre 1 Should I stay or Should I go ? Manipulating individual state during migration influences breeding decisions in a long lived bird species.

Accepté dans Functional Ecology

FE-2022-00103 - Should I breed or should I go ? Manipulating individual state during migration influences breeding decisions in a long-lived bird species.

Grandmont, Thierry; Fast, Peter; Grentzmann, Ilona; Gauthier, Gilles; Bety, Joel; Legagneux, Pierre

Auteur principal : Thierry Grandmont (TG) Coauteurs : Peter Fast (PF), Ilona Grentzmann (IG), Gilles Gauthier (GG), Joël Bêty (JB), Pierre Legagneux (PL)

Contribution des auteurs: PF, GG, JB et PL ont défini le projet. PF et PL ont collecté et rassemblé les données. TG, PF, IG et PL ont effectué les analyses statistiques. TG a rédigé l'article. PF, IG, GG, JB et PL ont révisé plusieurs versions de l'article.

Chapitre 2 Adjusting migration and reproduction phenology under climate change : can greater snow geese "wind the clock" ?

À soumettre

Auteur principal: Thierry Grandmont (TG). Coauteurs : Frédéric Dulude-de-Broin (FDB), Frédéric Letourneux (FL), Gilles Gauthier (GG), Joël Bêty (JB), Pierre Legagneux (PL)

Contribution des auteurs: TG, JB et PL ont défini le projet. TG, FDB, FL, JB et PL ont collecté les données. TG, JB et PL ont rassemblé les données. TG a effectué les analyses statistiques en collaboration avec FDB, FL et PL. TG a rédigé l'article. PL a révisé plusieurs versions du manuscrit.

Introduction

Un environnement aux perturbations multiples

Répondre aux perturbations de son milieu est une fonction centrale à tout organisme vivant. En écologie, on définit une perturbation comme un événement qui pousse un changement de densité ou de composition d’espèces dans une communauté (Glasby & Underwood 1996). Autrement dit, c’est un événement qui perturbe l’état d’équilibre qui est en place. On distingue principalement deux types de perturbation pouvant être exercés sur les écosystèmes ou communautés: les perturbations de pression (*press* en anglais) et les perturbations de pulsions (*pulse* en anglais). Ces deux perturbations diffèrent autant dans leurs causes que leurs effets. Les pressions sont des perturbations qui s’effectuent sur une longue période, elles réfèrent plus aux tendances à long terme. Ces pressions ont généralement des conséquences plus modérées sur les communautés, mais qui, au fil du temps, mèneront à des changements permanents et à un nouvel équilibre (Bender et al., 1984; Glasby & Underwood, 1996). Au contraire, les perturbations de pulsions sont plus soudaines et souvent plus extrêmes. Elles entraîneront des conséquences immédiates et aigües. Toutefois, une fois la perturbation terminée, les conséquences de celle-ci vont généralement tendre vers un retour à l’ancien équilibre (Bender et al., 1984; Glasby & Underwood, 1996). La résilience des écosystèmes dépendra donc de l’intensité et de la durée de telles pressions (Arnoldi et al. 2018).

Bien que ces concepts soient principalement utilisés pour décrire les perturbations affectant une communauté (Arnoldi et al. 2018), il est possible de relier cette théorie au niveau d’une espèce. En effet, au cours de sa vie, un individu subira autant des perturbations de pulsion, comme des tempêtes, des événements de prédation ou des froids extrêmes (Wingfield et al. 1998; Romero & Wingfield 2015), que des perturbations de pression, comme la dégradation graduelle de son habitat (Polfus et al. 2011) ou encore une diminution de l’abondance de ses proies (Grémillet et al. 2016). Ainsi, ces deux types de perturbations ne sont pas mutuellement exclusives et peuvent s’exercer sur un individu simultanément. C’est particulièrement le cas dans le contexte actuel de changements climatiques, où les organismes vivants font face à une augmentation constante des températures (pression) et des événements extrêmes plus fréquents (pulsion) (Harris et al. 2018). Dans les deux cas, ces perturbations poussent les individus hors de leur équilibre interne ou homéostasie.

Les changements climatiques s'accompagnent à la fois d'effets de pulsion et de pression. En effet, l'augmentation des températures au cours des années s'apparente à une perturbation par pression alors que les événements extrêmes (tempêtes, feux, sécheresses) correspondent à des pressions par pulsion. D'une part, le réchauffement s'effectue de manière hétérogène sur la planète (Kumar et al. 2013), certaines régions subissent donc un réchauffement plus prononcé. C'est notamment le cas en Arctique, où l'augmentation des températures est disproportionnée par rapport aux autres régions (Walsh et al. 2011), un phénomène nommé l'amplification arctique (Previdi et al. 2021). Les zones tempérées subissent également un réchauffement, mais celui-ci est moins prononcé qu'aux hautes latitudes (Hansen et al. 2006). De la même manière, les patrons et les tendances de précipitation et de vent sont amenées à être altérées au cours des prochaines années (Dore 2005, Vautard et al. 2010, Trenberth 2011, Kling & Ackerly 2020). D'autre part, le rapport du GIECC (2022) prévoit une augmentation des événements extrêmes. Une grande variété d'événements extrêmes devrait devenir plus fréquent dans les prochaines années : ouragans, inondations, sécheresses, tempêtes de vent, feux de forêt (Mann & Emanuel 2006, Mitchell et al. 2006, Flannigan et al. 2009, Schwierz et al. 2009, O'Gorman 2015, Dai et al. 2018). Ces deux types de perturbations résultant des changements climatiques s'opèrent de manière simultanées sur les espèces et les populations qu'elles composent. Harris et al. (2018) présente un cadre conceptuel montrant les composantes du changement climatique, de la variabilité du climat et de l'impact sur les systèmes biologiques (Fig. 0.1).

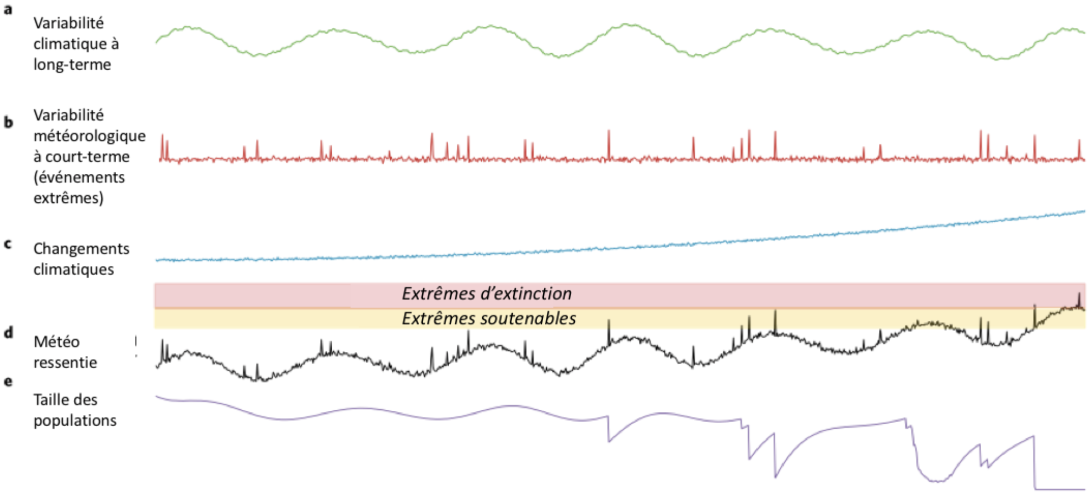

Figure 0.1 La structure pression-pulsion, montrant les composantes des changements climatiques et la variabilité climatique ressentie par les systèmes biologiques. Plusieurs organismes sont adaptés pour répondre à des changements à long terme (a) et de la variabilité

climatique à court terme (b), mais avec l'intensification des changements climatiques (c), il est attendu que la magnitude et la fréquence des événements extrêmes augmentent. Le seuil entre les événements soutenables (jaune) et les extrêmes d'extinction (rose) est donc franchi plus souvent, prévenant un rétablissement aux tailles de population précédentes. (e) L'effet cumulatif des perturbations de pression et de pulsion du climat pourrait entraîner des conséquences à long terme sur les tailles de population et potentiellement sur leur persistance. Adapté de Harris et al. (2018).

Le rôle des effets reportés

Toute perturbation a le potentiel d'engendrer des conséquences sur la valeur adaptative des individus, soit leur survie et leur capacité à se reproduire. Les perturbations de pulsion peuvent souvent forcer un animal à arrêter son mode de vie « normal » pour entrer dans un état d'urgence afin de rétablir son homéostasie, ce qui, tout dépendant de l'intensité et de la durée d'exposition à cette perturbation, peut mettre en péril sa survie ou encore son succès reproducteur (Wingfield et al. 1998). En effet, un tel événement mènera généralement un animal à développer une réponse physiologique. Par exemple, en augmentant les taux d'hormones de stress. Ceci mènera l'animal à diminuer l'énergie investie pour le maintien du métabolisme basal ou de son système immunitaire afin de la diriger vers l'augmentation du taux de glucose sanguin et donc vers ses muscles (Sapolsky 2000). Cette réponse physiologique s'effectue rarement sans qu'une réponse comportementale en découle, par exemple, le fait d'augmenter le temps passé en vigilance ou à rechercher de la nourriture (Wingfield et al. 1998). Ultimement, ces réponses au niveau individuel peuvent mener à des conséquences démographiques telles qu'une réduction du recrutement (Charbonnel et al. 2008). Parallèlement, les perturbations de pression peuvent graduellement perturber l'homéostasie et entrainer une réponse physiologique et comportementale chez un individu. Par exemple, une variation des conditions environnementales s'exerçant sur une période prolongée peut générer un stress basal plus élevé (Pravosudov et al. 2001), augmenter le taux métabolique (Swanson & Olmstead 1999) ou encore mener à un comportement de dissipation de chaleur corporelle (du Plessis et al. 2012).

Alors que la réponse aux pressions et aux pulsions vise généralement une meilleure survie dans l'immédiat (Bamberger et al. 1996), les effets de ces perturbations ou de la réponse à ces perturbations perdurent dans le temps. En effet, il arrive que des événements ou des processus survenant à un moment donné aient des impacts qui se détecteront plus tard. On parle alors d'effets reportés (*carry-over effects* en anglais), définis par O'Connor et al. (2014) comme étant toute situation où l'expérience passée d'un individu explique sa performance actuelle. Souvent sous-estimée dans la littérature, l'étude de ce phénomène a gagné en popularité lors des dernières décennies et il est maintenant reconnu que les effets reportés sont plus communs et répandus qu'on ne le pensait initialement (Harrison et al. 2011, O'Connor et al. 2014) avec des impacts sur la valeur reproductive aussi importants que des effets affectant directement la reproduction ou la survie (Harrisson et al. 2011). Les oiseaux migrateurs ont souvent été le sujet des études sur les effets reportés, car la migration facilite la séparation des événements du cycle annuel (Marra et al. 1998, Norris 2005, Inger et al. 2008, Harrison et al. 2011, Legagneux et al. 2012, Catry et al. 2013, Schultner et al. 2014, Latta et al. 2016).

Ainsi, pressions et pulsions peuvent engendrer chez les individus des effets reportés. Ces derniers peuvent se manifester entre n'importe quelle étape du cycle annuel. Par exemple, chez le Puffin cendré (*Calonectris borealis*), un investissement reproducteur réduit durant une année provoquera un devancement de tout le cycle annuel l'année suivante (Catry et al. 2013). De la même manière, le niveau d'hormone de stress (glucocorticoïdes) lors de la mue automnale (proxy des conditions environnementales) affecte négativement la date d'arrivée et la condition corporelle l'année suivante chez l'eider à duvet (*Somateria mollissima*) (Harms et al. 2015). Néanmoins, la majorité des études qui se sont penchées sur les effets reportés ont examiné les effets d'une perturbation lors de la période d'hivernage sur la reproduction. Les exemples de ce genre d'effets reportés sont multiples, et les causes autant que les effets sont variées: les conditions climatiques hivernales sur la condition corporelle printanière (Clausen et al. 2015), la qualité de l'habitat d'hivernage sur le succès reproducteur (Norris et al. 2004) ou sur la date d'arrivée (Gill et al. 2001), un stress expérimental sur la date de ponte (Descamps et al. 2011). Cependant, les mécanismes en jeu dans l'expression des effets reportés sont encore méconnus. En effet, même si les conséquences ultimes d'une perturbation sur la reproduction ont bien été étudiées (Legagneux et al. 2012), les processus de réponse aux perturbations, telles que les prises de décisions individuelles, sont moins bien documentés. Harrison et al. (2011) soulignent également le manque d'études expérimentales dans le domaine des effets reportés qui sont pourtant cruciales pour déterminer les processus écologiques responsables de tels effets.

Les prises de décisions pré-reproduction

Afin d'étudier les effets reportés d'une perturbation survenant en migration ou sur les aires d'hivernage sur la reproduction, nous avons décortiqué les prises de décision individuelles sous forme d'un schéma conceptuel (Fig. 0.2). Notre schéma s'applique plus particulièrement aux espèces d'oiseaux longévives, soit les espèces ayant une histoire de vie lente (croissance lente, maturité retardée et haut taux de survie; Spencer and Janzen 2010). Il est généralement reconnu que ces espèces soient plus portées à exprimer des effets reportés que les espèces à histoire de vie courte, bien que certaines études empiriques semblent démontrer des effets reportés sur les deux stratégies d'histoire de vie (Ramos et al. 2018). D'abord, nous établissons la prémisse qu'un événement perturbateur entraînera un stress physiologique. Ce stress physiologique, en fonction de son intensité et de sa fréquence, aura des conséquences directes sur l'allocation de l'énergie (Sapolsky 2000) ou encore le système immunitaire (Edes et al. 2018) avec des changements rapides de comportements et des effets à plus long terme sur des traits d'histoires de vie (Wingfield et al. 1998). Il a été démontré chez plusieurs espèces qu'à la suite d'une augmentation des hormones de stress dans le sang, les individus adoptent un comportement de recherche de nourriture (Astheimer et al. 1992, Hoarau et al. 2022). Ultimement, la perturbation, selon la nature de celle-ci, peut faire varier différents paramètres au sein de l'organisme. L'allocation de l'énergie, la condition corporelle (Landys et al. 2006, Owen-Ashley & Wingfield 2007) ou encore le comportement peuvent être affectés, ce qui peut même entraîner un délai dans sa phénologie (Krause et al. 2016), soit un délai dans la synchronie saisonnière des événements de son cycle annuel (Knudsen et al. 2011).

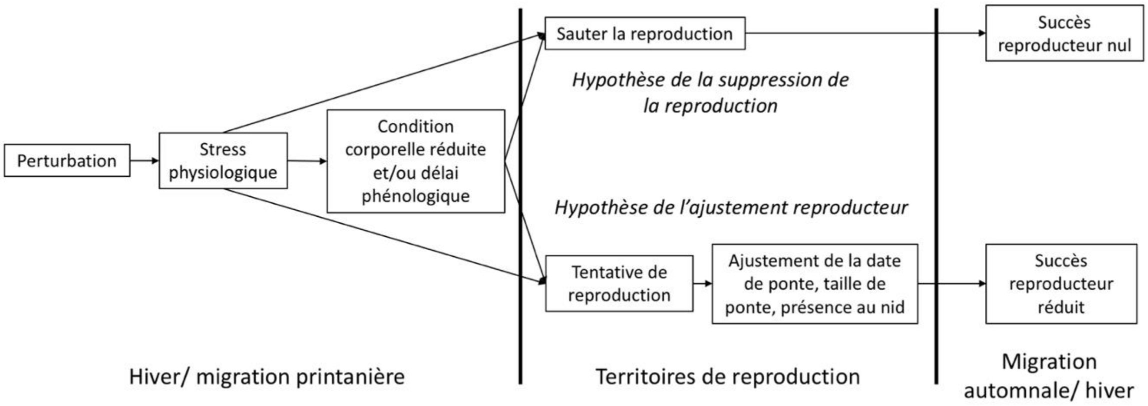

Figure 0.2 Figure conceptuelle montrant deux hypothèses alternatives de mécanisme sous-jacent à une réduction du succès reproducteur à la suite d'une perturbation.

Pour comprendre comment un stress physiologique, une diminution de la condition corporelle ou un retard en migration peuvent entraîner des répercussions sur la reproduction, il faut d'abord se pencher sur l'optimisation de la ponte chez les oiseaux. En effet, la production des œufs demande beaucoup d'énergie aux femelles, surtout lorsqu'elles utilisent en partie leurs réserves endogènes (Gauthier et al. 2003). Les espèces qui se reproduisent sur capital (capital breeders) doivent atteindre un certain seuil de condition corporelle afin de produire leurs œufs (Hennin et al. 2015). Pour atteindre ce seuil, les femelles doivent s'alimenter avant la reproduction pour amasser une quantité de réserve suffisante à la production des œufs (Rowe et al. 1994, Bêty et al. 2003, Descamps et al. 2011, Legagneux et al. 2016). Ainsi, en augmentant le taux d'engraissement en préparation à la ponte, les individus pourraient en théorie produire un nombre d'œufs plus important (Rowe et al. 1994). En principe, les oiseaux auraient avantage à s'alimenter le plus longtemps possible pour pondre plus d'œufs et augmenter leur succès reproducteur. Toutefois, en raison du déclin saisonnier du succès reproducteur, la valeur d'un œuf diminue avec le temps. Si bien qu'à un certain moment dans la saison, il devient plus avantageux d'arrêter la ponte plutôt que de passer plus de temps à accumuler l'énergie pour pondre un œuf supplémentaire (Drent & Daan 1980, Rowe et al. 1994). Ainsi, le moment optimal de la ponte et le nombre optimal d'œufs pondus résultent d'un compromis entre la vitesse d'engraissement, la condition corporelle au moment de la ponte et la date de ponte. Une perturbation qui aurait pour conséquence de modifier la date de ponte (décalage phénologique), de réduire la condition corporelle ou encore la vitesse d'engraissement pourrait donc avoir un impact sur les décisions de reproduction (Fig. 0.2).

Dans le cas d'une espèce longévive, une réduction du succès reproducteur en réponse à une perturbation pourrait résulter principalement de deux mécanismes : une diminution de la propension à se reproduire (i.e., sauter un événement reproducteur) ou une réduction de l'investissement reproducteur (i.e. taille de ponte; Rowe et al. 1994, Hennin et al. 2018). La première option est une stratégie assez commune chez les espèces longévives : elle permet d'économiser l'énergie lorsque l'investissement dans la reproduction devient non rentable à long terme (Warren et al. 2014, Legagneux et al. 2016, Jean-Gagnon et al. 2018; Fig. 0.2). Cette stratégie permet d'augmenter le taux de survie au détriment de la reproduction à court terme et donc de miser sur les prochaines années pour se reproduire. À l'inverse, la décision de nicher malgré une condition corporelle relativement fiable peut être possible grâce à une réduction de l'investissement dans la reproduction à court terme, incluant un décalage de la date de ponte et une réduction de la taille de ponte (Bêty et al. 2003, Descamps et al. 2011; Fig. 0.2).

Les conséquences de ces décisions sont multiples et peuvent être altérées par les changements climatiques. La décision de sauter la reproduction, une stratégie qui affecte le recrutement au niveau de la population (Sedinger et al. 2008), est influencée par les perturbations imprévisibles (Legagneux et al 2016). La fréquence des événements extrêmes étant projetée à augmenter (GIECC 2022), les conditions défavorables à la reproduction pourraient aussi survenir plus fréquemment (Visser et al. 2009). Alternativement, la diminution de l'investissement reproducteur peut induire une réduction du succès reproducteur annuel par différents mécanismes. Entre autres, un individu reportant sa reproduction verra la valeur saisonnière de ses œufs être réduite (Drent and Daan 1980, Harriman et al. 2017). Cette conséquence pourrait s'accentuer avec le devancement des saisons causé par les changements climatiques. En effet, les espèces des niveaux trophiques inférieurs étant plus réactives aux variations climatiques que les niveaux trophiques supérieurs, une désynchronisation entre le moment de la croissance des jeunes et le pic de qualité et de disponibilité des ressources peut avoir lieu (Both et al. 2005, Durant et al. 2007, Thackeray et al. 2010). Le phénomène a été bien étudié chez les gobemouches noirs (*Ficedula hypoleuca*) en Europe, où la désynchronisation trophique mène éventuellement à un déclin de population (Both et al. 2006).

Vu les implications des différentes prises de décision individuelles en réponse aux perturbations, il est primordial de comprendre les mécanismes sous-jacents à ces décisions. Toutefois, l'une de ces décisions, la propension à nicher, est un paramètre logistiquement difficile à mesurer en partie parce que les suivis ont lieu sur les sites de reproduction et les individus qui sautent un événement de reproduction ne sont généralement tout simplement pas observés (Etterson et al. 2011). Dans ce contexte, comprendre les mécanismes de réponse face aux perturbations, qu'elles soient d'origine naturelle ou anthropique, reste une tâche complexe qui demande le plus souvent de développer des approches expérimentales et requiert généralement un suivi individuel sur une longue période (Harrisson et al. 2011).

La Grande oie des neiges

Pour mieux comprendre les mécanismes sous-jacents à une réduction du succès reproducteur à la suite d'une perturbation, nous étudions spécifiquement, dans le cadre de ce mémoire, la Grande Oie des neiges (*Anser caerulescens atlanticus*), soit une espèce migratrice de longue-distance nichant dans l'Arctique canadien. Cette espèce s'avère être un bon modèle qui permet de faire un suivi au niveau individuel chez une espèce migratrice longévive, entre autres parce que sa taille permet l'utilisation de technologie de télémétrie depuis la fin des années 1990 (Blouin et al. 1999). De plus, un suivi de la reproduction et le baguage de plusieurs milliers d'individus depuis 1989 à la principale colonie de l'espèce à l'Île Bylot a non seulement permis une excellente compréhension de l'écologie de l'espèce, mais a aussi servi de base à la mise en place de manipulation expérimentales réalisées sur des individus en migration. En effet, comme les femelles sont hautement philopatriques (Bêty et al. 2004), les probabilités que les individus rencontrés en migration qui ont été bagués à l'Île Bylot retournent à cet endroit pour se reproduire sont élevées, ce qui permet un suivi de mêmes individus entre les haltes migratoires et le site de reproduction.

La grande oie des neiges effectue quelques haltes le long de son parcours migratoire reliant l'Arctique canadien et la Côte Est américaine. La plus longue et la plus importante d'entre elles se situent le long de la vallée du Saint-Laurent et aux basses terres du Lac-Saint-Jean. Les oies passent le printemps à s'alimenter de rhizomes dans les marais côtiers et de maïs et d'autres graminées dans les champs cultivés (Gauthier et al. 1992, 2005). Cette halte printanière est une période particulièrement importante pour l'espèce, car c'est là qu'elle accumule des réserves pour entreprendre sa migration, mais aussi, chez les femelles, pour emmagasiner des réserves pour la formation des œufs (Gauthier et al. 1992, 2003). En Arctique, la période de reproduction des oies est brève et il existe un fort déclin saisonnier du succès reproducteur (Lepage et al. 2000, Reséndiz-Infante and Gauthier 2020). L'effort reproducteur de la grande oie des neiges dépend autant de l'intégration des facteurs environnementaux tel que la température et le moment de fonte de la neige en Arctique (Dickey et al. 2008, Morrissette et al. 2010) que de facteurs internes tel que la condition corporelle printanière (Bêty et al. 2003) ou les stress rencontrés en migration (Juillet et al. 2012, Legagneux et al. 2012).

Depuis une cinquantaine d'années, la grande oie des neiges a fait face à plusieurs changements dans son environnement. Traditionnellement chassée en Arctique depuis des siècles, l'espèce fait, depuis quelques décennies, l’objet d’une chasse récréative qui s’opère depuis son retour automnal de l’Arctique à son départ printanier vers le Nord. Cette chasse printanière a été instaurée en 1999 pour limiter l’accroissement exponentiel de la population, largement dû aux modifications des pratiques agricoles (Lefebvre et al. 2017). Il a déjà été démontré que la chasse printanière affecte différents paramètres de reproduction des oies (Mainguy et al. 2002, Juillet et al. 2012). De plus, les changements climatiques exercent graduellement une pression sur plusieurs espèces d’oiseaux migrateurs, dont les oies. Le réchauffement hétérogène à travers la planète et particulièrement rapide en Arctique (Walsh et al. 2011) menace la synchronie entre les indicateurs de migration aux haltes migratoires et les conditions environnementales sur les territoires de nidification (Kumar et al. 2013, Bailey et al. 2022). Les migrateurs de longue-distance n’ayant pas d’information sur l’état des sites de reproduction situés plus au nord montrent un plus faible ajustement dans leurs dates de migration en réponse au réchauffement par rapport aux espèces résidentes (Both and Visser 2001, Rubolini et al. 2007). Chez l’oie des neiges, la date d’arrivée sur les sites de reproduction est un facteur important déterminant grandement la date de ponte, paramètre clef corrélé à l’investissement et le succès reproducteur (Bêty et al. 2003). Si les oies ne parviennent pas à devancer leur reproduction pour suivre l’avancée du printemps (Gauthier et al. 2013), une asynchronie entre le pic des ressources et la croissance des jeunes peut avoir lieu, affectant légèrement le succès reproducteur et la qualité des jeunes (Doiron et al. 2015).

