Impacts de la chasse sur les paramètres **démographiques d'une espèce migratrice: Le cas de la** grande oie des neiges

Thèse

Frédéric Le**T**ourneux

Doctorat en biologie
Philosophiæ doctor (Ph. D.)

Québec, Canada

Impacts de la chasse sur les paramètres **démographiques d'une espèce migratrice**

Le cas de la grande oie des neiges

Thèse de doctorat

Frédéric LeTourneux

Sous la direction de :

Gilles Gauthier, directeur de recherche

Roger Pradel, codirecteur de recherche

Résumé

Les populations animales peuvent parfois échapper aux mécanismes naturels de régulation, souvent à la suite d'actions humaines, entrainant ainsi leur surabondance. Ceci peut mener à une surexploitation des ressources et causer d'importants dommages aux écosystèmes qui abritent ces espèces. Dans certains cas, la chasse sportive peut s'avérer un outil efficace pour contrôler les populations surabondantes, mais pour avoir du succès, il faut bien comprendre les mécanismes par lesquels cette activité affecte leur démographie. La grande oie des neiges (*Anser caerulescens atlanticus*) est un modèle idéal pour explorer ces questions car c'est une espèce longévive, surabondante, chassée, et pour laquelle on dispose d'un suivi démographique à long terme. Pour éviter des dommages irréversibles à son habitat arctique, on a libéralisé les règlements de chasse pour cette espèce en instaurant des saisons de chasse spéciales au printemps au Canada en 1999 et à l'hiver aux États-Unis en 2009. Ces manipulations à grande échelle constituent un design quasi-expérimental unique pour étudier les impacts de la chasse sur les paramètres démographiques d'une population, et comment ceux-ci peuvent varier en fonction des moments dans le cycle annuel où l'on pratique cette activité. À l'aide de ce modèle d'étude, ma thèse, vise à (1) quantifier les impacts de la chasse sportive durant la migration printanière sur le comportement et la condition physique prénuptiale des oies, un important déterminant de la reproduction, (2) évaluer la présence d'interactions possibles entre les contraintes physiologiques imposées par la chasse et le marquage des oiseaux à l'aide de marqueurs auxiliaires dans leurs effets sur la survie des oies, (3) caractériser l'impact des changements de règlements de chasse des 20 dernières années sur la survie annuelle et saisonnière des adultes et (4) comparer l'impact des conditions environnementales estivales et de la chasse sur la survie des juvéniles. Pour ce faire, j'utilise les données de capture-marquage-recapture récoltées depuis 30 ans sur la halte migratoire printanière au Québec et sur la colonie de l'Île Bylot au Nunavut. Mes travaux montrent que la saison de chasse printanière affecte la condition physique prénuptiale des oies depuis son instauration en 1999, un effet relié à l'intensité de chasse. Les oies semblent également ajuster leur prise de risque en modulant l'utilisation de ressources profitables mais à haut risque (champs agricoles) en fonction de leur condition physique. Ensuite, mes résultats révèlent que l'augmentation de l'intensité de la chasse amenée par les changements de réglementation et le marquage avec colliers sont deux sources de stress qui ont un effet synergique négatif sur la survie des oies adultes. À l'échelle saisonnière, les changements de règlements de chasse ont causé une diminution de la survie des oies durant les saisons où ils ont été instaurés. Cependant, mes résultats révèlent également une compensation de la mortalité due à la chasse entre deux saisons consécutives, un phénomène qui demeurait jusqu'ici inconnu. Cette compensation est probablement due à une vulnérabilité différentielle à la chasse dans la population plutôt qu'à des effets dépendants de la densité tel que fréquemment observé. Par contre, les conditions environnementales liées à la phénologie durant le développement des jeunes en Arctique sont le principal déterminant de leur survie la première année alors que

les changements réglementaires de chasse ont eu peu d'impacts. Ma thèse permet d'expliquer le succès de la chasse comme outil de gestion pour contrôler la population de la grande oie des neiges, mais souligne également les limites de ces mesures. En effet, mes résultats fournissent plusieurs indices que les oies ont adapté leur comportement, ce qui leur permet de compenser au moins partiellement les effets négatifs de l'augmentation de la chasse sur leur survie. Cette adaptation a permis d'atténuer l'impact négatif des actions humaines sur le paramètre démographique ayant le plus fort potentiel d'affecter la dynamique de population tel que prédit par la théorie de la canalisation environnementale.