Globalement, l’oie des neiges est sujette à des changements environnementaux importants tout au long de son cycle annuel. Bien que les perturbations se produisant sur les haltes printanières peuvent affecter leur reproduction (Bêty et al. 2003, Legagneux et al. 2012, LeTourneux et al. 2021), les mécanismes de réponse à différents types de perturbations et leur impact relatif sur la reproduction restent à être éclaircies, comme c’est le cas pour bien d’autres espèces longévives.

Objectifs

Ce projet cadre dans les initiatives visant à mieux comprendre les effets de perturbations multiples sur la faune et à identifier les mécanismes qui génèrent des effets reportés sur leur reproduction. Par une approche individuelle, ce projet porte plus spécifiquement sur les effets reportés de deux types de perturbation rencontrée durant la migration sur la reproduction de la grande oie des neiges, une espèce longévive. Dans le premier chapitre, nous évaluons les mécanismes en jeu en réponse à une pression de pulsion, soit une manipulation expérimentale en simulant un stress environnemental sur les haltes migratoires. Plus spécifiquement, nous tentons de déterminer si la réduction du succès reproducteur à la suite d'une perturbation (Legagneux et al. 2012) passe par une réduction de l'investissement reproducteur ou une réduction de la propension à se reproduire. Dans le deuxième chapitre, nous nous intéressons à l'impact d'une perturbation de type pression, le réchauffement climatique. Nous avons comparé la phénologie de migration et de reproduction des oies au cours des 26 dernières années, période marquée par un réchauffement général dans les régions arctiques, afin de déterminer si les oies ont, contrairement à plusieurs migrateurs de longue-distance (Rubolini et al. 2007), ajusté leur migration en réponse aux changements globaux. Nous avons également investigué si différents facteurs environnementaux (température, fonte de neige et vents) pouvaient affecter la phénologie de migration et de reproduction. Ce chapitre repose sur le suivi d'individus marqués et équipés de colliers émetteurs permettant de suivre leurs décisions depuis les haltes migratoires dans le sud du Québec jusque dans le haut Arctique.

Chapitre 1 - Should I breed or should I go ? Manipulating individual state during migration influences breeding decisions in a long-lived bird species.

1.1 Résumé

La documentation des effets reportés (Carry-Over Effect en anglais, COE), définis comme étant un effet résultant d'un événement qui s'est produit à un moment antérieur, a été effectuée principalement par observation et la compréhension des mécanismes spécifiques sous-jacents aux COE est toujours manquante. Pour investiguer ceci, nous avons simulé une perturbation environnementale durant la migration d'une espèce longévive et avons observé les effets subséquents sur différents paramètres de reproduction. Nous avons capturé des femelles grande oie des neiges (*Anser caerulescens atlanticus*) sur leur halte migratoire printanière et avons maintenu des individus en captivité jusqu'à quatre jours avant de les relâcher. Nous avons réobservé ces femelles 3000 km au Nord, sur leur territoire de nidification arctiques, pour déterminer leur propension à se reproduire (la probabilité d'initier un événement reproducteur pour une année donnée), leur date d'arrivée, leur date de ponte, leur taille de ponte et leur succès d'éclosion. Seuls les proxys de la propension à se reproduire ont été affectés par notre manipulation, diminuant lorsque le temps passé en captivité augmentait. Cependant, les femelles étaient capables de compenser pour l'effet du temps passé en captivité lors de deux des trois années d'étude avec des conditions environnementales normales ou bonnes sur les sites de nidification. Faisant face au défi additionnel des conditions environnementales défavorables sur les territoires de nidification, plusieurs individus manipulés durant la migration semblent avoir abrégé leurs efforts de nidification en sautant la reproduction. Cette expérience est la première à montrer que la propension à se reproduire est un paramètre important afin de remédier aux COE résultant d'un événement stressant avant la reproduction chez une espèce longévive.

1.2 Abstract

Documentation of Carry-Over Effects (COEs), defined as effects resulting from events that occurred in a previous time period, has largely been observational and understanding of specific mechanisms underlying COEs is still lacking. To investigate this, we simulated an environmental perturbation during the spring migration of a long-lived bird species and looked at the subsequent effects on various breeding parameters. We captured female greater snow geese (*Anser caerulescens atlanticus*) on their spring staging sites and maintained individuals in captivity for up to four days before releasing them. We re-observed females 3000 km North, on their Arctic breeding grounds, to estimate their breeding propensity (i.e., probability of initiating a reproductive event for a given year), and measure their arrival date, laying date, clutch size, and nesting success. Only proxies of breeding propensity were affected by our manipulation, which decreased as the time spent in captivity increased. However, females were able to overcome the effects of captivity in two out of the three years of experimentation with normal or good environmental conditions at the breeding site. When facing the additional challenge of poor environmental conditions, many individuals manipulated during migration apparently curtailed their reproductive effort by skipping breeding. This experiment is the first to show that breeding propensity is an important parameter affected by COEs resulting from stressful events prior to reproduction in long-lived species.

1.3 Introduction

Organisms can cope with environmental changes through different mechanisms, ranging from molecular to physiological and behavioural adaptations. Those mechanisms typically aim to maintain homeostasis in response to short term environmental changes (Cockrem, 2013; Wingfield et al., 1998) with possible impacts on some life-history traits. Reproductive traits in particular are energetically demanding and can be affected not only by events occurring during the present time but also by events during a previous time period. Their outcome can thus be influenced by multiple stressors encountered over the whole annual cycle. Such Carry-Over Effects (COEs) were largely neglected in biological studies until recently and are now considered to have fitness impacts comparable to more proximate factors (Harrison et al., 2011; Norris, 2005; O'Connor et al., 2014).

COEs have been reported in many taxa (O'Connor et al., 2014), particularly in migratory species, with effects from wintering or staging grounds carrying over to breeding grounds (Bearhop et al., 2004; Marra et al., 1998) or *vice versa* (Catry et al., 2013; Inger et al., 2010). The mechanisms underlying COEs on reproductive performance in iteroparous species are still poorly understood, although a reduction in breeding propensity (probability of initiating a reproductive event for a given year) as well as other adjustments of the reproductive investment (such as clutch size) can result in an overall decline in breeding success. While the reduction of reproductive investment among individuals that do initiate reproduction can be readily assessed by monitoring individuals on their breeding grounds, breeding propensity is more difficult to assess (Jean-Gagnon et al., 2018; Souchay et al., 2014) because non-breeding individuals are often more secretive, erratic and may completely avoid their breeding territories (Chastel, 1995; Reed et al., 2004; Wheat et al., 2017).

In long-lived bird species, stressors that occur before reproduction, such as harsh weather, decreased food availability, or increased predation pressure, can be carried over onto reproduction and ultimately reduce the number of offspring produced (Fig. 1). Indeed, perturbations can limit an individual's condition gain by reducing the fattening rate or by delaying resource acquisition (Krause et al., 2017). As egg production and incubation require high amounts of energy (Williams, 2005), a stressful event can compromise acquisition of the endogenous reserves required to initiate reproduction (Hennin et al., 2016; Legagneux et al., 2016; Rowe et al., 1994). Furthermore, unpredictable perturbations can trigger acute physiological stress responses and suppress sexual hormone secretion, thus jeopardising reproduction (Wingfield et al., 1998). As a result, at the individual level, two mutually exclusive mechanisms could be involved in the reduction of reproductive success following a stressor. The first possible mechanism is the **breeding suppression hypothesis** (dotted line, Fig.1.1). Life-histories of long-lived species are based on high survival probability and low fertility. It is thus common for these species to skip the reproductive event for a given year, when investment into the reproduction becomes too demanding for the individual (Converse et al., 2009; Gauthier et al., 2010; Jenouvrier et al., 2008; Souchay & Gauthier, 2014), for example after a perturbation or when conditions on the breeding site are less favourable. This leads to increased survival probability by saving the extra energy otherwise invested in reproduction and preparing for future breeding attempts, under more favourable conditions (Cubaynes et al., 2011; Reed et al., 2004). Secondly, the **reproductive adjustment hypothesis** (dashed line, Fig.1.1) can be described as follows: an individual could have to compromise on its reproduction due to the constraints imposed by stress experienced prior reproduction (McKellar et al., 2013). Theoretical models predicting that individuals in lower condition prior to breeding will lay later and a have smaller clutch size (Drent & Daan, 1980; Rowe et al., 1994) have received empirical support in the literature (Bêty et al., 2003; Descamps, Bêty et al., 2011; Devries et al., 2008).

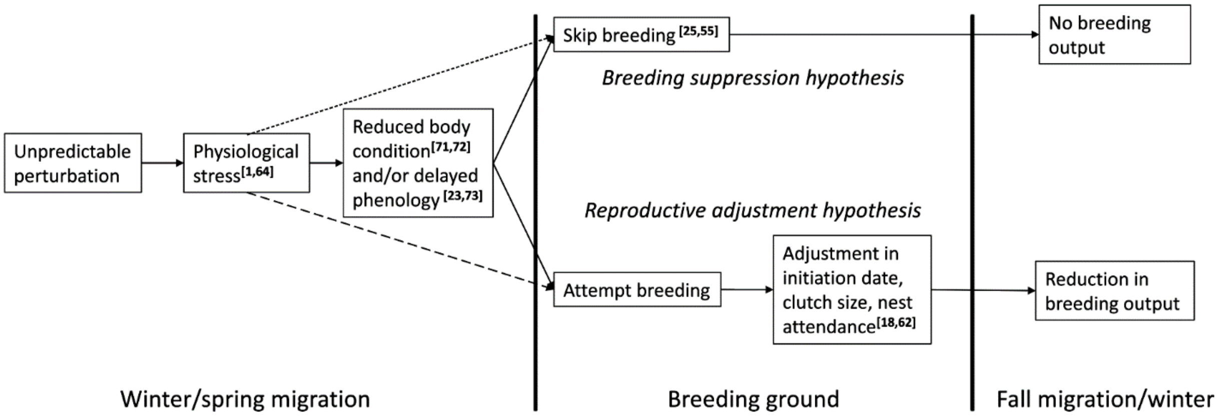

Figure 1.1 Conceptual figure showing two alternative hypotheses for the mechanisms underlying a reduction of breeding output due to the carried-over effect of a perturbation during migration. Dashed line: reproductive adjustment hypothesis; dotted line: breeding suppression hypothesis. Numbers within brackets in the figure refer to the reference list.

In this study, we examine the mechanisms involved in the reduction of breeding success following an experimental perturbation during migration in the greater snow goose (*Anser caerulescens atlanticus)*. Such experimental studies are still rare in the wild (Descamps et al., 2011; Legagneux et al., 2016; Studds & Marra, 2005) and provide invaluable information by characterising the life history traits most affected by COEs. Here, we seek to test two mechanisms (Fig. 1) that could mediate COEs in greater snow geese, a long-lived migratory species that relies on a combination of endogenous nutrients acquired during migration and nutrients acquired through feeding on the breeding grounds to lay their eggs (Choinière & Gauthier, 1995; Gauthier et al., 2003) and for which COEs were already documented in one of our previous studies (Legagneux et al. 2012). Over three consecutive years, we captured birds in the spring at their stopover sites were maintained in captivity for up to 4 days. We found that the time spent in captivity reduced the reproductive output (measured as the proportion of successful breeders observed in the fall) by 45–71% in two years. To identify the mechanisms involved in such carry-over effects, we conducted new analyses using additional information from individuals treated in spring and subsequently monitored on their Arctic breeding ground. To test the breeding suppression hypothesis (dotted line, Fig.1), we investigated the effect of time spent in captivity and the detection probability of individuals at the goose breeding colony, a proxy of breeding propensity in our study system. To test the reproductive adjustment hypothesis (dashed line, Fig.1), we compared arrival date, laying date, clutch size and nesting success between individuals that spent time in captivity and their spring stopover control individuals.

1.4 Material and methods

1.4.1 Study species and study sites

Greater snow geese are herbivorous, long-distance migrants breeding in the High Arctic. The largest greater snow goose colony is located on Bylot Island, Nunavut, Canada (78º08’N 80º00’ W), which hosts 15-20% of the breeding population (Reed et al., 2002). Greater snow geese winter along the

Atlantic coast of the United States and use St. Lawrence Valley in Quebec as staging site for both their spring and fall migrations. During spring staging, which lasts six to eight weeks from late March to late May, they feed in croplands and wetlands, which allow them to accumulate endogenous reserves (Gauthier et al., 1992). Geese were captured at Île-aux-Oies, (47º00'N 70º33' W) an important feeding and resting area located in the middle of the St. Lawrence River, 60 km northeast of Québec City.

1.4.2 Capture, measurements, and marking

As described in Legagneux et al. 2012, we captured spring staging geese using baited cannon-nets from late April to mid-May 2007, 2008, and 2009. For snow geese, spring migration is the typical period of family break-up (Gauthier & Tardif, 1991), therefore, juveniles were released immediately following capture. Shortly after capture, adults were sexed based on cloacal examination, females were weighed to the nearest gram with an electronic scale, and culmen, head and tarsus were measured to the nearest 0.1 mm. Females were individually marked with USGS metal bands and alphanumeric yellow neck collars (hereafter called standard neck collar) allowing multi-resighting events throughout their annual cycle.

1.4.3 Experimental treatments

We maintained geese within eight fenced indoor enclosures, keeping male and females in separate enclosures but with social (visual and vocal) contacts to minimize divorce risk. All individuals from the same capture group were later released simultaneously following captivity (see details in Legagneux et al., 2012). Females were assigned to one of three treatments: i) Control group (N = 672), released with their males immediately after banding (typically < 5 h after capture), ii) Fed groups (N = 681) kept in enclosures with *ad libitum* food (crushed corn) and water or iii) Fasting groups (N = 685) kept in enclosures with only water. Fed and Fasting groups were kept in captivity for up to four days, and females were weighed again before release. The same treatment was assigned to all females of a capture group. Food and water were provided to males from all treatment groups kept in captivity. To ensure a relatively balanced design and minimize differences in sample size among treatments, we followed a pre-ordered list (see list of treatment assigned to each capture group; Table 1.S1) to determine which treatment was assigned to each capture group. Following this design, mean time in captivity varied little among years (49.9 hours in 2007, 47.2 in 2008, and 64.33 in 2009).

Each year, all captures and releases were completed at least one week before mass departure from the staging sites for the arctic-breeding ground (Bêty et al., 2004).

1.4.4 Radio-tracking

We radio-marked 27 adult females on the spring staging site in 2006, 2007 and 2008 (N = 5, 10 and 12, respectively). Birds were selected among those captured on the spring staging site in 2007 and 2008 (see above). In 2006, radio-marked birds were captured using the exact same methods. All radio-marked birds had been previously banded (either as adults or young) at the Bylot Island breeding colony in the high Arctic when adults are moulting and juveniles are growing (see Menu et al., 2005 for details). Since female snow geese are philopatric to the breeding colony (Lecomte et al., 2008), the likelihood of detecting and resighting these females back on their breeding site was higher compared to females randomly chosen among those captured in spring. VHF radio transmitters were affixed to a neck collar (total weight 60±7 g, 2.5±0.4% of bird body mass; mean ± SD; (Demers et al., 2003)) and their longevity was 16–24 months. Following pre-ordered lists when assigning treatments, VHF individuals were released between 0-2.5 days after capture and had access to water only while in captivity (fasting group).

Each year in late May, we erected two automated telemetry towers on Bylot Island, located 30 km apart on high ground before the arrival of the geese. Each system included two pole-mounted antennas and was set to automatically scan and record the presence of radio-marked geese arriving on Bylot Island. These detections served the dual purpose of providing arrival dates on the breeding grounds (defined as the first detection date) and determining which individuals had not reached their breeding grounds (no detection on Bylot Island). Handheld receivers were also used daily during spring arrival, and at least bi-weekly during nesting. No additional individuals were detected by handheld surveys suggesting that automated telemetry towers provided reliable information and potentially better than handheld survey methods for which the average daily detection probability was already 81 ± 24% on Bylot Island (Bêty et al., 2003). To increase detection probability of marked birds, systematic searches were conducted on foot in the breeding colony during the prelaying, laying, and incubation periods.

1.4.5 Reproductive effort assessment

For this part of the study, we used the data from 2007, 2008 and 2009 to have enough individuals for each year. To assess breeding parameters, field staff conducting long-term monitoring of goose nesting (see methods and description in (Bêty et al., 2001)) identified 25 females marked with standard neck collars that were held in captivity during our experiment in spring. Using spotting scopes, we also scanned all zones of the main nesting colony where signals had been detected to find radio-marked birds on their nest, finding 6 of those birds. Nests of all marked females found (N = 31) were positioned with a handheld GPS and visited weekly to determine several breeding parameters: laying date of the first egg, clutch size (total number of eggs laid), and nesting success (based on whether ≥1 egg hatched or not). For more details, see Reséndiz-Infante et al., (2020). Compiling all observations of standard neck collared and radio-marked birds on Bylot during the summer (between initiation and incubation periods), 47 experimental females (2007 = 9, 2008 = 19, 2009 = 19; fed= 16, fasting = 13, control = 18) were found by field staff. These numbers included 25 standard neck collared individuals confirmed as nesting and the remaining individuals were of unknown breeding status.

1.4.6 Proxy of breeding propensity

To investigate the breeding suppression hypothesis, we used the presence at the breeding colony as a proxy of breeding propensity. In our study system, females are highly philopatric (Lecomte et al., 2008), and birds avoiding the colony almost all move directly to moulting sites, not attempting breeding (Chalifour, 2012). Conversely, a high proportion of birds going to the colony do attempt to breed there (Reed et al., 2003). Furthermore, the small proportion of non-breeding birds that can be encountered at the breeding colony leave the colony early to moulting sites (i.e., before the onset of the incubation period; Reed et al. 2003, Chalifour, 2012, Legagneux et al. unpub. data). Birds still present at the colony during the laying or incubation periods are more likely to have initiate a nest. We used two proxies of breeding propensity i) birds resighted at the colony considered as breeders and non-resighted birds considered as non-breeders and ii) by including birds as breeders only if confirmed on a nest or resighted at the colony late into the laying period or after. Individuals with unknow breeding status and only observed at the colony early in the season (i.e., before the onset of nest initiation) were removed since they could not be assigned to one category (breeders or non-breeders) with confidence.

1.4.7 Statistical analyses

A previous study using the same dataset (Legagneux et al., 2012) identified time in captivity as a primary driver of COEs in this system. Since geese were captured at various time of the day but never released at night, we used the number of hours spent in captivity (i.e., time elapsed from capture to release in hours) to account for variation in captivity duration between capture groups. Given that even short durations of captivity can have an impact on wild animals (Buttler et al., 2011), using the number of hours was more accurate than the number of days. We used 95% confidence intervals to determine significance in our results. Sample sizes for each parameter are listed in Table 1.S2. Since no individual had multiple nesting events across years, we did not consider individual identity as a random effect in our analyses.

Legagneux et al. (2012) found no effect of feeding treatment and spring body condition (i.e. mass corrected for capture date and body size, for more details, see (LeTourneux et al., 2021)) on overall reproductive success. We first validated that those same covariates did not affect breeding parameters (arrival date, laying date, clutch size, and nesting success in our study.

Breeding suppression hypothesis

We first tested for the effect of time spent in captivity (in hours) on the presence on Bylot Island (a proxy of breeding propensity, see section above) using only radio-marked birds (2006-2008) using Generalized Linear Mixed Model (GLMM). Year was considered as a random effect. We used a binomial distribution for the detection probability. Since birds detected at the colony could still be non-breeders, we conducted a subsequent analysis on a subsample of those birds located on Bylot that were either confirmed as nesting birds or detected during late laying or incubation. Finally, we conducted a complementary analysis on a larger dataset using all marked birds encountered on Bylot Island (i.e., including females for which we did not find a nest) to further explore possible annual differences in breeding propensity. We combined information from telemetry towers, systematic nest searches, and long-term monitoring protocols to establish the presence of individuals each year on Bylot Island. We then compared time spent in captivity of all marked individuals at the spring staging site with marked individuals encountered on Bylot Island. To control for unbalanced sample size, we performed a permutation test, approximating a null distribution of the statistical test by a Monte-Carlo resampling (10,000 Monte-Carlo replications).

Reproductive adjustment hypothesis

To look at the effect of time spent in captivity on arrival date, we used the relative arrival date (relative to the annual median) of the radio-marked birds only using GLMM. We used a normal distribution for arrival date. Additionally, we tested for the effect of time spent in captivity, on relative laying date (relative to the annual median), total clutch size, and nesting success using nesting data from all experimental females, including radio-marked and standard neck collars. Similarly, we used GLMMs for those analysis and year was considered as a random effect except for the relative laying date analysis. Normal distributions (without any transformation) were used for all independent variables except for nesting success for which a binomial distribution was used.

Effect of time spent in captivity on survival

We examined potential effects of the time spent in captivity on annual survival with multi-event capture-recapture models (Pradel, 2005), using E-SURGE V.2.2.3 (Choquet et al., 2009). Due to the absence of capture events after 2009 at the capture site, we used collar reobservations during the springs following the birds' initial capture and banding. These observations, reported by hunters and birdwatchers, are included in our database. We also included the mortality information reported by hunters. The model selection was made sequentially on recoveries, recaptures (here only visual reobervations) and on survival models using QAICc. The general model contained an effect of time in captivity, defined by the number of hours between capture and release, as a continuous individual covariate, an effect of the number of hours spent in captivity (using E-SURGE's age short-cut) and an effect of the year. We tested the goodness-of-fit of the model using U-CARE V2.3.5 (Choquet et al., 2009) and we corrected our models with the calculated dispersion coefficient (c-hat) of 1.672.

We further investigated potential effects of time spent in captivity on the survival of radio-marked birds by combining detection on Bylot Island with all subsequent detections during the non-breeding season, including hunter recoveries (that is, if a bird was detected alive on Bylot or if it had been subsequently encountered, dead or alive, elsewhere). To do so, we used GLMM with year as a random effect, using the binomial family.

1.5 Results

A priori analyses revealed that the food treatment did not affect any of the observed reproduction parameters (arrival date, laying date, clutch size, and nesting success; GLMM, with year as a random effect: all F < 1.00; all P > 0.18). Furthermore, body condition at capture in spring and body condition loss due to captivity did not influence any of the above-mentioned parameters (GLMM, with year as a random effect: all F < 2.78; all P > 0.11). This is similar to the results found in Legagneux et al. (2012).

1.5.1 Breeding suppression hypothesis

We first investigated the effect of time spent in captivity on detection rate of radio-marked birds. We detected: 19 of the 27 radio-marked birds on Bylot Island over the three years. The detection probability on Bylot Island was negatively affected by the time spent in captivity (β = -0.049 [-0.096; -0.001]; Fig. 1.2A). This result was similar if we restrained the analysis to the individuals detected only with the telemetry towers (β = -0.042 [-0.085; 0.001]). No difference in detection probability was found among years (β = -0.29 [-2.84; 2.26]). An *a posteriori* analysis also revealed that capture date did not affect the probability of being detected on Bylot Island (β = -0.009 [0.13; -0.14]).

Secondly, when removing radio-marked birds with unknown breeding status (8 individuals resighted during early initiation period at the colony) and considering the 5 individuals resighted after the initiation period (Fig. 1.S1) as breeders along with confirmed nesting individuals (N = 6), we found the same negative impact of captivity on breeding propensity (β = -0.05 [-0.001; -0.11]; Fig. 1.2B).

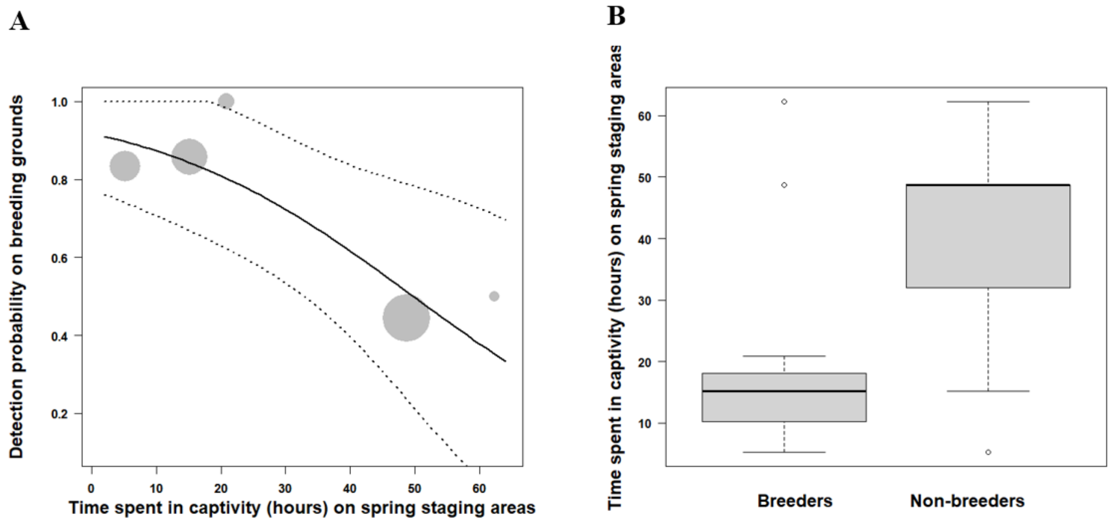

Figure 1.2. (A) Relationship between the detection probability of radio-marked snow geese on their arctic breeding ground and the time spent in captivity on their temperate spring staging areas. Grey circle sizes are mean values and proportional to N grouped by captures. Logistic regression is presented ± 95% confidence intervals (dotted line). N = 27. (B) Boxplot of time spent in captivity on temperate spring staging areas between non-breeding individuals (N = 8) that avoided the colony and individuals considered breeding, either confirmed on nest or found late during the laying period (N = 11).

Lastly, for each year, we compared the mean time spent in captivity of all experimental females captured at the spring staging site (N = 716, 649, 673 in 2007, 2008 and 2009 respectively) with the mean time spent in captivity of females that were encountered on Bylot Island during the next summer (N = 10, 19, 19, in 2007, 2008, 2009 respectively). A significant difference was detected in 2009 (permutation test: Chi^2= 13.3; P = 0.001) but not in 2007 (Chi^2 = 1.78; P = 0.43) and 2008 (Chi^2 = 0.56; P = 0.76). In 2009, mean time spent in captivity by all females was 64.3 ± 1.5 h compared to 34.0 ± 7.2 h for females encountered on Bylot Island (Fig. 1.3).

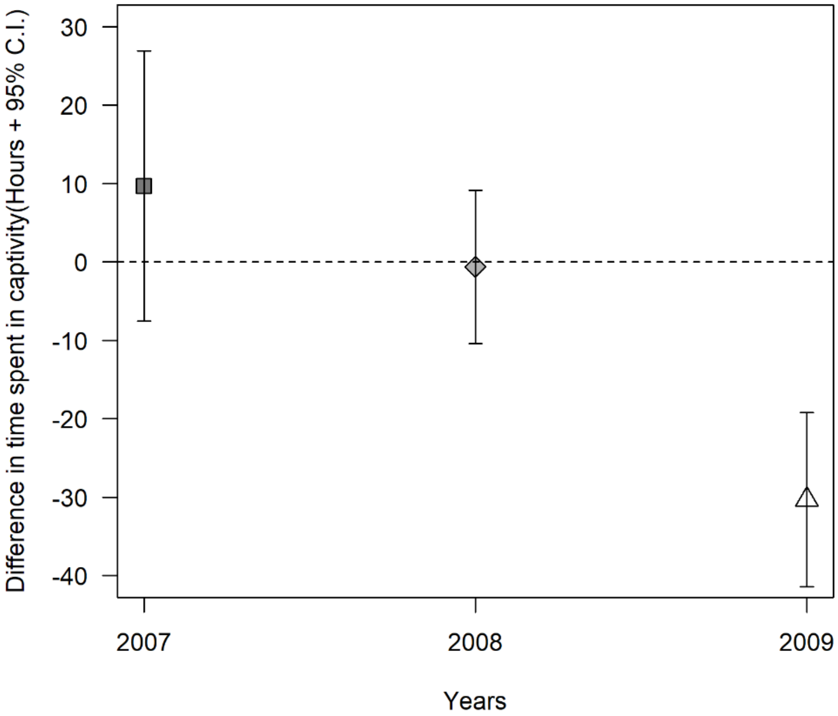

Figure 1.3: Yearly differences in the time spent in captivity (hours) by snow geese on their spring staging areas between all experimental birds captured in spring and those detected on their breeding grounds on Bylot Island. The associated 95% C.I. was obtained from permutation tests (10,000 Monte-Carlo replications) to control for unbalanced sample size within the two groups (spring vs. breeding). A negative value indicates a lower time spent in captivity for those detected on the breeding ground.

1.5.2 Reproductive adjustment hypothesis

For birds detected by radio towers (N = 17), arrival date (median: June 11; range: June 6-22) did not depend on the time spent in captivity ($\beta = -0.043$ [-0.13; 0.048]; Fig. 1.4A). Time spent in captivity did not influence laying date (N = 23, $\beta = 0.014$ [0.045; -0.016]; Fig. 1.4B). Similarly, total clutch size was not affected by time spent in captivity (N = 28, $\beta = -0.0052$ [0.0067; -0.017] Fig. 1.4C). Finally, nesting success did not vary with time spent in captivity (N=30, $\beta = -0.0050$ [0.023; -0.033]; Fig. 1.4D).

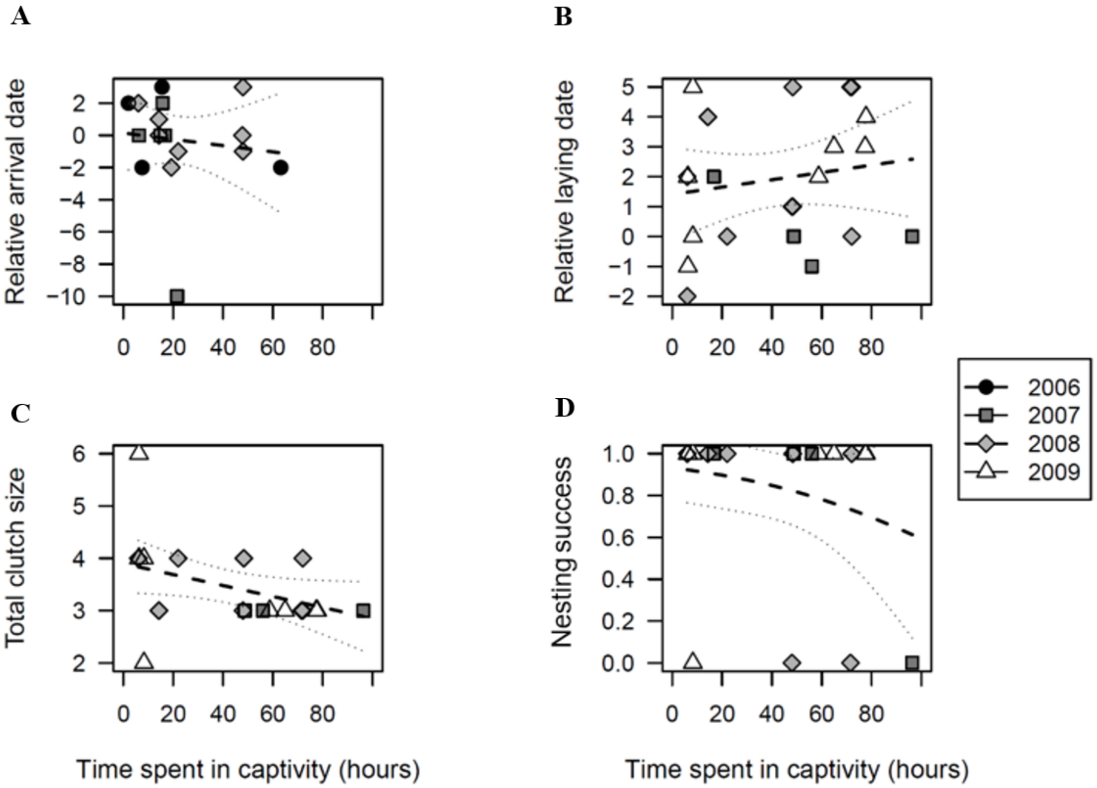

Figure 1.4. Relationship between various snow goose breeding parameters ((A) relative arrival date, (B) relative laying date, (C) total clutch size, and (D) nesting success) and time spent in captivity (hours) on their temperate spring staging areas. Arrival and laying dates are expressed in days relative to the annual median arrival or laying dates. Arrival dates were available from 2006-2008 and the other parameters were available from 2007-2009. Dashed lines indicate a non-significant relationship and dotted lines is the 95% confidence intervals.

1.5.3 Effect of time spent in captivity on survival

The most parsimonious model (M1, QAICc = 6060.29; Table 1.1) of the annual survival analysis included an effect of number of hours spent in captivity on recovery and recapture probabilities, but no effect on survival (see Table 1.S3 in Supplementary Materials for the complete model selection). A model including an effect of the number of hours spent in captivity had a ΔQAICc of 1.1 with the most parsimonious model. As the ΔQAICc between the first and the second model was <2, this indicates little difference between models with or without an effect of time spent in captivity on survival. However, the slope for the parameter HOURS was not significant (β = -0,044, [-0,14;

0,046]), which suggests little impact of this variable on survival. Finally, we found no effect of time spent in captivity on the probability of subsequently reencountering radio-marked birds when including all detections (on the breeding ground or elsewhere; N = 27, β = -0.12 [-1.86; 1.63]).

Table 1.1 Model selection testing the effects of number of years since first capture (a)[*], year (t) and hours spent in captivity (HOURS) on annual survival, recapture and recovery probabilities of snow geese marked with neckbands in 2007-2009. The notation "t" indicates an effect on the year as a factor. All models include a year effect on recaptures and an effect of time since capture on recoveries (see model selection on recoveries and recaptures; Table S3). All models also contain an intercept noted "i". K = number of parameters, ΔQAICc = difference in QAICc between the current and the top-ranked model.

Model name	Survival	Recaptures	Recoveries	K	deviance	ΔQAICc
M1	**i**	**t**	**a(2,3 to 5)**	**15**	**10154.93**	**0.00**
M2	i+HOURS	t	a(2,3 to 5)	16	10153.40	1.10
M3	i+a(1,2 to 5).HOURS	t	a(2, 3 to 5)	17	10151.64	2.07
M4	i+a(1,2 to 5)	t	a(2, 3 to 5)	17	10164.31	9.64
M5	i+a(1,2 to 5).t	t	a(2, 3 to 5)	28	10132.85	13.12
M6	i+t	t	a(2, 3 to 5)	26	10143.08	15.18
M7	i+t.HOURS	t	a(2, 3 to 5)	27	10145.50	18.66
M8	i+a(1,2 to 5).t.HOURS	t	a(2, 3 to 5)	29	10140.48	19.72
M9	i+a(1,2,3 to 5).t.HOURS	t	a(2, 3 to 5)	31	10139.44	23.17
M10	i+a.t.HOURS	t	a(2, 3 to 5)	35	10137.46	30.14

[*] a(2, 3 to 5) represents two groups : a(2) recovered individuals that were marked the previous year and a(3 to 5): recovered individuals that were marked 2 to 4 years ago. See also the table in supplementary materials for the choice of the different groups

1.6 Discussion

Our experimental manipulation during migration aimed to identify the mechanisms underlying COEs affecting reproductive success. We tested whether an unpredictable perturbation known to affect productivity at the population level (Legagneux et al. 2012) was mediated through an adjustment in reproductive investment or a suppression of breeding, two key parameters driving productivity in long-lived species. Capture, handling, and captivity during migration represent acute stress for individuals, and likely represent a strong perturbation induced on a wildlife species like snow geese. By combining radio-tracking and intensive survey on birds manipulated in their spring staging area and detected on their breeding site located 3000km away, our results provide evidence that the perturbation (measured as time spent in captivity) seems to primarily affect our proxies of breeding propensity and not breeding parameters once the birds had initiated nesting.

1.6.1 Breeding suppression hypothesis

To test the breeding suppression hypothesis, we first used the proportion of radio-marked geese detected on Bylot Island as a proxy of breeding propensity, and secondly refined this analysis on a subsample of true breeders and non-breeders. Both analyses conveyed the same result that reproduction was suppressed by the time spent in captivity. However, this was based on a small number of individuals (N = 27 and 19 respectively) that were kept in captivity for a maximum of 2.5 days. To overcome this sample size limitation, we also compared the time spent in captivity between all experimental birds (N = 2038) and the ones detected on Bylot Island (N = 47). All three approaches provided support for the breeding suppression hypothesis as birds held for a long time in captivity in spring were less likely to be encountered at the breeding colony. Birds breeding on Bylot Island being a random subsample of all captured birds, time spent in captivity between all captured birds and those detected on Bylot Island should be the same.

The difference that we found could result from the fact that birds non-detected on Bylot Island i) emigrated to other breeding sites, ii) had higher mortality rates or iii) skipped reproduction (Reed et al., 2004) and moved directly to moulting sites (Chalifour, 2012). Adult females are highly philopatric to their breeding colony (Alisauskas et al., 2012; Reed, et al., 2003, Lecomte et al. 2008), therefore we view the first possibility as very unlikely. Our results also eliminate the second option since we found no effect of time spent in captivity on the annual survival rate of all treated birds, nor on the probability of reencountering radio-marked birds anywhere after the experimental manipulation. The most likely explanation is that many individuals decided to skip reproduction in response to the spring perturbation. A previous study established that a very high proportion of marked geese returning to Bylot Island were found nesting (from 47% to 100% depending of the year; Reed et al. 2003). We must also consider that these are minimum values, because the nests of some returning birds may have not been found if they were predated early during nesting. In contrast, another study showed that marked birds not returning to the Bylot Island colony directly moved to known moulting sites, where they almost certainly did not breed (Chalifour, 2012). Therefore, although we cannot be certain that all birds that went to Bylot after the perturbation nested that year, it is likely that most of them did so, or were physiologically ready to breed. Moreover, this potential limitation is true for all individuals regardless of the time spent in captivity and is not likely to impact the comparison between control and treated groups. Indeed, both groups had similar proportions of confirmed nesting birds: 62% (17 out of 29) for the ones held in captivity and 72% (10 out of 18) for the control birds (χ^2= 0.04, p-value = 0.83). Therefore, our results confirm earlier observations studies suggesting that environmental perturbations negatively affected breeding propensity in greater snow geese (Reed et al. 2004, Souchay et al. 2014).

The analysis relying on all experimental birds (radio and collared-marked birds) suggested a strong suppression of breeding only in 2009, a year characterised with particularly unfavourable environmental conditions at the breeding grounds. Breeding conditions in the Arctic, such as timing of snow melt and predation pressure, are important drivers of greater snow goose reproductive success (Bêty et al., 2001; Dickey et al., 2008; Morrissette et al., 2010). Late snow melts are known to reduce breeding propensity in geese (Madsen et al., 2007; Prop & de Vries, 1993; Reed et al., 2004). This fits well with our results given that the date of snowmelt on Bylot Island was very late in 2009 (Table 2), as opposed to 2007 and 2008. This indicates that individuals dealing with both the COE of a stress-inducing perturbation during spring staging and unfavourable summer conditions could not mitigate the effects of these combined stressors, which led to a major breeding suppression. We thus experimentally demonstrated that environmental conditions on the breeding grounds can modulate the carry-over effects of events happening before reproduction through the decision of skipping reproduction.

Table 1.2 Spring environmental conditions affecting greater snow goose reproduction (updated from (Legagneux et al., 2012)).

Year	Snowmelt date[1] (day of the year)	Spring snow depth[2] (cm)	Spring NAO[3]
2007	171	12.65 ± 1.10	0.66
2008	164	4.41 ± 1.02	-1.73
2009	179	30.60 ± 1.58	1.68

[1] Date of 50% snow cover

[2] Mean daily snow depth from measures taken every two days at 50 stations along two 250m transects at the beginning of snow melt (between June 1st and 13th)

[3] Negative values are associated with warm temperatures and an early spring in the eastern Canadian Arctic; (Visbeck et al., 2003)

1.6.2 Reproductive adjustment hypothesis

Phenological delays can originate from multiple stressors encountered during the period preceding the breeding season (Béchet et al., 2004) and often lead to reduced breeding success (McKellar et al., 2013; Newton, 2006; Nooker et al., 2005). The time spent in captivity could have delayed individuals in their pre-migration fattening process, which can in turn delay breeding phenology or reduce clutch size (Hennin et al., 2018; Lamarre et al., 2017; Witter & Cuthill, 1993). Our experimental manipulation did not affect breeding phenology, as neither arrival nor laying dates were delayed by increased time spent in captivity. Arctic-nesting species often face unpredictable and harsh weather during migration or upon arrival on the breeding grounds (Martin & Wiebe, 2004) and are more likely to cope with unfavourable conditions than their temperate counterparts (Wingfield & Hunt, 2002). In these cases, a capital breeding strategy may be beneficial (Jönsson, 1997). Snow geese present a mixed income-capital strategy (Gauthier et al., 2003), which may allow individuals to cope better with temporal variation in food availability at different stages of their migration (Drent et al., 2006). This strategy may also depend on spring phenology: in early springs, geese will have more opportunity to feed locally after their arrival and switch to a more income dominated strategy (Hupp et al., 2018; Lameris et al., 2018), which could potentially increase their breeding propensity. It is thus possible that manipulated geese that bred on Bylot Island were able to partly overcome, or compensate for, the effect of captivity, especially in years with favourable breeding conditions (e.g., early snow-melt). Our results show no effect of time spent in captivity during the spring on any of the breeding parameters measured in the breeding grounds for birds that attempted to breed. Therefore, the reduction in the number of offspring observed in the fall following the perturbation encountered in spring (Legagneux et al., 2012) was apparently not due to a reduction in reproductive investment (see pathway on Fig.1.1).

1.6.3 Potential mechanisms mediating reproductive decisions

Long-lived species can skip a reproductive event when the required investment is too high and thus avoid a prohibitive reproductive cost in terms of reduced subsequent survival or future reproduction (Cubaynes et al., 2011; Jean-Gagnon et al., 2018; Öst et al., 2018). Unsurprisingly, the decision to skip reproduction is more common under unfavourable environmental conditions, for instance when nutrient acquisition is more strenuous or when access to nesting sites is compromised (Warren et al., 2014). For species relying on nutrient accumulation for breeding (i.e. capital breeders), environmental conditions prior to reproduction can also affect reproductive investment (Harrison et al., 2011; Inger et al., 2008). Therefore, it can be expected that individuals of long-lived species will skip a breeding event when experiencing stressors jeopardizing body condition gain before reproduction (Legagneux et al., 2016).

Although our experimental design allows us to separate which response most likely explains the fitness cost of a perturbation mediated through a COE, investigating the mechanisms involved in the decision to skip reproduction was beyond the scope of our study. Two non-exclusive mechanisms could be involved here. First, manipulated birds experienced hormonal stress, which has the potential to downregulate reproductive hormones (Wingfield & Sapolsky, 2003). Exposition to a perturbation will activate the hypothalamic–pituitary–adrenal (HPA) axis, which will then heighten the level of glucocorticoid hormones (Romero, 2004; Sapolsky, 2000). These hormones promote an “emergency life-history stage” characterised by behaviours favouring survival, while suppressing other nonessential activities, such as reproduction (Wingfield & Sapolsky, 2003; Wingfield et al., 1998). Reproductive inhibition in response to stress could depend on the value of the current reproductive investment, and would be more likely in long-lived species where breeding events are more numerous throughout an individual lifetime compared to short-lived species (Bókony et al., 2009).

Secondly, we know that captivity-induced weight loss occurs, even when fed *ad libitum* (Legagneux et al., 2012) (fed birds lost on average 14.4g during captivity, while fasting birds averaged a loss of 147.7g), which may lead to deteriorating body condition and potentially compromising the minimal condition threshold for breeding (Gorman et al., 2008; Legagneux et al., 2016; Rowe et al., 1994). Spring body condition in our focal species is known to partly and directly affect reproductive investment (Bêty et al., 2003, 2004; Reed et al., 2004). Since we did not find any effect on reproduction of the feeding regime imposed to birds during captivity (Legagneux et al., 2012) and that none of the tested breeding parameters was affected by our manipulation, the effect through body condition could only result from a strong impact on the minimal condition threshold (Jean-Gagnon et al., 2018; Rowe et al., 1994). Since our experiment occurred on average 10 days prior to mass departure, we can anticipate that several manipulated individuals could still have time to reach their optimal condition prior to departure (LeTourneux et al. 2021).

1.6.4 Conclusion

Our study is the first to experimentally demonstrate that events occurring prior to reproduction could alter the decision to breed based on detections on the breeding site, a proxy for breeding propensity in this study. We show that a perturbation during migration most likely reduced the breeding propensity of a long-lived species and that the COEs induced by the perturbation are stronger when coupled with unfavourable conditions at the breeding site. Even though breeding propensity is important for overall reproductive success and population growth (Sedinger et al., 2008), it is still one of the least understood breeding parameters (Souchayet al. 2014) due to logistical constraints (Etterson et al., 2011). Increasingly small and efficient tracking devices, which allow to track individuals in real time throughout their life cycle with minimal effects on individuals, should open new ways for future studies with the aim of measuring breeding propensity and studying the mechanisms that drive this reproductive decision. In conclusion, our findings emphasize how conditions experienced during migration can have severe consequences on reproductive output of long-distance migrants (Lameris et al. 2018) and how environmental conditions can modulate the magnitude of COEs (Legagneux et al. 2012; Briedis et al., 2018).

1.7 Acknowledgment

We are grateful to all the fieldworkers especially Gérald Picard, Johanne Dussureault, Marie-Claude Martin, and Eliane Valiquette. We thank M.-C. Cadieux for managing the database. We acknowledge funding from the Sentinelle North Research Chair from the Canada First Research Excellence Fund; the Fonds de Recherche du Québec - Nature et Technologies (FRQNT) [2020-NC-271544]; the Natural Sciences and Engineering Research Council of Canada (NSERC); and ArcticNet from the Networks of Centres of Excellence of Canada. This experiment was approved by the Committee of Animal Protection of the Université du Québec à Rimouski (Authorization number: CPA-42-10-78).

1.8 Supplementary material

Table 1.S1: List of treatments assigned to each capture group. Captivity indicates if the group was released after banding (No) or if it was kept in captivity (Yes), either fed or fasting.

Capture group	Year	Treatment	Captivity	Time spent in captivity (h)
2007C1	2007	Control	No	14.8
2007C2	2007	Fed	Yes	48.7
2007C3	2007	Control	No	48.0
2007C4	2007	Control	No	15.7
2007C5	2007	Fasting	Yes	48.6
2007C6	2007	Fasting	Yes	6.2
2007C7	2007	Control	No	49.3
2007C8	2007	Fasting	Yes	96.3
2007C9	2007	Control	No	21.5
2007C10	2007	Fed	Yes	115.3
2007C11	2007	Fed	Yes	90.1
2007C12	2007	Fasting	Yes	61.4
2007C13	2007	Fasting	Yes	73.5

2007C14	2007	Fed	Yes	45.4
2007C15	2007	Control	No	16.7
2007C16	2007	Fed	Yes	89.7
2007C17	2007	Fed	Yes	90.0
2007C18	2007	Fasting	Yes	52.2
2007C19	2007	Fed	Yes	56.0
2008C1	2008	Control	No	19.2
2008C2	2008	Fed	Yes	48.0
2008C3	2008	Fasting	Yes	48.0
2008C4	2008	Fasting	Yes	95.5
2008C5	2008	Fed	Yes	95.7
2008C6	2008	Fed	Yes	72.3
2008C7	2008	Control	No	22.0
2008C8	2008	Fasting	Yes	48.9
2008C9	2008	Fasting	Yes	72.0
2008C10	2008	Fed	Yes	48.3
2008C11	2008	Control	No	3.50
2008C12	2008	Fasting	Yes	47.7
2008C13	2008	Fed	Yes	71.5
2008C14	2008	Control	No	14.2
2008C15	2008	Fed	Yes	95.5
2008C16	2008	Fed	Yes	71.8
2008C17	2008	Fasting	Yes	48.0
2008C18	2008	Fed	Yes	47.5
2008C19	2008	Control	No	6.00
2008C20	2008	Control	No	6.00
2009C1	2009	Control	No	16.5
2009C2	2009	Fed	Yes	67.7
2009C3	2009	Fasting	Yes	58.7

2009C4	2009	Fasting	Yes	111.5
2009C5	2009	Fed	Yes	100.0
2009C6	2009	Fed	Yes	89.5
2009C7	2009	Control	No	4.6
2009C8	2009	Fasting	Yes	87.5
2009C9	2009	Fed	Yes	61.8
2009C10	2009	Fasting	Yes	64.0
2009C11	2009	Fed	Yes	77.7
2009C12	2009	Fed	Yes	110.9
2009C13	2009	Fed	Yes	64.9
2009C14	2009	Fasting	Yes	111.7
2009C15	2009	Fed	Yes	123.7
2009C16	2009	Control	No	13.3
2009C17	2009	Control	Yes	77.4
2009C18	2009	Control	No	6.2
2009C19	2009	Control	No	14.0
2009C20	2009	Control	No	8.2
2009C21	2009	Control	No	10.2
2009C22	2009	Control	No	9.6

Table 1.S2: Sample sizes used for the analyses of the phenological and reproduction parameters. The sample used for such analyses is also provided (radio = birds with a VHF radio collar; standard = birds with alphanumeric coded collar).