Abstract

Animal populations can sometimes escape natural regulation mechanisms, often as a result of human action, leading to their overabundance. This can lead to overexploitation of resources and cause significant damage to the ecosystems that harbor these populations. In some cases, sport hunting can be an effective tool for controlling overabundant populations, but to be successful, one must understand the mechanisms by which this activity affects their demography. The greater snow goose (*Anser caerulescens atlanticus*) is an ideal model for exploring these issues, as it is a long-lived, overabundant, hunted species, and for which long-term demographic monitoring is available. To avoid irreversible damage to their Arctic habitat, hunting regulations for this species were liberalized by introducing a special spring hunting season in Canada in 1999 and in winter in the USA in 2009. These large-scale manipulations provide a unique, quasi-experimental design for studying the impacts of hunting on the demographic parameters of a population, and how they may vary based on the timing of the annual cycle when hunting takes place. Using this study model, my thesis aims to (1) quantify the impact of sport hunting during spring migration on the behavior and pre-breeding body condition of geese, an important determinant of reproduction, (2) assess the presence of possible interactions between the physiological constraints imposed by hunting and marking with auxiliary markers in their effects on survival, (3) characterize the impact of changes in hunting regulations over the past 20 years on the annual and seasonal survival of adults, and (4) compare the impact of summer environmental conditions and hunting on juvenile survival. To do this, I use capture-mark-recapture data collected over the past 30 years on the spring staging area in Quebec and on the Bylot Island colony in Nunavut. My work shows that the spring hunting season has affected the pre-breeding body condition of geese since its inception in 1999, an effect related to hunting intensity. Geese also seem to adjust their risk-taking behavior by modulating the use of profitable but high-risk resources (agricultural fields) based on their body condition. Secondly, my results reveal that increased hunting intensity brought by regulatory changes and collar marking results are two sources of stress that had a negative synergistic effect on adult survival. On a seasonal scale, changes in hunting regulations caused a decrease in goose survival during the seasons when they were introduced. However, my results also reveal a compensation of hunting mortalities between two consecutive seasons, a phenomenon that was not previously described. This compensation is probably due to differential vulnerability to hunting within the population, rather than to density-dependent effects as frequently reported. On the other hand, environmental conditions in the Arctic related to plant phenology during the early development of juveniles are the main determinant of survival in the first year, while changes in hunting regulations had little impact. My thesis helps explain the success of hunting as a management tool to control the greater snow goose population, but also highlights the limits of these measures. Indeed, my results provide several indications that geese have adapted their behavior, enabling them to at least partially compensate for the negative effects of increased hunting on their survival. This adaptation has allowed

mitigating the negative impact of human actions on the demographic parameter with the greatest potential to affect population growth, as predicted by the theory of environmental canalization.

Table des matières

Résumé ii
Abstract iv
Table des matières vi
Liste des tableaux x
Liste des figures xii
Remerciements xx
Avant-propos xxvi
Introduction 1
Dynamique des populations 1
Gestion des populations par la chasse sportive 4
Estimation de la survie en condition naturelles 7
Le cas de la grande oie des neiges 9
Mesures de gestion pour contrôler la surabondance des oies des neiges 12
Objectifs de la thèse 15
Chapitre 1 – COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species 17
1.1 Résumé 18
1.2 Abstract 19
1.3 Introduction 20
1.4 Methods 22
1.5 Results 27
1.6 Discussion 30
1.7 Conclusion 33
1.8 Acknowledgements 34
1.9 Supplementary material 34
1.10 Bibliography 35
Chapitre 2 – Additional data confirms the impact of the COVID19 lockdown on the behavior and fattening of migratory snow geese 39
2.1 Résumé 40
2.2 Abstract 41
2.3 Introduction 42
2.4 Methods 43
2.5 Results 45
2.6 Discussion 45
2.7 Conclusion 48