Parameter	Sample size	Type of sample
Detection rate at the breeding site	27	Radio
Detection rate at the breeding site + elsewhere	27	Radio
Detection during late laying period	19	Radio
Arrival date at the breeding site	19	Radio
Laying date	23	Standard & Radio

Clutch size	28	Standard & Radio
Nesting success	30	Standard & Radio
Time spent in captivity for all females	2038	Standard & radio
Time spent in captivity of females observed on Bylot	47	Standard & radio
Survival analysis	1970	Standard

Table 1.S3: Detailed model selection for survival testing the effects of the number of years since capture (a), year (t) and hours in captivity (HOURS) on annual survival, recovery and recapture probabilities of snow geese marked with neckbands in 2007-2009. a(2, 3 to 5) thus represents two groups: individuals captured the year before – group a(2) – and individuals captured 2 to 4 years prior – group a(3 to 5). The notation "t" indicates an effect on the year as a factor. The notation "a" represents all classes of time since capture separately: equivalent of a(2,3,4,5,6). All models include a time effect on recaptures and an effect of time since capture on recoveries (see model selection on recoveries and recaptures; Table S1). All models also contain an intercept noted "i". In bold: the selected models at each step (first model selection: recoveries, second model selection: recaptures, third model selection: survival). K = number of parameters, ΔQAICc = difference in QAICc between the current and the top-ranked model.

Model name	Survival	Recaptures	Recoveries	K	deviance	ΔQAICc
M1	**i**	**t**	**a(2,3 to 5)**	**15**	**10154.93**	0.00
M2	i+HOURS	t	a(2,3 to 5)	16	10153.40	1.10
M3	i+a(1,2 to 5). HOURS	t	a(2, 3 to 5)	17	10151.64	2.07
M4	i+a(1,2 to 5)	t	a(2, 3 to 5)	17	10164.31	9.64
M5	i+a(1,2 to 5).t	t	a(2, 3 to 5)	28	10132.85	13.12
M6	i+t	t	a(2, 3 to 5)	26	10143.08	15.18
M7	i+t.HOURS	t	a(2, 3 to 5)	27	10145.50	18.66
M8	i+a(1,2 to 5).t. HOURS	t	a(2, 3 to 5)	29	10140.48	19.72
M9	i+a(1,2,3 to 5).t. HOURS	t	a(2, 3 to 5)	31	10139.44	23.17
M10	**i+a.t. HOURS**	**t**	a(2, 3 to 5)	**35**	**10137.46**	30.14

M11	i+a.t. HOURS	a(2, 3 to 5).t	a(2, 3 to 5)	37	10135.23	32.89
M12	i+a.t. HOURS	a.t	a(2, 3 to 5)	43	10131.56	42.98
M13	i+a.t. HOURS	a(2, 3 to 5)	a(2, 3 to 5)	26	10218.31	60.17
M14	i+a.t. HOURS	HOURS	a(2, 3 to 5)	24	10874.16	448.37
M15	i+a.t. HOURS	a(2, 3 to 5).HOURS	a(2, 3 to 5)	25	10874.11	450.37
M16	i+a.t. HOURS	a(2, 3 to 5).t. HOURS	a(2, 3 to 5)	39	10840.27	458.66
M17	i+a.t. HOURS	t.HOURS	a(2, 3 to 5)	35	10856.40	460.13
M18	i+a.t. HOURS	a(2, 3 to 5).t. HOURS	a(2, 3 to 5)	37	10849.57	460.13
M19	i+a.t. HOURS	a.t.HOURS	a(2, 3 to 5).t	55	10791.54	462.40
M20	**i+a.t. HOURS**	**a.t.HOURS**	**a(2, 3 to 5)**	**43**	**10833.63**	462.88
M21	i+a.t. HOURS	a.t.HOURS	T	53	10847.68	491.85
M22	i+a.t. HOURS	a.t.HOURS	a(2,3,4 to 5).t. HOURS	56	11108.07	653.78
M23	i+a.t. HOURS	a.t.HOURS	a(2,3 to 5).t. HOURS	54	11116.57	654.73
M24	i+a.t. HOURS	a.t.HOURS	a.t.HOURS	60	11100.95	657.80
M25	i+a.t. HOURS	a.t.HOURS	t.HOURS	52	11144.19	667.05

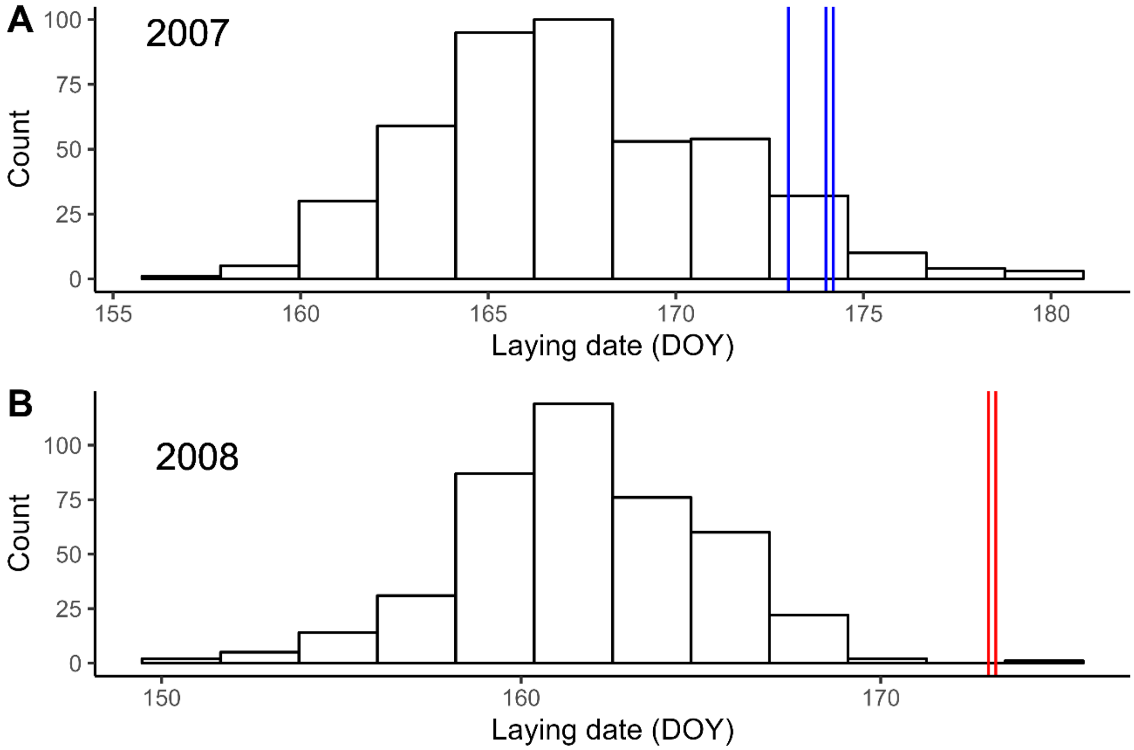

Figure 1.S1: Frequency distribution of snow goose laying date on Bylot Island in A) 2007 and B) 2008. Blue and red lines represent, for 2007 and 2008 respectively, the dates at which radio-marked individuals used in our detection analysis were detected by the telemetry tower (same-day detection of two individuals are jittered). These dates are all in the last percentile of laying dates for the population on their given year.

Chapitre 2 Adjusting migration and breeding phenology under climate change : can Greater snow geese “wind the clock” ?

2.1 Résumé

Les changements climatiques, hétérogènes à travers le globe, réduisent la fiabilité de certains indicateurs qu’utilisent les oiseaux migrateurs pour ajuster leur migration et maximiser leur reproduction. Si les liens entre les décisions de migration et de reproduction sont bien établis pour certaines espèces, il reste à démontrer si les changements climatiques peuvent modifier ces relations et entrainer un retard ou décalage phénologique par rapport aux conditions environnementales optimales pour se reproduire. Chez une espèce migratrice de longue-distance, l’oie des neiges (*Anser caerulescens atlanticus*), nous avons comparé les dates de départ des haltes migratoires, les durées de migrations, les dates d’arrivée aux sites de nidification, les durées de période préponte et les dates de ponte au cours des 24 dernières années (1997-2021). De plus, nous avons quantifié le rôle de la température locale, des vents rencontrés en migration et de la date de la fonte de neige sur le site de reproduction sur les paramètres phénologiques étudiés. Sur trois périodes (1997-1999 (n=75), 2007-2008 (n=27), 2019-2021 (n=31)), nous avons suivi des femelles munies de colliers émetteurs depuis leur départ des haltes migratoires au Québec jusqu’à leur site de reproduction dans le haut Arctique sur l’Île Bylot. Malgré la légère tendance à la hausse de la température sur le site de reproduction au cours de la période d’étude, les paramètres environnementaux sont restés relativement stables. Les relations entre phénologie de migration et de reproduction sont restées inchangées depuis la fin des années 1990 avec une influence marquée de la date d’arrivée au site de reproduction et de la date de fonte de la neige sur la date de ponte. En revanche, nous observons une forte corrélation négative entre la date d’arrivée des oies et les conditions de vent en migration. Ce facteur environnemental, jusqu’ici négligé, explique à lui seul une grande partie des décisions de reproduction chez une espèce migratrice de longue distance. Cette étude révèle un mécanisme potentiel de modulation de l’effet du réchauffement climatique sur la migration des oiseaux.

2.2 Abstract

Climate change is highly heterogenous across the globe and reduces the reliability of environmental cues used by migratory birds to time their migration and maximize their reproduction. If the links between migration and reproduction decisions are well-known for some species, it remains to show if climate change could modify or alter such relationships leading to a phenological delay or a mismatch regarding optimal environmental conditions. In a long-distance migrant, the greater snow goose, (*Anser caerulescens atlanticus*), we compared departure dates from the staging grounds, migration duration, arrival date on the breeding grounds, prelaying period duration, and laying dates over the last 24 year (1997-2021). Furthermore, we quantified the role of local temperature, wind encountered during migration and date of snowmelt on the breeding grounds on these phenological parameters. Over three periods (1997-1999 (n=75), 2007-2008 (n=27), 2019-2021 (n=31)), we followed females equipped with tracking devices from their departure from the staging grounds in Québec to their nesting site in the high Arctic on Bylot Island. Although temperature on the breeding site presented a slight warming trend over the period considered, environmental parameters remained relatively stable. Relationships between migration and reproduction phenology remained unchanged since the end of 1990 with a prominent role of arrival date and snowmelt on laying date. However, we found a strong negative correlation between arrival date and wind conditions experienced during migration. This often-overlooked environmental parameter explains a large amount of reproduction phenology in a long-distant migrant. This study reveals a potential mechanism modulating the effects of climate warming on bird migration.

2.3 Introduction

Many life history traits such as growth, maintenance, and reproduction tightly depend on time, a variable that is now considered as a key ecological resource for multiple organisms (Post 2019). Phenology, the seasonal synchrony of the different events in organisms' life cycle (Knudsen et al. 2011), has a great impact on organisms, especially on the time available to allocate energy on highly demanding life stages (Visser & Both 2005). Dictated by a large number of cues such as photoperiod, temperature, water or habitat availability (Tauber et al. 1998, Dawson et al. 2001, Post 2017), phenology often depends on local environmental conditions (Schwarz 2003). These include temperature, wind direction, and extreme events such as droughts or storms, which are exacerbated by climate change (Kumar et al. 2013, Bailey et al. 2022). For instance, global warming is responsible for advancing the onset of spring, such as the flowering of trees (Menzel 2000), the migration/emergence of arthropods (Roy and Sparks 2000, Høye and Forchhammer 2008, Leingärtner et al. 2014), or the onset of reproduction in birds (Crick et al. 1997, Both et al. 2005, Shipley et al. 2020).

For species breeding in seasonal environments, offspring production should be timed with the most favorable environmental conditions (Klinkhamer et al. 1997, Post et al. 2001, Visser and Both 2005). In birds, offspring value usually declines over the season (Drent and Daan 1980, Harriman et al. 2017) with early-breeding birds laying on average more eggs and producing offspring presenting better quality and higher survival rates than late breeding's ones (Winkler et al. 2014, Dubiec & Cichoñ 2001, Öberg et al. 2014). Optimal timing of reproduction often follows peak abundance of food (Martin 1987). Incidentally, climate change-induced phenological advancement of resources pressures bird species to adjust reproduction accordingly. While lower trophic levels' phenology is directly related to temperature variation, higher trophic levels (either primary consumers or predators) need to cope with such changes by shifting their own phenology at the same rate to avoid mismatch (Visser and Both 2005, Thackeray et al. 2010) that could lead to phenological cascades at the community level (Post 2017). Phenological asynchrony between spring green-up and arrival is increasing in many migratory bird species (Mayor et al. 2017).

In order to avoid phenological asynchrony, migratory birds should time their migration with breeding grounds' environmental change (Knudsen et al. 2011). Arrival date on the breeding ground is a key parameter with important consequences on breeding phenology and success (Bêty et al. 2003, Smith and Moore 2005, Descamps et al. 2011, Hennin et al. 2015). Some species can adjust both timing and duration of migration with environmental cues such as photoperiod, daily temperature increase, favorable winds, etc. but others present less flexibility (Gwinner 1996). Since climate change affects the environment heterogeneously across the globe, phenology cues for the onset of spring can vary between regions and species (Kumar et al. 2013, Bailey et al. 2022). If the synchronicity of environmental conditions between staging and breeding grounds is altered, then species with a more rigid regulation of migration could be more affected. It is namely the case for some long-distance migrants, which have been shown to display weaker migration phenology adjustments (Both and Visser 2001, Jonzén et al. 2007, Rubolini et al. 2007).

Many migratory species are already displaying a phenological response to recent environmental changes (Parmesan 2006, Knudsen et al. 2011, Shipley et al. 2020). Some species' change in phenology could be the result of increasingly better conditions encountered during migration (Sinelschikova et al. 2007). Arctic-breeding migrants, mainly composed of long-distance species, have seen their breeding grounds undergo stronger temperature increases than anywhere else on the planet (Walsh et al. 2011). The region’s narrow window of favorable conditions for breeding pressures organisms to adjust rapidly to temperature variation (Walker et al. 2006). This, combined with the current warming trends, has led to important environmental changes in the Arctic (snowmelt: Cleland et al. 2007, Gauthier et al. in prep.; plant growth and primary production: Gauthier et al. 2013, Oberbauer et al. 2013, arthropod emergence: Høye et al. 2007). Arctic-breeding birds therefore face increasing pressure to match their migration and reproduction with changing environmental conditions (Saalfeld et al. 2019).

Different warming rates between staging and breeding grounds is potentially one of the most challenging features of climate change that long-distance migrants have to cope with (Ahola et al. 2004, Both et al. 2005). Understanding the mechanisms that drive population level response to climate change also requires knowledge of individuals’ decisions and their associated fitness (Stillman and Goss-Custard 2010). This requires tracking individuals from staging areas to their breeding ground and comparing their reproductive decisions over the last decades. Here, we investigate potential shifts in migration phenology and its individual-level impact on reproductive decisions in a long-distance migrant species, the greater snow goose (*Anser caerulescens atlanticus*), monitored over the past 26 years. Particularly, we revisited the relationships between migration and reproduction phenology obtained by Bêty et al. (2003) with new tracking data collected since 1999. Our study system is ideal to investigate such questions since i) birds can be captured on their spring staging area, equipped with radio-collars and retrieved on their main breeding colony (Bêty et al. 2003; Grandmont et al. chapter 1), ii) snow geese accumulate endogenous reserves acquired on staging areas that are partly invested for egg production (Gauthier et al. 2003), and iii) this species exhibits a strong seasonal decline in clutch size (Lepage et al. 2000). Furthermore, in snow geese, the onset of reproduction is strongly related with snowmelt (Bêty et al. 2003), the species being able to advance their reproduction during years of early plant growth, although such response is moderate (Gauthier et al. 2013, Doiron et al. 2015, Reséndiz-Infante et al. 2020).

In this study, we gathered a 10-year dataset of radio-tracking data on 145 individuals distributed in three periods (1997-1999, 2006-2008, 2019-2022). We first investigated potential changes, over the last 26 years, in departure date, migration duration, arrival date, pre-laying duration, laying date and in the relationships between those variables. Since environmental conditions are known to modulate reproductive decisions (Legagneux et al. 2012, Grandmont et al. chapter 1), we then investigated temperature, snow cover, and wind regime trends over the study and their role as potential modulators of phenology and reproductive decisions. We expected snow geese's departure from the staging site and arrival on the breeding grounds to remain relatively stable over time because of a strong endogenous control of migration decisions and the expected slower warming rate in temperate areas (Bauer et al. 2008a, Eichhorn et al. 2009). Given the generally stronger warming rate in the Arctic (Previdi et al. 2021) and the seasonal decline in egg value, we expected laying dates to be earlier now than over the past 2-3 decades. We therefore expected the prelaying period to be shortened, if lay dates are advanced but arrival dates stay the same. Regarding environmental factors trends, we expected little change in staging ground temperature and wind regime, but increasing breeding ground temperature and advanced snowmelt date. Lastly, following literature on arctic-nesting geese, we expected warmer staging grounds temperatures to advance departure dates (Bauer et al. 2008b), favorable wind conditions to shorten migration duration and advance arrival dates (Geisler et al. 2022), and, mainly, we expected laying dates to be tightly linked to breeding ground temperature and snowmelt date (Madsen et al. 2007).

2.4 Methods

2.4.1 Study species and study site

Greater snow geese are herbivorous, long-distance migrants breeding in the High Arctic. The largest greater snow goose colony is located on Bylot Island, Nunavut, Canada (78º08’N 80º00’ W), which hosts 15-20% of the breeding population (Reed et al. 2002). Greater snow geese winter along the Atlantic coast of the United States and use Canada’s St. Lawrence Valley, in the province of Quebec, as a staging site for both their spring and fall migrations. During spring staging, which lasts six to eight weeks from late March to late May, they feed in croplands and wetlands to accumulate endogenous reserves (Gauthier et al. 1992). Depending on the study-period (see below), geese were captured either on Bylot Island or on Île-aux-Oies, (47º00’N 70º33’ W), an important feeding and resting area located in the middle of the St. Lawrence River, 60 km northeast of Québec City.

2.4.2 Capture, measurement, and marking

For the 1997-1999 period, geese were captured on Bylot Island in August 1996 and 1997, during geese’s flight feather molting period (see Blouin et al. (1999) for details). Only family groups were captured, and thus all marked adult females were at least 2 years old or more (Reed et al. 2003b). A subsample of captured females was then equipped with tracking-devices.

During 2007-2009 and 2019-2022, we captured spring staging geese using baited cannon nets from late April to mid-May. Shortly after capture, adults were sexed based on cloacal examination, females were weighed to the nearest gram with an electronic scale, and culmen, head and tarsus were measured to the nearest 0.1 mm. Females were individually marked with USGS metal bands and alphanumeric yellow neck collars. Each capture group was released together immediately after handling if it ended during the day, and the following morning if it ended at night to avoid disorienting the birds. Given that female greater snow geese are highly philopatric (Bêty et al. 2004), we put the tracking-device on females previously banded on Bylot Island to increase the likelihood of detecting and resighting tracking-collar equipped females on Bylot Island.

2.4.3 Radio and GPS tracking

For this study, two different tracking devices were used: VHF collars (same design used for all year; weight 60±7 g, 2.5±0.4% of bird body mass; mean ± SD; see Demers et al. (2003) for details) in 1997-1999, 2006-2008 and 2019 and GPS-GSM collars (OrniTrack-N44 - neck collar solar-powered trackers, weighing 45 g (approximately 1.5% body mass)) in 2019-2022. GPS locations were taken every 5 minutes below the 50th parallel (staging grounds) and every 15 minutes above the 50th (northward migration and breeding grounds). Locations were sent through cellular network and birds' movement over the summer was thus collected upon individuals' return within cellular coverage areas in the fall.

In 1997-1998, on a daily basis from the end of March to the departure of the last radio-marked birds at the end of May, five to six crews tracked birds on the staging area using vehicle- mounted receiving systems. Aerial tracking by plane was also conducted every week (see Bêty et al. 2003 for details). The same effort was not conducted during the second and third periods, preventing having departure dates for radio-tracked individuals in 2006-2008 and 2019. However, departure dates were obtained in 2019-2022 from individuals equipped with GPS-tracking-devices. Each year of the study period (except for 2020 and 2021 because of COVID-19 lockdown), we erected two automated telemetry towers on Bylot Island on high ground levels before the arrival of geese. Each system located 30 km apart, included two pole-mounted antennas and was set to automatically scan and record the presence of radio-marked geese arriving on Bylot Island.

For VHF collars, we defined departure date as the last date that a radio was detected on the staging area and arrival date as the first date that it was detected on the breeding grounds. To balance GPS collars' increased precision with VHF technology, we defined departure date as the day the geese left the St. Lawrence estuary and arrival date as the date GPS tracking fell within a 20 km radius of the VHF telemetry towers. Migration duration was defined as the difference between arrival and departure dates.

2.4.4 Reproductive effort assessment

For breeding parameters assessment, for every year except 2020 and 2021, field staff conducting long-term monitoring of goose nesting (see methods and description in Bêty et al. 2001) identified tracking-device-equipped females. Using spotting scopes, additional field staff scanned all zones of the main nesting colony where signals had been detected to find radio-marked birds on their nest. Nests of all tracking-device-equipped birds were positioned with a handheld GPS and visited weekly to determine nesting phenology and success. For more details, see Reséndiz-Infante et al., (2020). Prelaying duration was defined as the difference between laying date (date of the first egg laid) and arrival date.

In 2020-2021, no field work occurred during the nesting period of the geese on Bylot Island. We therefore used GPS tracking to determine laying dates. Nesting attempts and laying dates were determined by analyzing the movements of GPS-marked birds once they had reached the Arctic. Geese usually wander around when feeding during the prelaying period. When the goose movements started to be clustered (within a radius of ~75 m) around one location (presumed to be the nest location), it can provide a reliable proxy of the laying date (Schreven et al. 2021).

2.4.5 Wind favorability index

Wind data was collected from the NCEP Reanalysis I database (Kalnay et al. 1996) using R package RNCEP (Kemp et al. 2012). This dataset contained u and v wind components (where the u wind component is the windspeed along an East/West axis, and the v wind component is the windspeed along a North/South axis, both expressed in m/s) every 6 hours (4-times daily) with a resolution of 2.5° (~200km^2). We extracted wind data, at the 850 mb pressure level (approximately between altitudes of 1000 and 1500 m), between -82° and -65° in longitude and divided the wind map into two sections because of different wind circulations over and below the Hudson strait (Smith & Schwing 1991). The Northern tip of Nunavik (62° N) delineated the two sections with a southern section from the St. Lawrence valley to Nunavik (between 45 to 62° N) and a northern section from Nunavik to the northern end of Bylot Island (between 62° and 73°N).

We calculated the Wind Assistance, an index of wind favorability related to the direction of the migration. While some studies performing similar analyses use the number of days when winds are within a favorable angle for bird's migration (Haest et al. 2020), we used an index that encompasses both wind speed and direction. This component has been used in previous studies investigating the effect of wind on bird migration (Kemp et al. 2010, Gutierrez Illan et al. 2017, Bradarić et al. 2020). The component was determined using the following formula: $V_w*\cos(\beta)$, where V_w is wind speed and β is the difference between orientation of migration (in our case, 340 degrees) and wind directions.

We then assigned to each bird's migration the WA encountered (Bradarić et al. 2020). For all birds, including the ones only tracked on their arrival on the breeding grounds, we subtracted to the arrival date the mean migration duration obtained from all birds tracked from their staging areas (22 days ± 0.67). WAs values were taken from the southern section (i.e. below the Hudson Strait) for the first 11 days and from the northern section for the last 11 days. Daily WAs were then averaged, providing an estimate of the wind conditions that individuals encountered during migration. For birds with known departure and arrival dates, we split the migration in two equal time periods and assigned WAs values from the specific sections similarly as described above. We compared both indices to see if they were correlated. To validate our WA indices, we conducted a validation study using GPS-equipped birds for which a full migration track was available. From the GPS track, we first subsampled the GPS tracks to have one point every 15 minutes. Then, for every 6 hours of the GPS-equipped birds' migration (which corresponds to the time interval of our wind data), we associated the WA value closest to the GPS location of the bird. All WAs associated with a GPS point between the individuals' arrival and departure were averaged. For each GPS-equipped bird, we compared the WA obtained from GPS tracks with the WA obtained from fixed (22 days) or true migration durations.