2.8 Acknowledgements 48
2.9 Supplementary material 48
2.10 Bibliograpy 49
Chapitre 3 – Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species 52
3.1 Résumé 53
3.2 Abstract 54
3.3 Introduction 55
3.4 Methods 57
3.5 Results 61
3.6 Discussion 67
3.7 Conclusion 69
3.8 Acknowledgements 70
3.9 Supplementary material 70
3.10 Bibliography 71
Chapitre 4 – Evidence for seasonal compensation of hunting mortalities in a long-lived migratory bird 74
4.1 Résumé 75
4.2 Abstract 76
4.3 Introduction 77
4.4 Methods 79
4.5 Results 82
4.6 Discussion 85
4.7 Conclusion 90
4.8 Acknowledgements 90
4.9 Supplementary material 91
4.10 Bibliography 92
Chapitre 5 – Environmental conditions outweigh the effect of hunting on juvenile survival in greater snow geese 97
5.1 Résumé 98
5.2 Abstract 99
5.3 Introduction 100
5.4 Methods 102
5.5 Results 106
5.6 Discussion 108
5.7 Conclusion 113
5.8 Acknowledgements 114
5.9 Supplementary material 114
5.10 Bibliography 115

Conclusion 121
Effets directs et indirects de la chasse sur les paramètres démographiques 121
Apprentissage et habituation à la chasse 123
La chasse: un outil de gestion puissant et flexible, mais avec ses limites 124
Importance de la saisonnalité 125
Limitations 126
Perspectives 128
Recommandations 130
Bibliographie 132
Annexe S1 – Documentation supplémentaire pour le Chapitre 1 152
Annexe S1.1 – Dates of data acquisition 153
Annexe S1.2 – Selected model to adjust mass for the effect of date 154
Annexe S1.3 – Weather data 155
Annexe S1.4 – Hunting pressure metrics 156
Annexe S1.5 – Analysis of habitat use for all GPS-marked birds 158
Annexe S1.6 – Abdominal profile scores 159
Annexe S2 – Documentation supplémentaire pour le Chapitre 2 160
Annexe S2.1 – Supplementary figures 161
Annexe S2.2 – Calculation of hunting effect on average annual body condition 162
Annexe S3 – Documentation supplémentaire pour le Chapitre 3 163
Annexe S3.1 – Multievent model definition 164
Annexe S3.2 – Harvest rate estimation 168
Annexe S3.3 – Goodness-of-fit tests 169
Annexe S3.4 – Encounter probabilities 172
Annexe S3.5 – E-SURGE syntax for model M14 (Table 3.1) 175
Annexe S3.6 – Complete model selection tables 177
Annexe S4 – Documentation supplémentaire pour le Chapitre 4 180
Annexe S4.1 – Multievent model definition 181
Annexe S4.2 – Discrete analysis of continuous live encounter data 186
Annexe S4.3 – Goodness-of-fit tests 189
Annexe S4.4 – Additional modelling considerations 192
Annexe S4.5 – Survival of collared geese and encounter probabilities for all birds 194
Annexe S4.6 – Compensation relationships 199
Annexe S4.7 – Complete model selection table 202
Annexe S5 – Documentation supplémentaire pour le Chapitre 5 203
Annexe S5.1 – Multievent model definition 204
Annexe S5.2 – Encounter and emigration probabilities 206

Annexe S5.3 – Relationships between phenology and hatching 209
Annexe S5.4 – Model validation: analysis of simulated data 211
Annexe S5.5 – Trace plots and density plots from the analysis of the real dataset 218

Liste des tableaux

CHAPITRE 1

Table 1.1 Parameter estimates of the linear mixed model comparing adjusted body mass of greater snow geese among years. *Intercept (2020)* represents the average body condition (in g) in 2020. Other estimates represent the difference (in g) in average body condition with 2020. Estimates in bold are significantly different than 2020 (n = 3460). 28

Table 1.2 Parameter estimates of the linear mixed model testing the influence of year, date and their interaction on adjusted body mass of greater snow geese. *Date(2020)* is the average daily increase in body condition (g/d) in May 2020. The interactions *date*2007 – 2009* and *date*2019* represent differences in daily increase in body condition between 2020 and 2007 – 2009 or 2019, respectively. Significant effects are in bold. Model parameters other than effects of interest are in pale gray (n = 2616). 29

CHAPITRE 3

Table 3.1 Results of model selection for the analysis of collar loss, survival, and live and dead encounter in adult female greater snow geese marked between 1990 and 2018. For each model, deviance, number of estimated parameters (NP) and difference in QAIC (ΔQAIC) with the most parsimonious model (M14) are provided. The complete model selection is provided in Table S3.3. 62