Finally, we extracted wind data from mid-May to mid-June for every year between 1997 and 2022 and calculated daily WAs. For each section of the map, WAs were averaged by year to compare wind conditions over time.

2.4.6 Other environmental data

The snow cover index used was the date at which snow cover reached 50% of the Quarlikturvik Valley, on Bylot Island. We extracted MODIS (Moderate Resolution Imaging Spectroradiometer) data from 2000 to 2022. As MODIS data wasn't available before 2000, we used the same measure estimated during field monitoring at the research station for 1997-1999. Date of 50% snow cover estimates from the two different methods are highly correlated between 2000 and 2021 (see Cadieux et al. (2020) for more details).

Daily temperatures were obtained in April and May from two different weather stations (Quebec/Jean Lesage Intl and Ste-Anne-de-Bellevue 1) located along the St. Lawrence Valley in Quebec and in June from the weather station of Pond Inlet (located 80 km from Bylot Island's goose colony) for every year between 1997 and 2022. Data was extracted from Canada's government meteorological website: https://climat.meteo.gc.ca/historical_data/search_historic_data_f.html.

2.4.7 Statistical analysis

Before performing the analyses, we examined the data for any outliers or data points with a strong potential lever effect. One individual completed its migration within two days in 2020 which represents the fastest migration record for this species. This individual had a strong leverage effect in the analyses. We thus conducted the analyses by removing this individual from the analyses. Since the inclusion or the exclusion of this particular individual did not change the outcome of any of the results (analyses not shown), we decided to keep it in all our analyses.

We performed general linear mixed models (GLMM) with year as a random factor to test for the effect of the period (or blocks) on the different phenological parameters (departure date, migration duration, arrival date, prelaying duration, and laying date). We performed linear models to detect any trend in mean temperatures, snowmelt date, and WA over time. We also tested for relationships among the different phenological parameters and environmental variables (Wind Assistance, staging grounds temperatures, breeding grounds temperatures, day of 50% snowmelt) using GLMMs with year taken as a random factor. For each phenological variable, we only investigated proximal environmental drivers,, that is, the environmental information that could directly impact phenological decisions (e.g. we did not test the relationship between breeding ground temperatures and departure dates). We performed *a posteriori* analyses on one of the phenological parameters, arrival date, to investigate potential interactions between environmental parameters. We did so by comparing models with and without an interaction between the environmental parameters with Akaike Information

Criterion. All covariates were scaled prior analyses. Sample size for each variable is represented in Table 2.S1.

2.5 Results

2.5.1 Testing phenological changes over time

Departure dates were similar between the first and last period (β = 3.30 [8.01; -1.41]; Fig. 2.1A) with a median departure date on May 17 for both periods. Migration duration also remained similar between the first and last period (β = -7.84 [2.02; -17.71]; Fig. 2.1B) with a mean of 22 days. Compared to the first period, arrival dates did not vary in second period (β = 3.06 [9.87; -3.75]; Fig. 2.1C) nor in the last periods (β = -3.96 [2.32; -10.23]; Fig. 2.1C) . Pre-laying duration did not significantly change among the three periods (β = -0.35 [3.31; -4.01] between the first and second periods and β = 2.38 [4.99; -0.24] between the first and third periods; Fig. 2.1D). Similarly, laying dates remained stable among all three periods (β = 1.72 [8.46; -5.03]; Fig 2.1E) with a median laying date on June 12th. Note that in three years of low reproductive success (1999, 2007, 2022), no radio-tracked females were found nesting.

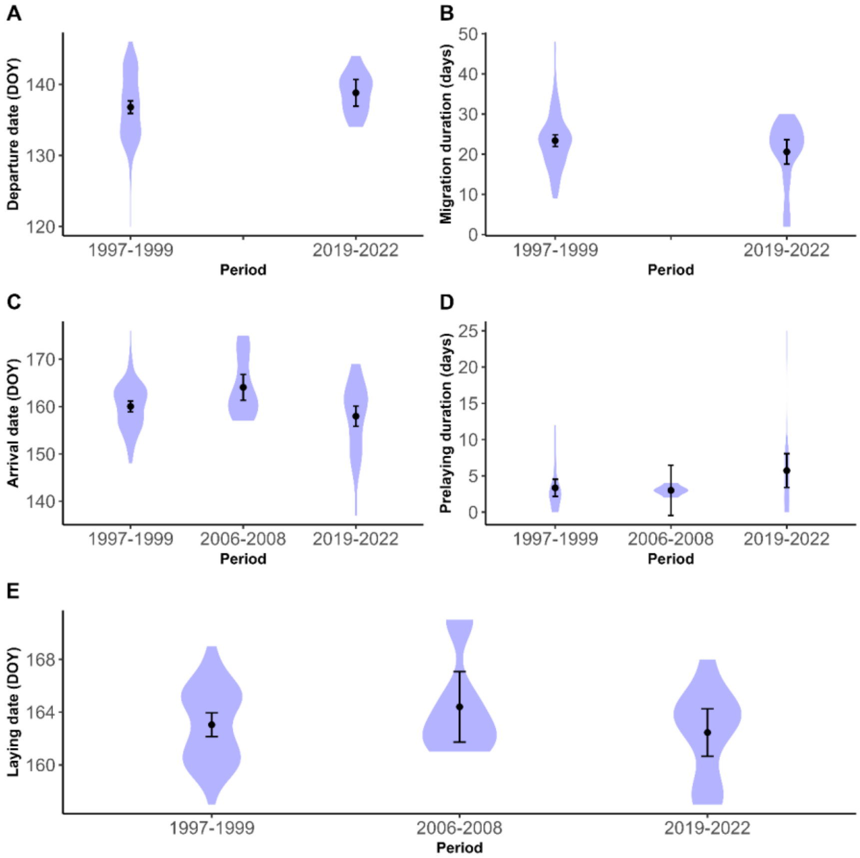

Figure 2.1. Tracked female greater snow goose's migration and reproduction phenology parameters over the three periods of the study (1997-1999, 2006-2008, 2019-2022): (A) departure date from the spring staging area, (B) migration duration (arrival - departure dates), (C) arrival date on the breeding grounds, (D) prelaying duration (lay date - arrival dates), and (E) laying date. Error bars show 95% confidence intervals.

2.5.2 Testing relationships among phenological parameters

Migration duration was significantly related to departure date (β = -0.73 [-0.44; -1.01]). However, arrival date was not significantly related with departure date (weak positive trend: β = 0.23 [0.51; -0.04]; Fig. 2.2A) but arrival date was strongly correlated with migration duration (β = 0.70 [0.80; 0.61]; Fig. 2.2B). Prelaying duration was significantly affected by both migration duration (β = -0.65 [-0.50; -0.80]; Fig. 2.2C) and arrival date (β = -0.71 [-0.59; -0.83]; Fig. 2.2D). Finally, laying date was significantly related to arrival date (β = 0.32 [0.43; 0.21]; Fig. 2.2E) but not with prelaying duration (β = -0.07 [0.09; -0.24]; Fig. 2.3F).

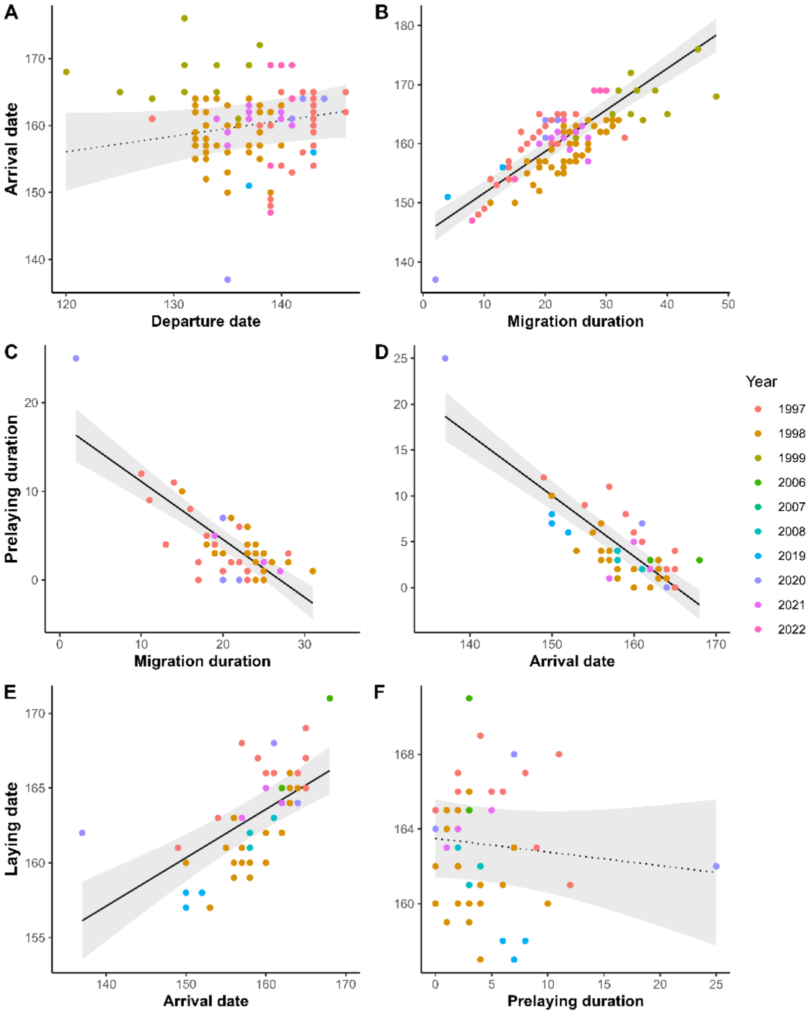

Figure 2.2. Relationships between migration and reproductive phenology in tracked female greater snow geese. For all 6 scatterplots, each dot represents a specific individual for a given year. Regression lines (dotted lines represent non-significant relationships) and 95% confidence interval are presented. Relationships between departure and arrival and dates (A), arrival dates vs. migration duration (B), prelaying vs. migration durations (C), prelaying duration vs. arrival date (D), laying vs. arrival dates (E) and laying date vs prelaying duration (F). Note that in three years of low reproductive success (1999, 2007, and 2022), no radio-tracked females were found nesting.

2.5.3 Environmental conditions over time

Temperatures in Southern Quebec changed little since the beginning of the study, with great variation among years leading to no significant change over time (β = -0.01 [0.071; -0.069]; Fig. 2.3A). Pond Inlet temperatures, slowly increased since 1997, and went from 3.2 °C in the first study-period to 4.0 °C in the last one, but the temporal trend was also not significant over 25 years (β = 0.035 [0.086; -0.016]; Fig. 2.3B). Similarly, study-period mean date of 50% snow was varied from 159 to 163, and no significant trend was observed across the 25 years of environmental data (β = 0.13 [0.37; -0.10]; Fig. 2.3C). Lastly, since 1997, WAs for both the northern and southern sections showed weak, unsignificant decreasing trends (β = -0.23 [0.14; -0.59]; Fig. 2.4A and β = -0.14 [0.13; -0.42]; Fig. 2.4B respectively).

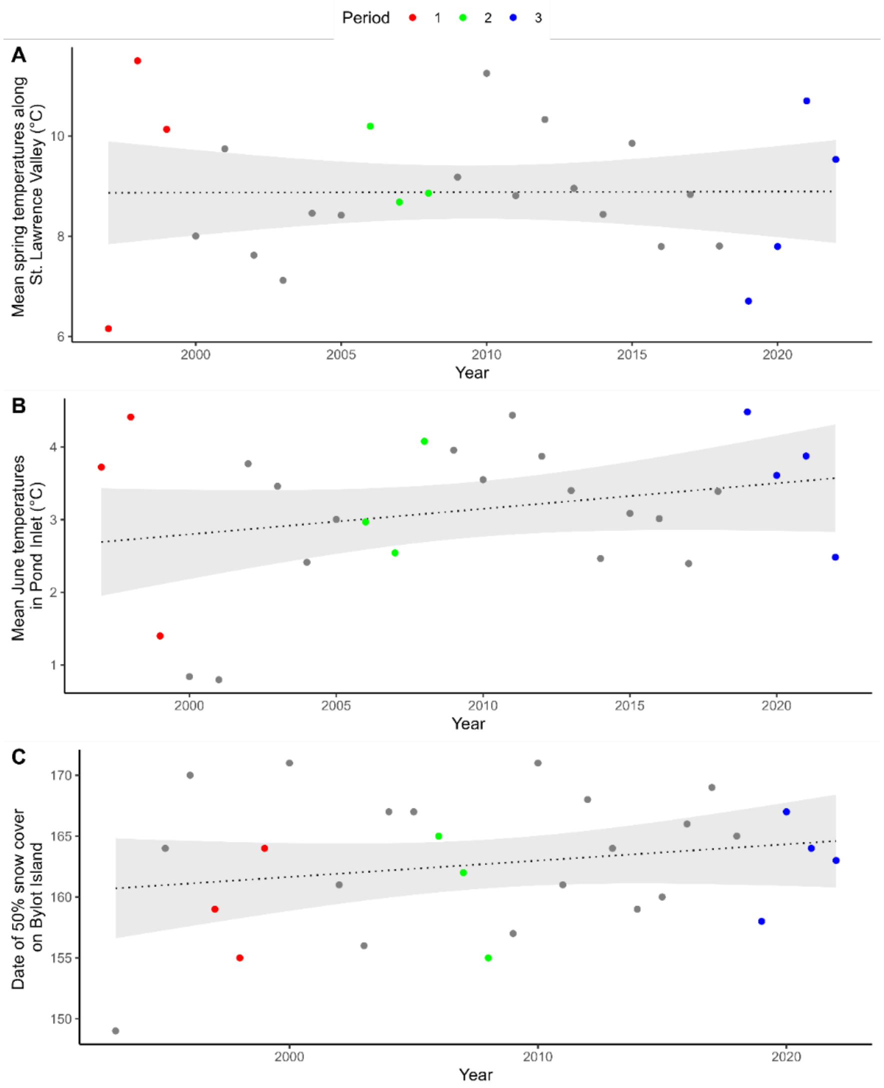

Figure 2.3. Temperature and snowmelt conditions across the study. (A) shows the yearly average of temperatures for April and May in Quebec City and Montreal, (B) shows yearly average of Pond Inlet June temperatures, and (C) shows days of 50% snow cover at Bylot Island’s research station. The first, second and third period of the study are colored in red, green, and blue respectively. Non-significant trends for the 26 years of data are represented with the dotted black line and 95% confidence intervals are shown.

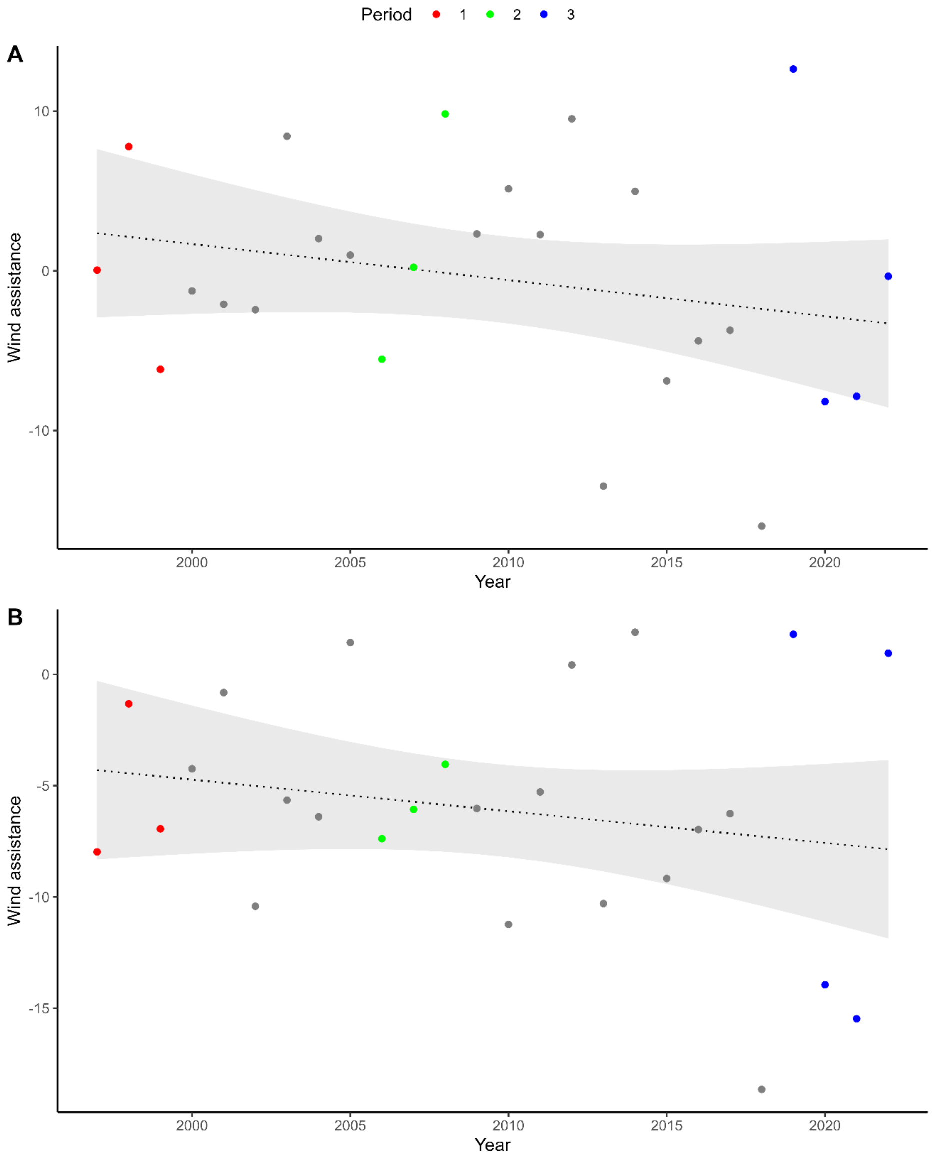

Figure 2.4. Wind assistance across the study. (A) shows the yearly average of wind assistances from mid-May to mid-June in the northern section of snow geese’s migratory route, between the tip of Nunavik and Bylot Island, (B) shows the yearly average of wind assistances from mid-May to mid-June in the southern section of snow geese’s migratory

route, between the St. Lawrence Valley and the tip of Nunavik. The first, second, and third period of the study are colored in red, green, and blue respectively. Non-significant trends for the 26 years of data are represented with the dotted black line and 95% confidence intervals are shown.

2.5.4 Testing the effect of environmental variables on phenology parameters

Wind assistance (WA) calculated either with real migration duration of individuals or using a fixed migration duration of 22 days based on individual arrival date were highly correlated (β = 0.93 [1.00;0.87]; $F_{1,135}$ =790.01; $P < 0.0001$; Adj. R^2 = 85%; Fig. 2.S1. Those two WA metrics were also highly correlated with WA obtained for GPS-tracked individuals with known migration routes (both metrics $F_{1,12} > 120$; $P < 0.0001$ with same β = 0.41 [0.47; 0.35]; see Fig 2.S2 and Fig. 2.S3 for more details). Therefore, we used the Wind assistance for a fixed migration duration of 22 days which allow to include all tracked individuals.

We tested for the effect of different environmental conditions on the phenological and reproductive parameters. Mean temperature in Quebec was significantly correlated with earlier departures (β = -2.88 [-0.88; -4.89]). Mean temperature in Pond Inlet significantly affected laying dates (β = -2.78 [-0.82; -4.74]), but not other parameters such as migration duration (β = -2.02 [2.44; -6.47]); arrival date (β = -1.11 [4.32; -6.54]) or prelaying duration (β = -2.02 [1.19; -5.24]). Date of 50% snow cover was significantly correlated with both prelaying duration (β = 1.22 [4.02; 1.22]) and laying dates (β = -1.25 [-0.38; -2.12]). Finally, WA significantly affected migration duration (β = -6.93 [-5.21; -8.65]; Fig. 2.5A), arrival date (β = -7.79 [-6.53; -9.05]; Fig. 2.5B), prelaying duration (β = 3.59 [4.87; 2.32]), and laying date (β = -2.19 [-1.41; -2.97]; Fig. 2.5C). Due to a relationship between arrival date and WAs in 2007 opposite to that of the other years of the study (Fig. 2.5B), we tested for a possible interaction between WA and mean temperature in Pond Inlet on arrival date over the study period. We found that the model with WA alone was a better predictor of arrival date than the one including an interaction between WA and temperature (AICc = 790.92 vs AICc = 795.05 respectively, ΔQAICc = 4.14). The ΔQAICc between the first and the second model superior to 2 indicates that there is a difference between the models.

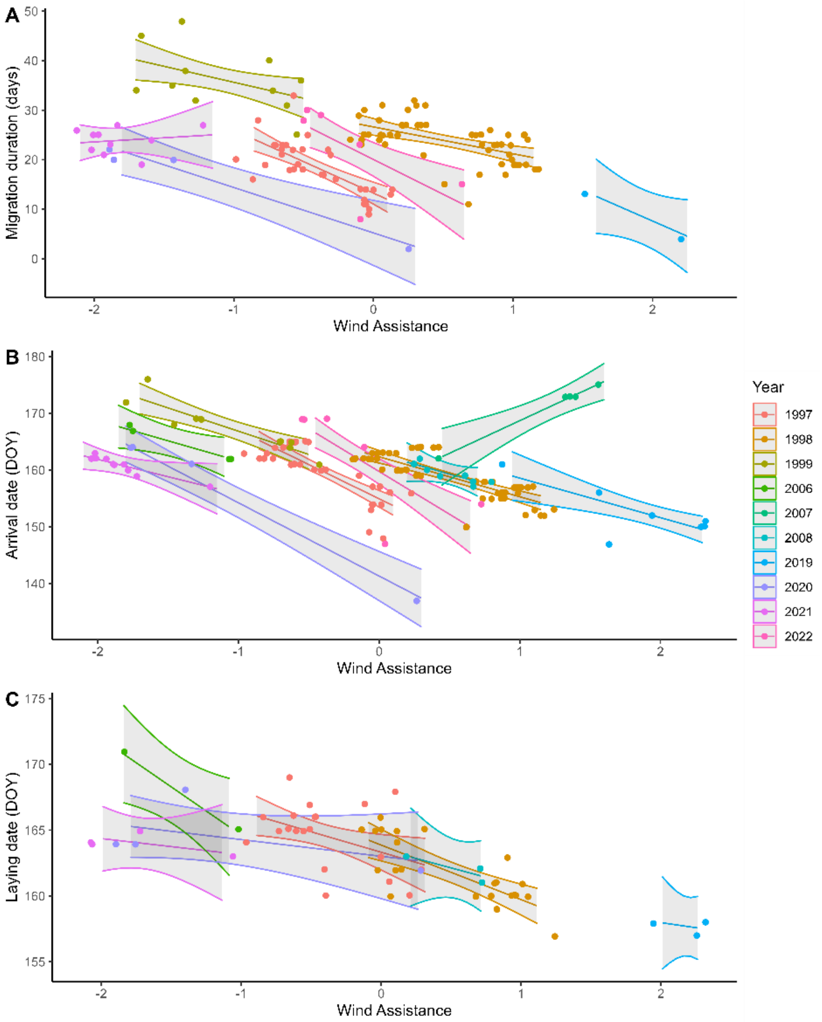

Figure 2.5. Migration duration (A), arrival dates on the breeding grounds (B) and laying dates (C) measured for tracked female greater snow geese are presented in relationship with scaled mean Wind assistance for each year (with specific regression lines and confidence intervals). Wind assistance was compiled for the 22 days prior individual arrival dates. Note that in three years of low reproductive success (1999, 2007, and 2022), no radio-tracked females were found nesting. 95% confidence intervals are shown.

2.6 Discussion

There is widespread evidence that birds are changing their migration and reproduction phenology in response to climate change (Crick et al. 1997, Rubolini et al. 2007, Hurlbert and Liang 2012, Shipley et al. 2020). However, some species display weaker phenological adjustment than others, which is generally the case for long-distance migrants (Both and Visser 2001, Møller et al. 2008). Our results indicate that, in greater snow geese nesting in the High Arctic, phenology parameters of both migration and reproduction have mostly remained stable at the individual level since the late 1990s. The lack of temporal trend in reproductive phenology was also reported in other vertebrate species breeding in the same area (Gauthier et al. 2013). A slight reduction in migration duration observed between study-periods (2019-2021 compared to 1997-1999) could be due to more favorable wind conditions. Except for one year, en route wind assistance was a strong predictor of individual arrival date, a key parameter of reproductive phenology. Relationships between migration phenology and reproduction did not display major changes, as our 10-year data shows a strong effect of arrival dates on laying dates, as in Bêty et al. (2003).