CHAPITRE 4

Table 4.1 Results of model selection for the analysis of seasonal survival, live encounter (physical capture of leg-ringed-only birds), and dead encounter (recovery) probabilities of adult greater snow geese marked between 1990 and 2018. For each model, deviance, number of estimated parameters (K) and difference in QAIC (ΔQAIC) between the current and the most parsimonious model (M10) are provided. Full time variation and heterogeneity in interaction with seasons was applied to live encounter probabilities of collared birds in all models. The complete model selection is provided in Table S4.3. 83

CHAPITRE 5

Table 5.1 Reclassification of mismatch values into 11 bins to model the effect of trophic mismatch on survival of juvenile greater snow geese. The Value in model column shows the mismatch value used as the mismatch covariate in the model for individuals classified in each bin. This was done to estimate a continuous mismatch effect. Bins 3 to 9 represent observed mismatch values from birds of known age. Bins 1, 2, 10 and 11 were added to allow predicted ages to yield mismatch values beyond those observed. 106

ANNEXE S3

Table S3.1 Multi-state goodness-of-fit test and variance inflation factors calculated for our dataset of adult female greater snow geese marked from 1990 to 2018 on Bylot Island. Test 3G examines homogeneity in survival between newly marked and previously marked individuals while test M verifies homogeneity of re-encounter between captured and missed individuals on each occasion. For each test component, chi-squared test statistic (χ^2), degrees of freedom (df) and p-values (*p*) are provided. *Overall ĉ* is the overall variance inflation factor and *Adjusted ĉ* is the variance inflation factor adjusted for inclusion of heterogeneity in live-encounter probabilities (see text). 170

Table S3.2 Results of the general model with and without heterogeneity in live-encounter probabilities. Both models have the same structure for collar loss, survival, live-encounter and dead recovery probabilities than model M1 (Table 3.1) except for heterogeneity on live-encounters. 171

Table S3.3 Complete set of models tested for the analysis of collar loss, survival, and live- and dead-encounter probabilities in adult female greater snow geese marked between 1990 and 2018. For each model, deviance, number of estimated parameters (NP) and difference in QAIC (ΔQAIC) with the most parsimonious model (M13) are provided. Models already present in Table 3.1 are identified by their names in column 'Name'. 177

Table S3.4 Complete set of models tested for the analysis of hunting and natural mortality probabilities in adult female greater snow geese marked between 1990 and 2018. Constraints on collar loss were identical to model M14 in Table 3.1. For each model, deviance, number of estimated parameters (NP) and difference in QAIC (ΔQAIC) with the most parsimonious model (P10) are provided. 179

ANNEXE S4

Table S4.1 Results of the goodness-of-fit test for multi-state models and variance inflation factors computed for encounter histories of adult greater snow geese marked between 1990 and 2018. Tests were conducted separately for leg-ringed-only males and females (because their live encounter probabilities are estimated separately in all models) and for collared females (because they can be observed during all encounter occasions unlike birds wearing only a leg-ring). For leg-ringed-only birds, GOF tests were conducted on an annual dataset because Test M fails when individuals are not detectable in all occasions. For all groups and all test components, the chi-squared statistic (χ^2), degrees of freedom (df) and p-values (p) are provided. *Overall ĉ* is the variance inflation factor calculated from overall GOF tests and *Adjusted ĉ* is the inflation factor corrected for the inclusion of heterogeneity in live-encounter probability in our model (see text for calculation). 190

Table S4.2 Number of parameter and deviances of models with the same constraints except for the presence of heterogeneity in live-encounter probabilities (K = number of parameters). 191

Table S4.3 Complete results of model selection for the analysis of seasonal survival and dead encounter (recovery) probabilities of adult greater snow geese marked between 1990 and 2018. For each model, model number from Table 4.1 in the main text, number of estimated parameters (K) and difference in QAIC (ΔQAIC) between the current and the most parsimonious model (M10) are provided. Full time variation and heterogeneity in observation in interaction with seasons was applied to live encounter probabilities of collared birds in all models. Similarly, full time variation for summer occasions, heterogeneity in live encounter probability and a sex effect were applied to live encounter of leg-ringed-only birds in all models, except for model M1 where the sex effect was absent. 202

Liste des figures

INTRODUCTION

Figure 0.1 Taille de population de la grande oie des neiges au printemps entre 1967 et 2023. Les estimations sont fournies par le Service Canadien de la Faune et sont obtenues par survol aérien (détails dans l'Appendice S3.2). 11