2.6.1 Phenology parameters over time

The fact that migration phenology of greater snow geese remained fairly stable over the study period was expected for a long-distance migrant species that could not rely on cues from their breeding grounds to adjust their migration timing (Gwinner and Ditrami 1990, Rubolini et al. 2007, Bauer et al. 2008b). Long-distance migrants rely mostly on endogenous factors and environmental conditions on staging areas to influence migratory departures (Knudsen et al. 2011). Their weak adjustment in arrival dates is therefore often linked to fixed departure dates (Both & Visser 2001). In greater snow geese, arrival dates were not correlated with departure dates, which is consistent across our study-periods (see also Bêty et al. 2003). Arrival dates were, on the other hand, highly correlated with migration duration, hinting that arrival dates were likely the result of environmental conditions encountered at departure from staging to the arrival on breeding grounds. An Eurasian arctic-nesting goose species, the Barnacle Goose (*Branta leucopsis*), has been shown to migrate faster as a response to climate change and earlier springs (Van der Graaf et al. 2006, Si et al. 2015, Lameris et al. 2018). However, this seems to be mostly the case for species whose migratory route contains many stopover sites. These species can better fine-tune their migration with environmental conditions, possibly because conditions at one stopover can more reliably indicate the conditions at the next one, (Tombre et al. 2008, van Wijk et al. 2012). Such feature, known as the green-wave hypothesis (Van der Graaf et al. 2006, Shariatinajafabadi et al. 2014, Si et al. 2015), is likely difficult to perform when migration routes include fewer stopovers and longer flight bouts (Tombre et al. 2008), which is the case for greater snow geese (Reséndiz Infante 2020).

On the other hand, reproduction phenology showing no sign of advancing trend was against our expectations. With the overwhelming evidence of increasing temperatures and advancing springs in the Arctic (Cleland et al. 2007, Gauthier 2013), we would have expected greater snow geese to initiate reproduction earlier (Bêty et al. 2001, Dickey et al. 2008, Morrissette et al. 2010) with a potentially shortened prelaying duration.

2.6.2 Environmental conditions trends and snow goose phenology

Against our expectations, we found no clear trend in Arctic temperatures or snowmelt date at the study site, as both of environmental parameters presented high variation across the 26 years encompassed in the present study. Snowmelt plays an important role in arctic geese breeding phenology, possibly restricting access to both nesting areas (Madsen et al. 2007) and food resources (Prop and de Vries 1993). Our long-term records on snowmelt contrast with most arctic snowmelt studies (Foster et al. 1990, Stone & Dutton 2001, Brown et al. 2010, Brown and Robinson 2011) that showed advanced snowmelt timing. This was also the case for Bylot Island for the period 1993- 2011 (Gauthier et al. 2013). Some studies have suggested that the absence of snowmelt trend in some parts of the Arctic could be due to the amount of snow precipitation that increased over time and compensates for the increase in temperature (Foster et al. 2008, Morgner et al. 2010, Cooper et al. 2011), making snowmelt timing difficult to predict (Førland and Hanssen-Bauer 2003). Increase in annual snow depth can delay the date of snowmelt despite warming spring temperature (Bjorkman et al. 2015). Given the absence of change in snow cover and the fact that this element is key in driving goose reproduction phenology (Prop & de Vries 1993, Bêty et al. 2003; Madsen et al. 2007), it is not that surprising to find a certain stability in reproductive timing (prelaying duration and laying dates) in our studied species.

On the St. Lawrence valley staging areas, predicted early springs are likely to lengthen plants growing season (Ouranos, 2015). This better and longer access to food resources could lead geese to increase their fattening rate and their spring body condition (LeTourneux et al. 2021). The resources acquired this way are partly used for egg formation (Gauthier et al. 2003) and to perform the migration to the breeding grounds. Incidentally, our results indicate that spring temperatures can play a role on geese's departure date. The lack of adjustments in individual departure dates observed in this study could be due to the little variation in spring conditions on staging areas over the 26 yr period. It is noteworthy that the staging grounds spring temperature trend in our results contrast with other studies investigating long-term temperature trends in the same area (Ouranos, 2015). This difference might be explained by the additional ten years of data between the two studies and the relatively short time window of our study.

2.6.3 Wind assistance, a driver of migration duration and timing of reproduction

Studies investigating the effect of climate change on migration and breeding phenology often compare arrival dates and an index of spring initiation, such as temperature, snowmelt or greenness (Marra et al. 2005, Conklin et al. 2021, La Sorte & Graham 2021). Wind patterns, however, are often overlooked in long-distant migrants, even if it can play an important role in migration speed (Kemp et al. 2010) and timing (Sinelschikova et al. 2007). In this study, we show that wind assistance is a strong driver of both migration duration and arrival date. Our index represents winds integrated over a large area (2.5-degree resolution) and is a reliable proxy of wind condition experienced by geese during their migration (see Appendix). Wind assistance was the environmental parameter that explained most of phenological variation between years. Even if this index represents winds over a large area and estimates the position of the bird during its migration, wind favorability index still explains, more than temperature, variation in arrival dates between years. This is similar to what has been found in long-distant migrant such as small European passerines (Haest et al. 2020). The correlation with arrival date also holds between individuals within a given year: individuals experiencing more favorable wind conditions migrate faster and arrive earlier. The only year where this trend doesn’t hold was in 2007, characterized by a late spring with low reproduction output (Legagneux et al. 2012). Furthermore, the sample size is low for this specific year and could explain the discrepancy compared to the rest of the dataset.

Arrival date is a key parameter for migratory birds. Theoretical models predict that individuals arriving early will be able to feed longer upon arrival, but still nest earlier than late arriving ones, ultimately impacting reproductive success (Rowe et al. 1994). In greater snow geese, similarly to other long-distance migrants (Both et al. 2005), this key parameter is mostly influenced by migration duration and the conditions encountered along the way. Since arrival dates are correlated with both wind favorability and laying dates, the strong effect of winds on arrival dates is also observed on laying dates. Although extremely late snowmelt date could jeopardize reproduction, generally, even when environmental conditions on the breeding grounds are not optimal, using favorable winds during migration could benefit geese by reducing the amount of energy spent flying (Liechti 2006) and allowing a better adjustment to local conditions (Van Noordwijk et al. 1995) to initiate reproduction. Studies investigating goose migration phenology with environmental conditions have found that geese do not strictly follow spring green up and arrive on the breeding grounds before optimal feeding conditions or snowmelt (Kölzsch et al. 2015, Si et al. 2015, Li et al. 2020). Wind assistance is likely to play a central role explaining such features in bird migration and reproduction strategies (Geisler et al. 2022).

Laying dates depend mostly on two key parameters: the arrival date on the breeding ground and habitat availability largely constrained by snow cover (Bêty et al. 2003). In this study, we have shown that arrival date varies greatly among years and individuals and largely depends on wind speed and direction experienced during migration. We also show that snowmelt is still a key parameter for snow geese that is not (yet) influenced by warming spring at the species' main breeding colony. Such results provide new insights on how a long-distant migrant species is tightly dependent of environmental conditions. Considering the lack of wind assistance trend in our results and the decreasing wind speed found by Wan et al. (2010) over snow geese's migratory route, this reliance on wind conditions could potentially limit their ability to respond to climate change. Future studies should investigate more in depth the relationship between migration of GPS-equipped birds and wind patterns, as well as its interaction with felt temperature (Knudsen et al. 2011).

2.7 Acknowledgment

We would like to thank all the fieldworkers that contributed to the data collection, namely Gérald Picard and Marie-Claude Martin. We thank Marie-Christine Cadieux for managing the database. We acknowledge funding from the Sentinelle North Research Chair from the Canada First Research Excellence Fund; the Fonds de Recherche du Québec - Nature et Technologies (FRQNT) [2020-NC-271544]; the Natural Sciences and Engineering Research Council of Canada (NSERC); and ArcticNet from the Networks of Centres of Excellence of Canada.

2.8 Supplementary material

From the 6-hour interval map of wind speed and direction (https://psl.noaa.gov/data/gridded/data.ncep.reanalysis.html), we computed several indices of wind assistance (WA) using the following formula Vw*cos(β), where Vw is wind speed and β is the difference between orientation of migration (in our case, 340 degrees) and wind directions.

To calculate mean WA for GPS tracks, we first subsampled the GPS tracks to have one point every 15 minutes. Then, for every 6 hours (which corresponds to the time interval of our wind data) of the GPS-equipped birds' migration, we associated the WA value closest to the GPS location of the bird. All WAs associated with a GPS point between the individuals' arrival and departure were averaged.

Mean WA for 22 days before arrival were calculated for all birds, including the ones only tracked on their arrival on the breeding grounds. We subtracted to the arrival date the mean migration duration obtained from all birds tracked from their staging areas (22 days). WAs values were taken from the southern section for the first 11 days and from the northern section for the last 11 days and then averaged providing an estimate of the wind conditions that individuals encountered during migration.

Mean WA for migration duration was calculated only for birds with known departure and arrival dates. We split the migration in two equal time periods and assigned WAs values from the specific sections similarly as described above.

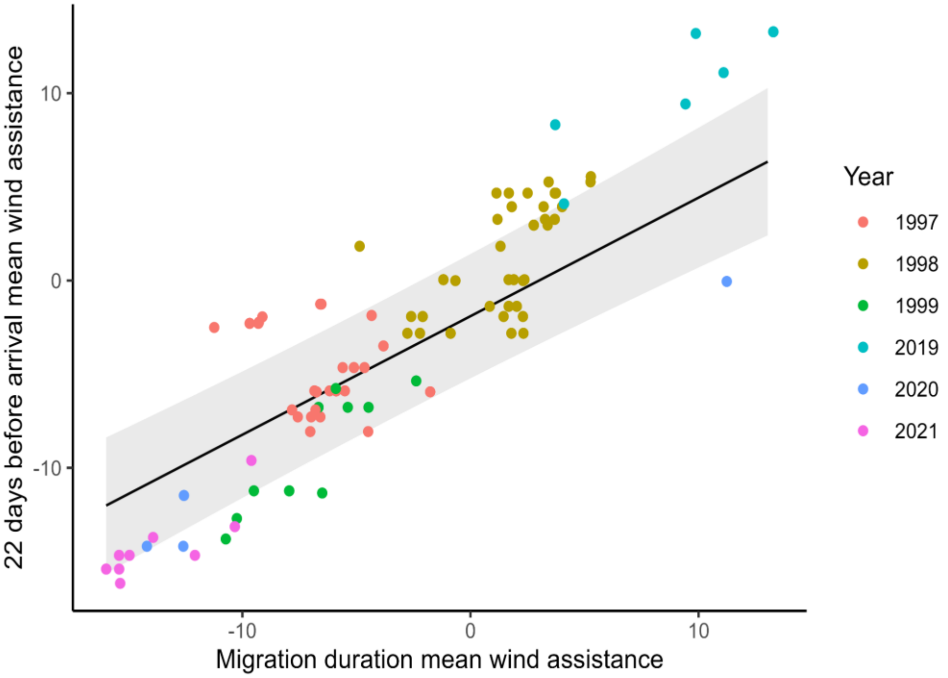

Figure 2.S1. Comparison between the mean of daily wind assistance for the specific migration duration of individuals and the mean of daily wind assistance for 22 days before the arrival of individuals on the breeding grounds. Both indices consider migration duration to be the time in days spent between Île-aux-Oies, QC and Bylot Island, Nunavut. A period of 22 days represents the mean migration duration of all individuals with known arrival date and departure date (n = 16). Adjusted $R^2 = 0.85$.

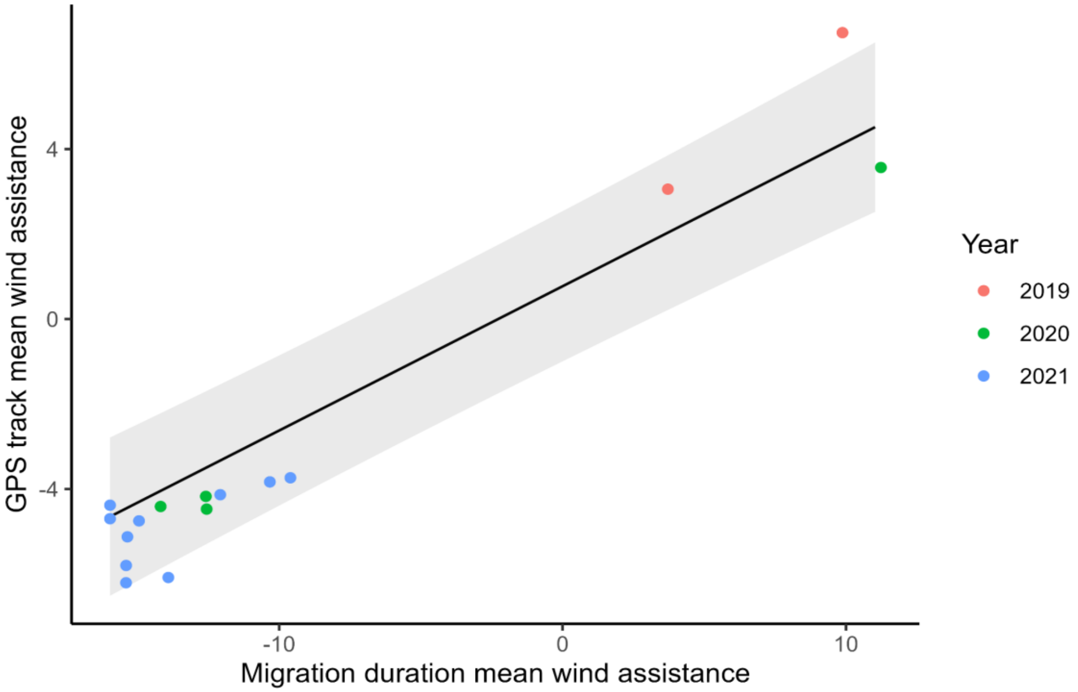

Figure 2.S2. Comparison between the mean of daily wind assistance for the specific migration duration of individuals and the mean of wind assistance associated with GPS location for individuals tracked during their spring migration. For the mean migration duration wind assistance, migration duration is considered to be the time spent traveling between Île-aux-Oies, QC and Bylot Island, Nunavut. For the GPS track mean wind assistance, GPS coordinates selected during spring migration are those between those same two locations. Adjusted $R^2 = 0.93$.

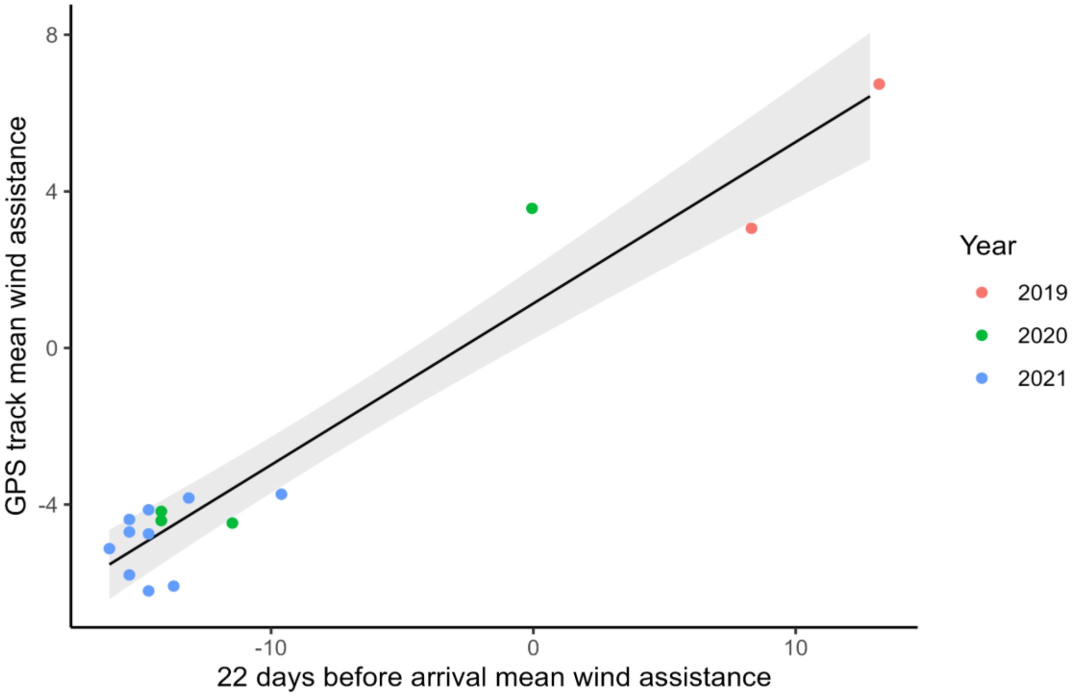

Figure 2.S3. Comparison between the mean of daily wind assistance for 22 days before the arrival of individuals on the breeding grounds and the mean of wind assistance associated with GPS location for individuals tracked during their spring migration. Both indices consider migration duration to be the time spent or the distance traveled between Île-aux-Oies, QC and Bylot Island, Nunavut. 22 days represent the mean migration duration of all individuals with arrival date and departure date in this study. Adjusted $R^2 = 0.92$.

Table 2.S1. Yearly sample sizes for each parameter investigated in the study, as well as sample size for both collar types.

Study-periods	1			2			3		
Years	1997	1998	1999	2006	2007	2008	2019	2020	2021
VHF collar	34	54	11	4	5	9	6	0	0
GPS collar	0	0	0	0	0	0	2	4	10
Departure date	34	53	11	0	0	0	2	4	10
Arrival date	33	54	11	4	5	8	8	4	10
Migration duration	33	53	11	0	0	0	2	4	10
Laying date	20	24	0	2	0	3	3	4	4
Prelaying duration	19	24	0	2	0	3	3	4	4

Conclusion

L’étude d’un phénomène aussi complexe que les effets reportés chez des espèces migratrices demande un effort considérable. Ce projet tente de distinguer les mécanismes de réponse à deux types de perturbations chez une espèce dont la répartition s’étend sur plus 3000 kilomètres en intégrant un suivi à long terme à la colonie, une manipulation expérimentale en migration, deux technologies de suivi individuel et trois périodes de collecte de données s’étendant sur une période de 25 ans. Les résultats amenés par cet effort permettent de lever le voile sur certains mécanismes permettant à une espèce longévive de répondre aux perturbations de pulsion et de pression (Harris et al. 2018).

Perturbations de pulsion

La première partie de ce projet s’intéresse aux effets reportés d’une perturbation de pulsion chez les individus, c’est-à-dire des événements soudains qui causent un stress aigu. Pour ce faire, nous avons simulé une perturbation imprévisible de haute intensité en gardant des oies sauvages en captivité (jusqu’à quatre jours) lors de leur halte migratoire au Québec. Ce chapitre fait suite à une étude qui a démontré que cette perturbation expérimentale avait un impact négatif sur le succès reproducteur mesuré à l’automne (Legagneux et al. 2012). En revisitant les données de Legagneux et al. (2012) et en y ajoutant des informations sur le suivi d’oies marquées sur le site de reproduction, nous avons ici voulu mettre en évidence les mécanismes pouvant expliquer cette diminution du succès reproducteur. Nous avons confronté deux hypothèses principales, soit une diminution de la propension à se reproduire ou une diminution de l’investissement reproducteur. Nous n’avons trouvé aucun effet de la manipulation expérimentale sur les paramètres d’investissement reproducteur, mais avons constaté une diminution de la détection à la colonie en réponse à cette manipulation. De plus, nous avons observé, pour une année aux conditions environnementales moins propices à la reproduction, une différence de temps passé en captivité entre les oies observées à la colonie et l’ensemble des oies manipulées. Ces résultats démontrent qu’un stress aigu subi sur les haltes migratoires peut amener une espèce longévive telle que l’oie des neiges à sauter un événement reproducteur plutôt que de réduire cet investissement par un plus petit effort reproducteur pour l’année en cours. En effet, les oies qui ont décidé de nicher malgré la perturbation avaient un effort reproducteur semblable aux oiseaux témoins.

Sauter une saison de reproduction lorsque les conditions sont défavorables est une stratégie relativement répandue chez les espèces longévives (Erikstad et al. 1998, Cubaynes et al. 2011, Jean-Gagnon et al. 2018). Contrairement aux autres paramètres de reproduction, celui-ci est beaucoup plus difficile à étudier en raison du fait que les individus non-nicheurs évitent souvent les territoires de nidification (Etterson et al. 2011). Cette étude est parmi les premières à démontrer expérimentalement qu'une perturbation rencontrée avant la reproduction peut affecter ce paramètre aux sites de reproduction et donc probablement la décision de nicher. En effet, si plusieurs études expérimentales soulèvent des effets reportés d'un stresseur rencontré en migration sur différents paramètres de reproduction telle que la date de ponte ou la taille de ponte, peu d'entre elles sont capables de détecter un effet sur la propension à se reproduire ou un proxy de celle-ci. Comme cette décision peut avoir des conséquences sur la croissance des populations (Sedinger et al. 2008), nos résultats soulignent l'importance de considérer ce paramètre dans l'étude des effets reportés sur la reproduction afin d'éventuellement mieux le comprendre.

Perturbations de pression

Dans le deuxième chapitre de ce mémoire, nous nous intéressons aux tendances de phénologie de migration et de reproduction des oies en fonction d'une perturbation de pression, soit les variations de température causées par les changements climatiques. Comme les migrateurs de longue-distance sont moins réactifs aux changements climatiques (Both and Visser 2001), nous voulions tester deux hypothèses. La première étant qu'en raison d'un contrôle plus interne des décisions de migration, ce migrateur de longue-distance ne changerait pas ses dates de migration avec le temps. La deuxième hypothèse que nous voulions tester était qu'avec le devancement des printemps arctiques et par conséquent de la valeur saisonnière des œufs, les oies ayant une migration inchangée réduiraient la période préponte afin de pondre plus tôt. De plus, nous voulions comparer la phénologie de migration avec différents paramètres environnementaux afin de déterminer lesquels avaient la plus grande influence sur les paramètres phénologiques. Alors que les dates individuelles de migration sont effectivement restées assez stables entre les périodes, les dates de pontes sont, contrairement à notre hypothèse, restées stables également. Par contre, notre étude révèle le rôle que jouent différents facteurs environnementaux sur la phénologie des oies. Le facteur affectant le plus la phénologie des oies est la direction et la vitesse des vents, permettant aux oies bénéficiant de conditions de vents favorables de grandement devancer leur date d'arrivée en Arctique et conséquemment leur date de ponte.

Alors que plusieurs études s'intéressant aux changements climatiques comparent la phénologie de migration et de reproduction avec des facteurs environnementaux reliés à la température (Marra et al. 2005, Conklin et al. 2021, La Sorte & Graham 2021), beaucoup moins se sont penchées sur l'effet des conditions de vents (Haest et al. 2018). Or, nos résultats indiquent que les vents, plus que la température, permettent aux oies de moduler leur date de migration. Des résultats similaires ont été trouvés chez des passereaux migrateurs de longue-distance (Haest et al. 2020). En effet, cette étude démontre que le vent est le facteur environnemental expliquant en plus grande partie l'ajustement de la phénologie de migration des espèces étudiées au cours des 50 dernières années. Notre étude révèle que les oies, une autre espèce migratrice de longue-distance, pourraient également bénéficier des vents favorables pour devancer leur phénologie de migration et de reproduction et suivre à l'avancée des saisons et de la valeur saisonnière des œufs.

Néanmoins, ce mécanisme d'ajustement phénologique ne permettrait aux oies de répondre aux changements climatiques qu'advenant que les tendances de conditions de vents dans les prochaines années demeurent similaires à leurs conditions actuelles. Contrairement aux projections de variation de température qui sont spatialement hétérogènes, une tendance généralement à la baisse de la vitesse des vents s'observe un peu partout sur le globe (Vautard et al. 2010, McVicar et al. 2012). C'est notamment le cas pour le Québec et l'Île de Baffin, soit le long du parcours migratoire des oies, où la vitesse des vents suit une tendance à la baisse depuis 1950 (Wan et al. 2010). De la même manière, nos résultats n'indiquent pas d'amélioration dans les tendances d'assistance de vent au cours de la période d'étude. Ainsi, si notre étude révèle un mécanisme utilisé par un migrateur de longue-distance pour ajuster sa durée de migration et sa date d'arrivée, elle soulève également, à l'instar de La Sorte et al. (2019), l'importance d'investiguer les tendances et projections de conditions environnementales dans un contexte écologique.

Limites de l'étude

Malgré les avantages que procure une approche individuelle, notamment une meilleure compréhension des mécanismes de réponse observés au niveau de la population, une telle approche comprend des inconvénients. Entre autres, il est plus difficile d'avoir un suivi à grande échelle, puisque chaque individu demande plus d'effort pour être suivi. Ceci affecte donc les tailles d’échantillon et la puissance statistique. Particulièrement avec des effets aléatoires comme l’année en cours, avoir un nombre limité d’individus requiert d’être prudent dans l’interprétation des résultats. Néanmoins, ce genre de limite est commun dans les études avec approche individuelle (Studds and Marra 2005) et nos analyses statistiques ne souffrent pas d’un manque de puissance même si certaines interactions entre variables environnementales sur la phénologie de reproduction n’ont pu être testées.

Ce projet, principalement le deuxième chapitre, tire avantage de l'information accumulée grâce à différents protocoles. Si plusieurs décennies de suivi de la colonie à l’Île Bylot permettent de comparer des données sur une longue période, d’autres données sont plus difficiles à contraster. Par exemple, le changement de méthode d’estimation de la condition corporelle printanière des oies en passant d’estimation de profils abdominaux (Féret et al. 2005) à un calcul de masse corrigée par la taille (LeTourneux et al. 2021) complique la comparaison des deux indices entre différentes périodes. C’est pourquoi nous avons été restreints dans l’utilisation de la condition corporelle printanière pour tester l’effet de celle-ci sur les paramètres de phénologie. Ainsi, la combinaison d’une approche individuelle et d’une compilation de différentes méthodes a empêché cette étude d’investiguer la relation entre la phénologie de migration, de reproduction et la condition corporelle printanière tel qu’effectué dans Bêty et al. 2003.

En plus des méthodes différentes, ce projet incorpore deux technologies de suivi individuel avec des précisions différentes : les colliers VHF et GPS. Afin de pallier cette différence de précision, nous avons appliqué des contraintes aux informations obtenues par les colliers GPS pour que les données soient similaires à celle de la technologie VHF. Bien que cette méthode permette de comparer de manière égale les données obtenues par les deux technologies, une réduction de la qualité de l’information pour les données GPS s’ensuit. De la même manière, alors que les données de reproduction des individus suivis par VHF ont été validées sur le terrain, les données des colliers GPS ont été estimées par le trajet GPS des oies. D’autres études se penchent sur des méthodes similaires pour déterminer la position d’un nid et une tentative de reproduction (de Boer et al. 2014, Kölzsch et al. 2019, Picardi et al. 2020). Cette méthode nécessite toujours une validation sur le terrain, mais il demeure que l’estimation de la date de ponte représente un paramètre assez visible sur les trajets GPS. Dans son ensemble, la différence entre les deux technologies doit être considérée dans l’interprétation des résultats, mais une méthode conservatrice de l’utilisation des données GPS produit des résultats en lesquels nous avons confiance, qui devraient être validés sur le terrain à l’été 2023.

Enfin, le premier chapitre de ce mémoire utilise deux approches pour estimer un paramètre difficile à mesurer, la propension à se reproduire. Les deux approches indiquent la même tendance, mais ces deux approches restent des proxys de la propension à se reproduire. Plusieurs études utilisent des proxys pour estimer ce paramètre difficile à mesurer (Souchay and Gauthier 2014). Dans cette étude, nous avons vérifié que le proxy utilisé, soit la probabilité d'observation sur les sites de reproduction, était représentatif de la propension à se reproduire en éliminant les autres possibilités pouvant expliquer le phénomène. En testant l'effet de la manipulation sur la survie des oies et compte tenu de ce que nous savons sur les fortes tendances philopatriques des oies (Bêty et al. 2004), nous pouvons être confiant que ce proxy est un bon indicateur de la propension à se reproduire. Néanmoins, il ne s'agit pas du vrai paramètre, ce qui encore une fois invite à la prudence dans les conclusions que l'on peut tirer des résultats.

Futures approches

Avec les nouvelles technologies de suivi individuel qui voient le jour, il sera bientôt possible d'investiguer des hypothèses jusqu'alors seulement effleurées. Pour faire suite au premier chapitre de ce mémoire, une nouvelle étude répétant la manipulation des oies avec des colliers GPS plutôt que VHF permettrait de déterminer directement la propension à se reproduire. De plus, la combinaison de la technologie GPS avec des données d'accélérométrie pourra non seulement permettre de déterminer la propension à se reproduire, mais également la date de ponte et le succès reproducteur (Schreven et al. 2021). Parallèlement, une étude mesurant le niveau de stress et de prédisposition à se reproduire des individus, en plus des mesures de masses comme effectuées dans notre étude (Legagneux et al. 2012), pourrait indiquer le mécanisme proximal affectant la décision de sauter la reproduction, que ce soit un stress hormonal aigu ou une réduction de la condition corporelle en dessous d'un certain seuil (Legagneux et al. 2016).

Les résultats du deuxième chapitre soulèvent de nouvelles questions concernant la réponse des oiseaux migrateurs de longue-distance aux changements climatiques. Grâce à la précision qu'apporte la technologie GPS, il sera possible de comparer la phénologie de migration des individus avec les conditions environnementales exactes que les individus rencontrent le long de leur trajet migratoire. Ainsi, comme nous l'avons fait pour valider notre indice de vent, il serait possible de voir le temps que prennent les individus à se rendre à leur site de reproduction en fonction des conditions de vent, de température et l'interaction entre celles-ci. En effet, comme plusieurs études montrent un effet de la température ou d'un indice d'initiation du printemps sur la phénologie de migration (Tombre et al. 2008, van Wijk et al. 2012, Polakowski et al. 2018), il est possible que ces deux facteurs agissent en interaction sur la décision des oies à progresser dans leur migration. Comme il est connu que les conditions extrêmes représentent un risque à une arrivée hâtive (Martin & Wiebe 2004, Krause et al. 2016), il serait également possible de voir quelles conditions forcent les oies à s'arrêter en route et de quelles manières celles-ci affectent la reproduction des oies. Autrement dit, plutôt que s'intéresser à des indices de conditions environnementales à grande échelle, cette technologie permettrait de comparer les conditions rencontrées à fine échelle et la réponse comportementale immédiate à ces conditions.

Conclusion générale

Par une approche individuelle, ce projet contribue à l'acquisition de connaissance des mécanismes des effets reportés chez les espèces migratrices et longévives. Dans le premier chapitre de ce mémoire, suivre des individus spécifiques a permis de comprendre par quel mécanisme le succès reproducteur a été réduit au niveau de la population à la suite d'une perturbation expérimentale. En effet, si la perturbation n'a pas mené les oies à se reproduire avec un investissement réduit, elle a plutôt affecté leur propension à se reproduire lorsque les conditions environnementales en Arctique étaient défavorables à la reproduction. À l'inverse, lors d'années de conditions favorables, les oies ont pu remédier aux effets de la perturbation et se reproduire sans conséquences visibles de la manipulation. Dans le second chapitre de ce projet, nos résultats ont indiqué très peu de changements dans la phénologie de migration et de reproduction des oies depuis 26 ans. Néanmoins, nous avons noté une forte corrélation entre les conditions de vents et la date d'arrivée et de ponte des oies. Ceci soulève donc un nouveau facteur à considérer dans la compréhension de la réponse des oies aux changements climatiques, où les conditions de vents pourraient à la fois permettre de moduler les effets d'un printemps hâtif ou empêcher un ajustement à celui-ci. En somme, nos résultats démontrent que les oies sont fortement dépendantes des conditions environnementales dans leur réponse aux perturbations de pression et de pulsion pesant sur la biodiversité. Nous suggérons aux futures études d'investiguer davantage en profondeur la réponse individuelle des oies aux perturbations grâce à la technologie GPS. Entre autres, il serait possible de contraster le trajet migratoire des oies avec les conditions de températures tout le long de leur trajet ou encore déterminer la vraie propension à se reproduire à la suite d'une perturbation expérimentale.

Pour conclure, ce projet se penchant sur les effets de perturbations rencontrés en migration sur la reproduction témoigne de la résilience d'une espèce migratrice de longue-distance. Il est reconnu que les espèces migratrices sont plus sensibles aux changements globaux qui s'opèrent présentement en raison de la complexité de leur cycle de vie (Carey 2009) et de leur dépendance à plusieurs sites différents pour survivre (Knudsen et al. 2011). Pour cette raison, les espèces migratrices sont généralement considérées comme étant plus vulnérables aux changements anthropiques (Møller et al. 2008, Saino et al. 2011). Plusieurs études prévoient de telles tendances chez les espèces migratrices de longue-distance (Both and Visser 2001), notamment les oies et les bernaches nichant en Arctique (Lameris et al. 2018). Or, une étude s'intéressant aux destins des espèces face aux changements climatiques soulève l'importance de comprendre la capacité des espèces à remédier aux perturbations (Moritz and Agudo 2013). La présente étude montre que la grande oie des neiges est, pour le moment, capable de surmonter des perturbations variées subites en migration en palliant ses décisions de migration et de reproduction avec les conditions environnementales qu'elle rencontre sur son trajet. Malgré tout, bien que cette espèce migratrice soit en mesure de répondre aux perturbations actuelles, sa dépendance aux conditions, notamment de vent et de fonte de neige, pourrait limiter sa réponse aux perturbations futures. Une meilleure connaissance des facteurs pouvant prédire l'évolution des paramètres environnementaux d'importance pour les oiseaux migrateurs est donc requise afin de comprendre comment ceux-ci réagiront aux changements climatiques.

Bibliographie

Ahola, M., T. Laaksonen, K. Sippola, T. Eeva, K. Rainio, and E. Lehikoinen. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. Global Change Biology 10:1610–1617.

Alisauskas, R. T., K. L. Drake, J. H. Caswell, and D. K. Kellett. 2012. Movement and persistence by Ross's Geese (*Chen rossii*) in Canada's arctic. Journal of Ornithology 152:573–584.

Arnoldi, J. F., A. Bideault, M. Loreau, and B. Haegeman. 2018. How ecosystems recover from pulse perturbations: A theory of short- to long-term responses. Journal of Theoretical Biology 436:79–92.

Astheimer, L. B., W. A. Buttemer, and J. C. Wingfield. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. Ornis Scandinavica 23:355.

Bailey, L. D., M. van de Pol, F. Adriaensen, A. Arct, E. Barba, P. E. Bellamy, S. Bonamour, J.-C. Bouvier, M. D. Burgess, A. Charmantier, C. Cusimano, B. Doligez, S. M. Drobniak, A. Dubiec, M. Eens, T. Eeva, P. N. Ferns, A. E. Goodenough, I. R. Hartley, S. A. Hinsley, E. Ivankina, R. Juškaitis, B. Kempenaers, A. B. Kerimov, C. Lavigne, A. Leivits, M. C. Mainwaring, E. Matthysen, J.-Å. Nilsson, M. Orell, S. Rytkönen, J. C. Senar, B. C. Sheldon, A. Sorace, M. J. Stenning, J. Török, K. van Oers, E. Vatka, S. J. G. Vriend, and M. E. Visser. 2022. Bird populations most exposed to climate change are less sensitive to climatic variation. Nature Communications 13:1–10.

Bamberger, C. M., H. M. Schulte, and G. P. Chrousos. 1996. Molecular determinants of glucocorticoid receptor function and tissue sensitivity to glucocorticoids. Endocrine Reviews 17:245–261.

Bauer, S., M. Van Dinther, K. A. Høgda, M. Klaassen, and J. Madsen. 2008a. The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. Journal of Animal Ecology 77:654–660.

Bauer, S., P. Gienapp, and J. Madsen. 2008b. The relevance of environmental conditions for departure decision changes en route in migrating geese. Ecology 89:1953–1960.

Bearhop, S., G. M. Hilton, S. C. Votler, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society B: Biological Sciences 271:215–218.

Béchet, A., J. F. Giroux, and G. Gauthier. 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. Journal of Applied Ecology 41:689–700.

Bender E.A., Case T.J., Gilpin M.E., B. E.A., C. T.J., and G. M.E. 1984. Perturbation experiments in community ecology: Theory and Practice. Ecology 65:1–13.

Bêty, J., G. Gauthier, and J. F. Giroux. 2003. Body condition, migration, and timing of reproduction in snow geese: A test of the condition-dependent model of optimal clutch size. American Naturalist 162:110–121.

Bêty, J., G. Gauthier, J. F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388–400.

Bêty, J., J. F. Giroux, and G. Gauthier. 2004. Individual variation in timing of migration: Causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behavioral Ecology and Sociobiology 57:1–8.

Bjorkman, A. D., S. C. Elmendorf, A. L. Beamish, M. Vellend, and G. H. R. Henry. 2015. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. Global Change Biology 21:4651–4661.

Blouin, F., J. Giroux, J. Ferron, G. Gauthier, and J. Doucet. 1999. The use of satellite telemetry to track Greater Snow Geese. Journal of Field Ornithology 70:187–199.

de Boer, R., S. Bauer, H. P. Van Der Jeugd, B. J. Ens, L. Griffin, D. Cabot, K. M. Exo, B. A. Nolet, and A. Kölzsch. 2014. A comparison of spring migration between three populations of barnacle geese *Branta leucopsis* using GPS satellite-transmitters. Limosa 87:99–106.

Bókony, V., Á. Z. Lendvai, A. Likér, F. Angelier, J. C. Wingfield, and O. Chastel. 2009. Stress response and the value of reproduction: are birds prudent parents? American Naturalist 173:589–598.

Both, C., R. G. Bijlsma, and M. E. Visser. 2005. Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. Journal of Avian Biology 36:368–373.

Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81–83.

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298.

Bradarić, M., W. Bouten, R. C. Fijn, K. L. Krijgsveld, and J. Shamoun-Baranes. 2020. Winds at departure shape seasonal patterns of nocturnal bird migration over the North Sea. Journal of Avian Biology 51:1–11.

Briedis, M., Krist, M., Král, M., Voigt, C. C., & Adamík, P. 2018. Linking events throughout the annual cycle in a migratory bird—non-breeding period buffers accumulation of carry-over effects. Behavioral Ecology and Sociobiology, 72: 1-12.

Brown, R. D., and D. A. Robinson. 2011. Northern Hemisphere spring snow cover variability and change over 1922-2010 including an assessment of uncertainty. Cryosphere 5:219–229.

Buttler, E. I., H. G. Gilchrist, S. Descamps, M. R. Forbes, and C. Soos. 2011. Handling stress of female common eiders during avian cholera outbreaks. Journal of Wildlife Management 75:283–288.

Cadieux, M.-C., G. Gauthier, É. Duchesne, M. Belke-Brea, T. Grandmont, J. Bêty, and P. Legagneux. 2020. Population study of Greater Snow Geese on Bylot and Ellesmere Islands (Nunavut) in 2020 : a Progress Report:1–55.

Carey, C. 2009. The impacts of climate change on the annual cycles of birds. Philosophical

Transactions of the Royal Society B: Biological Sciences 364:3321–3330.

Catry, P., M. P. Dias, R. A. Phillips, and J. P. Granadeiro. 2013. Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. Ecology 94:1230–1235.

Chalifour, É. 2012. Écologie de la mue chez la grande oie des neiges (*Chen caerulescens atlantica*). Diss. Université du Québec à Rimouski,

Charbonnel, N., Y. Chaval, K. Berthier, J. Deter, S. Morand, R. Palme, and J. F. Cosson. 2008. Stress and demographic decline: A potential effect mediated by impairment of reproduction and immune function in cyclic vole populations. Physiological and Biochemical Zoology 81:63–73.

Chastel, O. 1995. Influence of reproductive success on breeding frequency in four southern petrels. Ibis 137:360–363.

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

Choquet, R., J. D. Lebreton, O. Gimenez, A. M. Reboulet, and R. Pradel. 2009a. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. Ecography 32:1071–1074.

Choquet, R., Rouan, L., & Pradel, R. 2009b. Program E-SURGE: a software application for fitting multievent models. In Modeling demographic processes in marked populations (pp. 845-865). Springer, Boston, MA.

Clausen, K. K., J. Madsen, and I. M. Tombre. 2015. Carry-over or compensation? The impact of winter harshness and post-winter body condition on spring-fattening in a migratory goose species. PLoS ONE 10:1–13.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. Trends in Ecology and Evolution 22:357–365.

Cockrem, J. F. 2013. Individual variation in glucocorticoid stress responses in animals. General and Comparative Endocrinology 181:45–58.

Conklin, J. R., S. Lisovski, and P. F. Battley. 2021. Advancement in long-distance bird migration through individual plasticity in departure. Nature Communications 12:1–9.

Cooper, E. J., S. Dullinger, and P. Semenchuk. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. Plant Science 180:157–167.

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

Cubaynes, S., P. F. Doherty, E. A. Schreiber, and O. Gimenez. 2011. To breed or not to breed: A seabird’s response to extreme climatic events. Biology Letters 7:303–306.

Dai, A., Zhao, T., & Chen, J. 2018. Climate change and drought: a precipitation and evaporation perspective. Current Climate Change Reports, 4: 301-312.

Dawson, A., V. M. King, G. E. Bentley, and G. F. Ball. 2001. Photoperiodic control of seasonality in birds. Journal of Biological Rhythms 16:365–380.

Demers, F., J. F. Giroux, G. Gauthier, and J. Bêty. 2003. Effects of collar-attached transmitters on behaviour, pair bond and breeding success of snow geese *Anser caerulescens atlanticus*. Wildlife Biology 9:161–170.

Descamps, S., J. Bêty, O. P. Love, and H. G. Gilchrist. 2011. Individual optimization of reproduction in a long-lived migratory bird: A test of the condition-dependent model of laying date and clutch size. Functional Ecology 25:671–681.

Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in Mallards (Anas platyrhynchos). Auk 125:618–628.

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

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

Dore, M. H. 2005. Climate change and changes in global precipitation patterns: what do we know?. Environment international, 31: 1167-1181.

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

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

Dubiec, A., and M. Cichoñ. 2001. Seasonal decline in health status of Great Tit (*Parus major*) nestlings. Canadian Journal of Zoology 79:1829–1833.

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

Edes, A. N., B. A. Wolfe, and D. E. Crews. 2018. Evaluating allostatic load: A new approach to measuring long-term stress in wildlife. Journal of Zoo and Wildlife Medicine 49:272–282.

Eichhorn, G., R. H. Drent, J. Stahl, A. Leito, and T. Alerstam. 2009. Skipping the Baltic: The emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. Journal of Animal Ecology 78:63–72.

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

Etterson, M. A., S. N. Ellis-Felege, D. Evers, G. Gauthier, J. A. Grzybowski, B. J. Mattsson, L. R. Nagy, B. J. Olsen, C. M. Pease, M. P. van der Burg, and A. Potvien. 2011. Modeling fecundity in birds: Conceptual overview, current models, and considerations for future developments. Ecological Modelling 222:2178–2190.

Féret, M., J. Bêty, G. Gauthier, J.-F. Giroux, and G. Picard. 2005. Are abdominal profiles useful to assess body condition of spring staging Greater Snow Geese? The Condor 107:694.

Flannigan, M., Stocks, B., Turetsky, M., & Wotton, M. 2009. Impacts of climate change on fire activity and fire management in the circumboreal forest. Global change biology, 15: 549-560.

Førland, E. J., and I. Hanssen-Bauer. 2003. Past and future climate variations in the Norwegian Arctic: overview and novel analyses. Polar Research 22:113–124.

Foster, J. L., D. A. Robinson, D. K. Hall, and T. W. Estilow. 2008. Spring snow melt timing and changes over Arctic lands. Polar Geography 31:145–157.

Foster, J. L., J. W. Winchester, and E. G. Dutton. 1990. The date of snow disappearance on the Arctic tundra as determined from satellite, meteorological station and radiometric in situ observations. IEEE Transactions on Geoscience and Remote Sensing 30:793–798.

Gauthier, G., J. Bêty, M. C. Cadieux, P. Legagneux, M. Doiron, C. Chevallier, S. Lai, A. Tarroux, and D. Berteaux. 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. Philosophical Transactions of the Royal Society B: Biological Sciences 368.

Gauthier, G., J. Bêty, and K. A. Hobson. 2003. Are Greater Snow Geese capital breeders? New evidence from a stable-isotope model. Ecology 84:3250–3264.

Gauthier, G., J.-F. Giroux, and J. Bédard. 1992. Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. Canadian Journal of Zoology 70:2077–2087.

Gauthier, G., J. F. Giroux, A. Reed, A. Béchet, and L. Bélanger. 2005. Interactions between land use, habitat use, and population increase in greater snow geese: What are the consequences for natural wetlands? Global Change Biology 11:856–868.

Gauthier, G., and J. Tardif. 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. The Condor 93:701–711.

Geisler, J., Madsen, J., Nolet, B. A., & Schreven, K. H. 2022. Sea crossings of migratory pink-footed geese: seasonal effects of winds on flying and stopping behaviour. Journal of Avian Biology, 2022: e02985.

Gill, J. A., K. Norris, and P. M. Potts. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412:436–438.

Glasby, T. M., and A. J. Underwood. 1996. Sampling to differentiate between pulse and press perturbations. Environmental Monitoring and Assessment 42:241–252.

Gorman, K. B., D. Esler, P. L. Flint, and T. D. Williams. 2008. Nutrient-reserve dynamics during egg production by female Greater Scaup (*Aythya marila*): Relationships with timing of reproduction. Auk 125:384–394.

van der Graaf, A. J., J. Stahl, A. Klimkowska, J. P. Bakker, and R. H. Drent. 2006. Surfing on a green wave - how plant growth drives spring migration in the Barnacle Goose *Branta leucopsis*. Ardea-Wageningen-, 94: 567 .

Grémillet, D., C. Péron, A. Kato, F. Amélineau, Y. Ropert-Coudert, P. G. Ryan, and L. Pichegru. 2016. Starving seabirds: unprofitable foraging and its fitness consequences in Cape gannets competing with fisheries in the Benguela upwelling ecosystem. Marine Biology 163:1–11.

Gutierrez Illan, J., G. Wang, F. L. Cunningham, and D. T. King. 2017. Seasonal effects of wind conditions on migration patterns of soaring American white pelican. PLoS ONE 12:1–15.

Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. Ibis 138:47–63.

Gwinner, E., and J. Ditrami. 1990. Endogenous reproductive rhythms in a tropical bird. American Association for the Advancement of Science 249:906–908.

Haest, B., O. Hüppop, and F. Bairlein. 2018. The influence of weather on avian spring migration phenology: What, where and when? Global Change Biology 24:5769–5788.

Haest, B., O. Hüppop, and F. Bairlein. 2020. Weather at the winter and stopover areas determines spring migration onset, progress, and advancements in Afro-Palearctic migrant birds. Proceedings of the National Academy of Sciences of the United States of America 117:17056–17062.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D. W., & Medina-Elizade, M. 2006. Global temperature change. Proceedings of the National Academy of Sciences, 103: 14288-14293.

Harms, N. J., P. Legagneux, H. G. Gilchrist, J. Bêty, O. P. Love, M. R. Forbes, G. R. Bortolotti, and C. Soos. 2015. Feather corticosterone reveals effect of molting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird. Proceedings of the Royal Society B: Biological Sciences 282.

Harriman, V. B., R. D. Dawson, L. E. Bortolotti, and R. G. Clark. 2017. Seasonal patterns in reproductive success of temperate-breeding birds: Experimental tests of the date and quality hypotheses. Ecology and Evolution 7:2122–2132.

Harris, R. M. B., L. J. Beaumont, T. R. Vance, C. R. Tozer, T. A. Remenyi, S. E. Perkins-Kirkpatrick, P. J. Mitchell, A. B. Nicotra, S. McGregor, N. R. Andrew, M. Letnic, M. R. Kearney, T. Wernberg, L. B. Hutley, L. E. Chambers, M. S. Fletcher, M. R. Keatley, C. A. Woodward, G. Williamson, N. C. Duke, and D. M. J. S. Bowman. 2018. Biological responses to the press and pulse of climate trends and extreme events. Nature Climate Change 8:579–587.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4–18.

Hennin, H. L., J. Bêty, P. Legagneux, H. G. Gilchrist, T. D. Williams, and O. P. Love. 2016. Energetic physiology mediates individual optimization of breeding phenology in a migratory Arctic Seabird. American Naturalist 188:434–445.

Hennin, H. L., C. J. Dey, J. Bêty, H. G. Gilchrist, P. Legagneux, T. D. Williams, and O. P. Love. 2018. Higher rates of prebreeding condition gain positively impacts clutch size: A mechanistic test of the condition-dependent individual optimization model. Functional Ecology 32:2019–2028.

Hennin, H. L., P. Legagneux, J. Bêty, T. D. Williams, H. Grant Gilchrist, T. M. Baker, and O. P.

Love. 2015. Pre-breeding energetic management in a mixed-strategy breeder. Oecologia 177:235–243.

Hoarau, M., F. Angelier, F. Touzalin, T. Zgirski, C. Parenteau, and P. Legagneux. 2022. Corticosterone: foraging and fattening puppet master in pre-breeding greylag geese. Physiology and Behavior 246:113666.

Høye, T. T., and M. C. Forchhammer. 2008. Phenology of High-Arctic arthropods: Effects of climate on spatial, seasonal, and inter-annual variation. Advances in Ecological Research 40:299–324.

Høye, T. T., E. Post, H. Meltofte, N. M. Schmidt, and M. C. Forchhammer. 2007. Rapid advancement of spring in the High Arctic. Current Biology 17:449–451.

Hurlbert, A. H., and Z. Liang. 2012. Spatiotemporal variation in avian migration phenology: Citizen science reveals effects of climate change. PLoS ONE 7.

Inger, R., G. A. Gudmundsson, G. D. Ruxton, J. Newton, K. Colhoun, S. Auhage, and S. Bearhop. 2008. Habitat utilisation during staging affects body condition in a long distance migrant, *Branta bernicla hrota*: Potential impacts on fitness? Journal of Avian Biology 39:704–708.

Inger, R., X. A. Harrison, D. R. Graeme, J. Newton, K. Colhoun, G. A. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop. 2010. Carry-over effects reveal reproductive costs in a long distance migrant. Journal of Animal Ecology 79:974–982.

Jean-Gagnon, F., P. Legagneux, G. Gilchrist, O. P. Love, S. Bélanger, and J. Bêty. 2018. The impact of sea ice conditions on breeding decisions is modulated by body condition in an arctic partial capital breeder. Oecologia 186:1–10.

Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57.

Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, M. Stervander, A. Andersson, J. Waldenström, A. Lehikoinen, E. Edvardsen, R. Solvang, and N. C. Stenseth. 2007. Response to comment on “Rapid advance of spring arrival dates in long-distance migratory birds.” Science 315:598.

Juillet, C., R. Choquet, G. Gauthier, J. Lefebvre, and R. Pradel. 2012. Carry-over effects of spring hunt and climate on recruitment to the natal colony in a migratory species. Journal of Applied Ecology 49:1237–1246.

Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, and L. Gandin. 1996. The NCEP / NCAR 40-year reanalysis project. Bulletin of the American meteorological Society, 77: 437-472.

Kemp, M. U., E. Emiel van Loon, J. Shamoun-Baranes, and W. Bouten. 2012. RNCEP: Global weather and climate data at your fingertips. Methods in Ecology and Evolution 3:65–70.

Kemp, M. U., J. Shamoun-Baranes, H. Van Gasteren, W. Bouten, and E. E. Van Loon. 2010. Can wind help explain seasonal differences in avian migration speed? Journal of Avian Biology 41:672–677.

Kling, M. M., & Ackerly, D. D. 2020. Global wind patterns and the vulnerability of wind-dispersed species to climate change. Nature Climate Change, 10: 868-875.

Klinkhamer, P. G. L., T. Kubo, and Y. Iwasa. 1997. Herbivores and the evolution of the semelparous perennial life-history of plants. Journal of Evolutionary Biology 10:529–550.

Knudsen, E., A. Lindén, C. Both, N. Jonzén, F. Pulido, N. Saino, W. J. Sutherland, L. A. Bach, T. Coppack, T. Ergon, P. Gienapp, J. A. Gill, O. Gordo, A. Hedenström, E. Lehikoinen, P. P. Marra, A. P. Møller, A. L. K. Nilsson, G. Péron, E. Ranta, D. Rubolini, T. H. Sparks, F. Spina, C. E. Studds, S. A. Sæther, P. Tryjanowski, and N. C. Stenseth. 2011. Challenging claims in the study of migratory birds and climate change. Biological Reviews 86:928–946.

Kölzsch, A., S. Bauer, R. de Boer, L. Griffin, D. Cabot, K. M. Exo, H. P. van der Jeugd, and B. A. Nolet. 2015. Forecasting spring from afar? Timing of migration and predictability of phenology along different migration routes of an avian herbivore. Journal of Animal Ecology 84:272–283.

Kölzsch, A., G. J. D. M. Müskens, P. Szinai, S. Moonen, P. Glazov, H. Kruckenberg, M. Wikelski, and B. A. Nolet. 2019. Flyway connectivity and exchange primarily driven by moult migration in geese. Movement Ecology 7:1–11.

Krause, J. S., J. H. Pérez, H. E. Chmura, S. K. Sweet, S. L. Meddle, K. E. Hunt, L. Gough, N. Boelman, and J. C. Wingfield. 2016. The effect of extreme spring weather on body condition and stress physiology in Lapland longspurs and white-crowned sparrows breeding in the Arctic. General and Comparative Endocrinology 237:10–18.

Krause, J. S., J. H. Pérez, S. L. Meddle, and J. C. Wingfield. 2017. Effects of short-term fasting on stress physiology, body condition, and locomotor activity in wintering male white-crowned sparrows. Physiology and Behavior 177:282–290.

Kumar, S., V. Merwade, J. L. Kinter, and D. Niyogi. 2013. Evaluation of temperature and precipitation trends and long-term persistence in CMIP5 twentieth-century climate simulations. Journal of Climate 26:4168–4185.

Lamarre, V., A. Franke, O. P. Love, P. Legagneux, and J. Bêty. 2017. Linking pre-laying energy allocation and timing of breeding in a migratory arctic raptor. Oecologia 183:653–666.

Lameris, T. K., H. P. van der Jeugd, G. Eichhorn, A. M. Dokter, W. Bouten, M. P. Boom, K. E. Litvin, B. J. Ens, and B. A. Nolet. 2018. Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. Current Biology 28:2467-2473.e4.

Landys, M. M., M. Ramenofsky, and J. C. Wingfield. 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. General and Comparative Endocrinology 148:132–149.

Latta, S. C., S. Cabezas, D. A. Mejia, M. M. Paulino, H. Almonte, C. M. Miller-Butterworth, and G. R. Bortolotti. 2016. Carry-over effects provide linkages across the annual cycle of a Neotropical migratory bird, the Louisiana Waterthrush *Parkesia motacilla*. Ibis 158:395–406.

Lefebvre, J., G. Gauthier, J. F. Giroux, A. Reed, E. T. Reed, and L. Bélanger. 2017. The greater snow goose *Anser caerulescens atlanticus*: Managing an overabundant population. Ambio 46:262–274.

Legagneux, P., P. L. F. Fast, G. Gauthier, and J. Bêty. 2012. Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proceedings of the Royal Society B: Biological Sciences 279:876–883.

Legagneux, P., H. L. Hennin, H. G. Gilchrist, T. D. Williams, O. P. Love, and J. Bêty. 2016. Unpredictable perturbation reduces breeding propensity regardless of pre-laying reproductive readiness in a partial capital breeder. Journal of Avian Biology 47:880–886.

Leingärtner, A., J. Krauss, and I. Steffan-Dewenter. 2014. Elevation and experimental snowmelt manipulation affect emergence phenology and abundance of soil-hibernating arthropods. Ecological Entomology 39:412–418.

Lepage, D., G. Gauthier, and S. Menu. 2000. Reproductive consequences of egg-laying decisions in snow geese. Journal of Animal Ecology 69:414–427.

LeTourneux, F., T. Grandmont, F. Dulude-de Broin, M.-C. Martin, J. Lefebvre, A. Kato, J. Bêty, G. Gauthier, and P. Legagneux. 2021. COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species. Biological Conservation 255:108968.

Li, H., L. Fang, X. Wang, K. Yi, L. Cao, and A. D. Fox. 2020. Does snowmelt constrain spring migration progression in sympatric wintering Arctic-nesting geese? Results from a Far East Asia telemetry study. Ibis 162:548–555.

Liechti, F. 2006. Birds: Blowin’ by the wind? Journal of Ornithology 147:202–211.

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

Mainguy, J., J. Bêty, G. Gauthier, and J.-F. Giroux. 2002. Are body condition and reproductive effort of laying Greater Snow Geese affected by the spring hunt? The Condor 104:156–161.

Mann, M. E., & Emanuel, K. A. 2006. Atlantic hurricane trends linked to climate change. Eos, Transactions American Geophysical Union, 87: 233-241.

Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. Oecologia 142:307–315.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable- carbon isotopes. Science 282:1884–1886.

Martin, K., and K. L. Wiebe. 2004. Coping mechanisms of alpine and arctic breeding birds: Extreme weather and limitations to reproductive resilience. Integrative and Comparative Biology 44:177–185.

Martin, T. E. 1987. Food as a limit on breeding birds: a life history perspective.

Mayor, S. J., R. P. Guralnick, M. W. Tingley, J. Otegui, J. C. Withey, S. C. Elmendorf, M. E. Andrew, S. Leyk, I. S. Pearse, and D. C. Schneider. 2017. Increasing phenological asynchrony between spring green-up and arrival of migratory birds. Scientific Reports 7:1–10.

McKellar, A. E., P. P. Marra, and L. M. Ratcliffe. 2013. Starting over: Experimental effects of breeding delay on reproductive success in early-arriving male American redstarts. Journal of Avian Biology 44:495–503.

McVicar, T. R., Roderick, M. L., Donohue, R. J., Li, L. T., Van Niel, T. G., Thomas, A., ... & Dinpashoh, Y. 2012. Global review and synthesis of trends in observed terrestrial near-surface wind speeds: Implications for evaporation. Journal of Hydrology, 416: 182-205.

Menzel, A. 2000. Trends in phenological phases in Europe between 1951 and 1996. International Journal of Biometeorology 44:76–81.

Mitchell, J. F., Lowe, J., Wood, R. A., & Vellinga, M. 2006. Extreme events due to human-induced climate change. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 364: 2117-2133.

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

Morgner, E., B. Elberling, D. Strebel, and E. J. Cooper. 2010. The importance of winter in annual ecosystem respiration in the High Arctic: effects of snow depth in two vegetation types. Polar Research 29:58–74.

Moritz, C., and R. Agudo. 2013. The future of species under climate change: Resilience or decline? Science 341:504–508.

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

Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? Journal of Ornithology 147:146–166.

Nooker, J. K., P. O. Dunn, and L. A. Whittingham. 2005. Effects of food abundance, weather, and female condition on reproduction in Tree Swallows (*Tachycineta bicolor*). Auk 122:1225–1238.

van Noordwijk, A. J., R. H. McCleery, and C. Perrins. 1995. Selection for the timing of Great Tit breeding in relation to caterpillar growth and temperature. Journal of Animal Ecology 64:451–458.

Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. Oikos 109:178–186.

Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 271:59–64.

O'Connor, C. M., D. R. Norris, G. T. Crossin, and S. J. Cooke. 2014. Biological carryover effects: Linking common concepts and mechanisms in ecology and evolution. Ecosphere 5:1–11.

O'Gorman, P. A. 2015. Precipitation extremes under climate change. Current climate change reports, 1: 49-59.

Oberbauer, S. F., S. C. Elmendorf, T. G. Troxler, R. D. Hollister, A. V. Rocha, M. S. Bret-Harte, M. A. Dawes, A. M. Fosaa, G. H. R. Henry, T. T. Høye, F. C. Jarrad, I. S. Jónsdóttir, K. Klanderud, J. A. Klein, U. Molau, C. Rixen, N. M. Schmidt, G. R. Shaver, R. T. Slider, Totland, C. H. Wahren, and J. M. Welker. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. Philosophical Transactions of the Royal Society B: Biological Sciences 368.

Öberg, M., T. Pärt, D. Arlt, A. T. Laugen, and M. Low. 2014. Decomposing the seasonal fitness decline. Oecologia 174:139–150.

Öst, M., A. Lindén, P. Karell, S. Ramula, and M. Kilpi. 2018. To breed or not to breed: drivers of intermittent breeding in a seabird under increasing predation risk and male bias. Oecologia 188:129–138.

Ouranos. 2015. Vers l’adaptation. Synthèse des connaissances sur les changements climatiques au Québec. Édition 2015. Montréal, Québec : Ouranos. 415 p.

Owen-Ashley, N. T., and J. C. Wingfield. 2007. Acute phase responses of passerine birds: Characterization and seasonal variation. Journal of Ornithology 148:583–591.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.

Picardi, S., B. J. Smith, M. E. Boone, P. C. Frederick, J. G. Cecere, D. Rubolini, L. Serra, S. Pirrello, R. R. Borkhataria, and M. Basille. 2020. Analysis of movement recursions to detect reproductive events and estimate their fate in central place foragers. Movement Ecology 8:1–14.

du Plessis, K. L., Martin, R. O., Hockey, P. A., Cunningham, S. J., & Ridley, A. R. 2012. The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. Global Change Biology, 18: 3063-3070.

Polakowski, M., Z. Kasprzykowski, and A. Golawski. 2018. Influence of temperature on the timing of spring arrival and duration of migration in Arctic goose species at a central European stopover site. Ornis Fennica 95:32–40.

Polfus, J. L., Hebblewhite, M., & Heinemeyer, K. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biological Conservation, 144: 2637-2646.

Post, E. 2017. Implications of earlier sea ice melt for phenological cascades in arctic marine food webs. Food Webs 13:60–66.

Post, E., M. C. Forchhammer, N. C. Stenseth, and T. V. Callaghan. 2001. The timing of life-history events in a changing climate. Proceedings of the Royal Society B: Biological Sciences 268:15–23.

Pradel, R. 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics 61:442–447.

Pravosudov, V. V., Kitaysky, A. S., Wingfield, J. C., & Clayton, N. S. 2001. Long-term unpredictable foraging conditions and physiological stress response in mountain chickadees (*Poecile gambeli*). General and comparative endocrinology, 123: 324-331.

Previdi, M., Smith, K. L., & Polvani, L. M. 2021. Arctic amplification of climate change: a review of underlying mechanisms. Environmental Research Letters, 16: 093003.

Prop, J., and J. de Vries. 1993. Impact of snow and food conditions on the reproductive performance of Barnacle Geese *Branta leucopsis*. Ornis Scandinavica 24:110.

Ramos, R., V. Llabrés, L. Monclús, M. López-Béjar, and J. González-Solís. 2018. Costs of breeding are rapidly buffered and do not affect migratory behavior in a long-lived bird species. Ecology 99:2010–2024.

Reed, A., R. J. Hughes, and H. Boyd. 2002. Patterns of distribution and abundance of Greater Snow Geese on Bylot Island, Nunavut, Canada 1983-1998. Wildfowl 53:53–65.

Reed, E. T., J. Bêty, J. Mainguy, G. Gauthier, and J. F. Giroux. 2003a. Molt migration in relation to breeding success in greater snow geese. Arctic 56:76–81.

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

Reed, E. T., G. Gauthier, R. Pradel, and J. D. Lebreton. 2003b. Age and environmental conditions affect recruitment in Greater Snow Geese. Ecology 84:219–230.

Reséndiz-Infante, C., and G. Gauthier. 2020. Temporal changes in reproductive success and optimal breeding decisions in a long-distance migratory bird. Scientific Reports 10:1–10.

Reséndiz-Infante, C., G. Gauthier, and G. Souchay. 2020. Consequences of a changing environment on the breeding phenology and reproductive success components in a long-distance migratory bird. Population Ecology 62:284–296.

Reséndiz Infante, G. C. 2020. Migration , phénologie de la nidification et succès reproducteur d ’un migrateur de longue distance : la grande oie des neiges dans un environnement en changement. Diss. Université Laval.

Romero, L. M. 2004. Physiological stress in ecology: Lessons from biomedical research. Trends in Ecology and Evolution 19:249–255.

Rowe, L., D. Ludwig, and D. Schluter. 1994. Time, condition, and the seasonal decline of avian clutch size. American Naturalist 143:698–722.

Roy, D. B., and T. H. Sparks. 2000. Phenology of British butterflies and climate change. Global Change Biology 6:407–416.

Rubolini, D., A. P. Møller, K. Rainio, and E. Lehikoinen. 2007. Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among european bird species. Climate Research 35:135–146.

Saalfeld, S. T., D. C. McEwen, D. C. Kesler, M. G. Butler, J. A. Cunningham, A. C. Doll, W. B. English, D. E. Gerik, K. Grond, P. Herzog, B. L. Hill, B. J. Lagassé, and R. B. Lanctot. 2019. Phenological mismatch in Arctic-breeding shorebirds: Impact of snowmelt and unpredictable weather conditions on food availability and chick growth. Ecology and Evolution 9:6693–6707.

Saino, N., R. Ambrosini, D. Rubolini, J. Von Hardenberg, A. Provenzale, K. Hüppop, O. Hüppop, A. Lehikoinen, E. Lehikoinen, K. Rainio, M. Romano, and L. Sokolov. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. Proceedings of the Royal Society B: Biological Sciences 278:835–842.

Sapolsky, R. M. 2000. Stress hormones: Good and bad. Neurobiology of Disease 7:540–542.

Schreven, K. H. T., C. Stolz, J. Madsen, and B. A. Nolet. 2021. Nesting attempts and success of Arctic-breeding geese can be derived with high precision from accelerometry and GPS-tracking. Animal Biotelemetry 9:1–13.

Schultner, J., B. Moe, O. Chastel, S. Tartu, C. Bech, and A. S. Kitaysky. 2014. Corticosterone mediates carry-over effects between breeding and migration in the kittiwake *Rissa tridactyla*. Marine Ecology Progress Series 496:125–133.

Schwartz, M. D. (Ed.). 2003. Phenology: an integrative environmental science (p. 564). Dordrecht: Kluwer Academic Publishers.

Schwierz, C., Köllner-Heck, P., Zenklusen Mutter, E., Bresch, D. N., Vidale, P. L., Wild, M., & Schär, C. 2010. Modelling European winter wind storm losses in current and future climate. Climatic change, 101: 485-514.

Sedinger, J. S., N. D. Chelgren, D. H. Ward, and M. S. Lindberg. 2008. Fidelity and breeding probability related to population density and individual quality in black brent geese Branta bernicla nigricans. Journal of Animal Ecology 77:702–712.

Shariatinajafabadi, M., T. Wang, A. K. Skidmore, A. G. Toxopeus, A. Kölzsch, B. A. Nolet, K. M. Exo, L. Griffin, J. Stahl, and D. Cabot. 2014. Migratory herbivorous waterfowl track satellite-derived green wave index. PLoS ONE 9:1–11.

Shipley, J. R., C. W. Twining, C. C. Taff, M. N. Vitousek, A. Flack, and D. W. Winkler. 2020. Birds advancing lay dates with warming springs face greater risk of chick mortality. Proceedings of the National Academy of Sciences of the United States of America 117:25590–25594.

Si, Y., Q. Xin, W. F. De Boer, P. Gong, R. C. Ydenberg, and H. H. T. Prins. 2015. Do Arctic breeding geese track or overtake a green wave during spring migration? Scientific Reports 5:1–6.

Sinelschikova, A., V. Kosarev, I. Panov, and A. N. Baushev. 2007. The influence of wind conditions in Europe on the advance in timing of the spring migration of the song thrush (*Turdus philomelos*) in the south-east Baltic region. International Journal of Biometeorology 51:431–440.

Smith, P., and F. Schwing. 1991. Mean circulation and variability on the eastern Canadian continental shelf. Continental Shelf Research 11:977–1012.

Smith, R. J., and F. R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231–239.

Swanson, D. L., & Olmstead, K. L. 1999. Evidence for a proximate influence of winter temperature on metabolism in passerine birds. Physiological and Biochemical Zoology, 72: 566-575.

La Sorte, F. A., Horton, K. G., Nilsson, C., & Dokter, A. M. 2019. Projected changes in wind assistance under climate change for nocturnally migrating bird populations. Global change biology, 25: 589-601.

La Sorte, F. A., and C. H. Graham. 2021. Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds. Journal of Animal Ecology 90:343–355.

Souchay, G., and G. Gauthier. 2014. To breed or not : a novel approach to estimate breeding propensity and potential trade-offs in an Arctic-nesting species. Ecology 95:2745–2756.

Spencer, R. J., and F. J. Janzen. 2010. Demographic consequences of adaptive growth and the ramifications for conservation of long-lived organisms. Biological Conservation 143:1951–1959.

Stillman, R. A., and J. D. Goss-Custard. 2010. Individual-based ecology of coastal birds. Biological Reviews 85:413–434.

Stone, R., and E. Dutton. 2001. The advancing date of spring snowmelt in the Alaskan Arctic. Proc. 11th Atmospheric …:1–13.

Studds, C., and P. Marra. 2005. Nonbreeding habitat occupancy and population processes : An upgrade experiment with a migratory bird. Ecology 86:2380–2385.

Tauber, M. J., C. A. Tauber, J. P. Nyrop, and M. G. Villani. 1998. Moisture, a vital but neglected factor in the seasonal ecology of insects: hypotheses and tests of mechanisms. Environmental Entomology 27:523–530.

Thackeray, S. J., T. H. Sparks, M. Frederiksen, S. Burthe, P. J. Bacon, J. R. Bell, M. S. Botham, T. M. Brereton, P. W. Bright, L. Carvalho, T. Clutton-Brock, A. Dawson, M. Edwards, J. M. Elliott, R. Harrington, D. Johns, I. D. Jones, J. T. Jones, D. I. Leech, D. B. Roy, W. A. Scott, M. Smith, R. J. Smithers, I. J. Winfield, and S. Wanless. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16:3304–3313.

Tombre, I. M., K. A. Høgda, J. Madsen, L. R. Griffin, E. Kuijken, P. Shimmings, E. Rees, and C. Verscheure. 2008. The onset of spring and timing of migration in two arctic nesting goose populations: The pink-footed goose *Anser bachyrhynchus* and the barnacle goose *Branta leucopsis.* Journal of Avian Biology 39:691–703.

Trenberth, K. E. 2011. Changes in precipitation with climate change. Climate research, 47: 123-138.

Vautard, R., Cattiaux, J., Yiou, P., Thépaut, J. N., & Ciais, P. 2010. Northern Hemisphere atmospheric stilling partly attributed to an increase in surface roughness. Nature geoscience, 3: 756-761.

Visbeck, M., Chassignet, E. P., Curry, R. G., Delworth, T. L., Dickson, R. R., Krahmann, G., ... & Ottersen, G. 2003. The North Atlantic Oscillation: climatic significance and environmental impact. Geophys. Monogr, 134.

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

Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jónsdóttir, J. A. Klein, B. Magnússon, U. Molau, S. F. Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, Ø. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America 103:1342–1346.

Walsh, J. E., J. E. Overland, P. Y. Groisman, B. Rudolf, J. E. Walsh, J. E. Overland, P. Y. Groisman, and B. Rudolf. 2011. Ongoing Climate Change in the Arctic Ongoing Climate Change in the Arctic 40:6–16.

Wan, H., Wang, X. L., & Swail, V. R. 2010. Homogenization and trend analysis of Canadian near-surface wind speeds. Journal of Climate, 23: 1209-1225.

Warren, J. M., K. A. Cutting, J. Y. Takekawa, S. E. De La Cruz, T. D. Williams, and D. N. Koons. 2014. Previous success and current body condition determine breeding propensity in Lesser Scaup: Evidence for the individual heterogeneity hypothesis. Auk 131:287–297.

Wheat, R. E., S. B. Lewis, Y. Wang, T. Levi, and C. C. Wilmers. 2017. To migrate, stay put, or wander? Varied movement strategies in bald eagles (*Haliaeetus leucocephalus*). Movement Ecology 5:1–10.

van Wijk, R. E., A. Kölzsch, H. Kruckenberg, B. S. Ebbinge, G. J. D. M. Müskens, and B. A. Nolet. 2012. Individually tracked geese follow peaks of temperature acceleration during spring migration. Oikos 121:655–664.

Williams, T. D. 2005. Mechanisms underlying the costs of egg production. BioScience 55:39–48.

Wingfield, J. C., and K. E. Hunt. 2002. Arctic spring: Hormone-behavior interactions in a severe environment. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology 132:275–286.

Wingfield, J. C., D. L. Maney, C. W. Breuner, J. D. Jacobs, S. Lynn, M. Ramenofsky, and R. D. Richardson. 1998. Ecological bases of hormone-behavior interactions: The emergency life history stage. American Zoologist 38:191–206.

Wingfield, J. C., and R. M. Sapolsky. 2003. Reproduction and resistance to stress: When and how. Journal of Neuroendocrinology 15:711–724.

Winkler, D. W., K. M. Ringelman, P. O. Dunn, L. Whittingham, D. J. T. Hussell, R. G. Clark, R. D. Dawson, L. S. Johnson, A. Rose, S. H. Austin, W. D. Robinson, M. P. Lombardo, P. A. Thorpe, D. Shutler, R. J. Robertson, M. Stager, M. Leonard, A. G. Horn, J. Dickinson, V. Ferretti, V. Massoni, F. Bulit, J. C. Reboreda, M. Liljesthröm, M. Quiroga, E. Rakhimberdiev, and D. R. Ardia. 2014. Latitudinal variation in clutch size-lay date regressions in Tachycineta swallows: Effects of food supply or demography? Ecography 37:670–678.

Witter, M. S., and I. C. Cuthill. 1993. The ecological costs of avian fat storage. Philosophical Transactions - Royal Society of London, B 340:73–92.