CHAPITRE 1

Figure 1.1 Map of the breeding (purple), wintering (yellow) and staging areas (red star) of the migratory greater snow goose population. The hatched polygon represents the migratory flyway. This map was modified from Lefebvre et al. (2017)..... 23

Figure 1.2 Locations of the four GPS-collared snow geese tracked near the end of the staging period from May 6th to 24th in both 2019 (green dots) and 2020 (orange dots) in the St. Lawrence estuary. All geese were captured and marked at Île-aux-Oies, which explains the larger concentration of dots there in 2019, the year of marking. Restricting the analysis to only the Île-aux-Oies area did not affect the proportion of locations in agricultural fields in either year. Window: average daily proportion of locations recorded in fields by the same individuals (*n*=4) tracked in 2019 and 2020. Error bars are 95% CI and colored shading represents the density distribution of individual data points. 24

Figure 1.3 A: Annual spring harvest of greater snow goose from 1999 to 2020. Error bars represent 95% confidence intervals. Colored bars represent years for which data on body condition is available. B: Spring body condition of geese at the end of the staging period in relation to annual spring harvest. Values at 0 harvest (white violin) correspond to years without a spring Conservation Harvest (before 1999). The black line represents the mean model predictions based on individual data points with its 95% CI (shaded; regression slope [95%CI]: -0.009 g/goose harvested [-0.012, -0.006], n = 3460). Black dots and error bars are the mean body mass with their 95% CI for each harvest level and color shading represents the density distribution of individual data points. Source of hunting statistics: Smith and Gendron 2020. 27

Figure 1.4 Annual variation in greater snow goose body condition index during spring migratory stopover in Québec. Points are individual body masses corrected for skeletal size and adjusted to May 12th. The black dots and error bars represent average annual body mass with their 95% confidence intervals. 29

Figure 1.5 Body condition index (mass corrected for body size) of greater snow geese in relation with date for 2019 (green), 2020 (orange) and years with a spring Conservation Harvest and sampling dates comparable to 2020 (2007 – 2009; grey). Lines are the mean model predictions with their 95% CI (shading) and represent the increase in goose body condition at the end of their migratory stopover in Québec. Full lines represent significant relationships and the dashed line a non-significant relationship (2020)..... 30

CHAPITRE 2

Figure 2.1 Impacts of spring hunting pressure on body condition and behavior of spring-staging greater snow geese. A: Annual spring harvest of greater snow geese. Error bars are the upper 95% confidence intervals. Data obtained from Smith and Gendron (2022). B: Relationship between body condition index of captured geese and day of the year for 2019 (green), 2020 (orange), 2021 (blue), 2022 (purple) and other years with sampling dates comparable to 2020 (2007-2009; gray). Lines are the model prediction for each year along with their 95% confidence intervals (shading). The dotted line (2020) indicates a non-significant relationship. Individual data points for 2007-2009 were omitted to reduce clutter but are presented in LeTourneux et al. (2021). Day of year 132 = 12 May. C: Daily proportion of time spent in agricultural lands near the end of spring staging determined by radio-tracking in 2019 (n=10 birds), 2020 (n=7) and 2021 (n=7). Black dots are the mean model prediction by year with their 95% CI. Violins represent the distribution of individual data points. No comparable habitat use data is available for 2022. 46

CHAPITRE 3

Figure 3.1 Effect of neck collars on survival probability of adult female greater snow geese marked between 1990 and 2016. A: Effect of collar on survival probability for three periods defined by different hunting regulations. Points represent the coefficient of the collar effect (β_{col}) estimated by model M15 (Table 3.1). B: Annual survival probabilities from the best-supported model (M14, Table 3.1). Dashed lines separate the three time periods with different hunting regulations. Error bars are 95% C.I. 63

Figure 3.2 Effect of neck collars on hunting mortality probability of adult female greater snow geese marked between 1990 and 2016. A: Effect of collar on hunting mortality probability for three periods defined by different hunting regulations. Points represent the coefficient of the collar effect (β_{col}) estimated by model P5 (Table S3.4). B: Annual hunting mortality probabilities from the best-supported model (P10, Table S3.4). Dashed lines separate the three time periods with different hunting regulations. Error bars are 95% C.I. 64

Figure 3.3 Effect of neck collars on annual non-hunting mortality probability of adult female greater snow geese marked between 1990 and 2016. A: Effect of collar on natural mortality probability for three periods defined by different hunting regulations. Points represent the coefficient of the collar effect (β_{col}) estimated by model P5 (Table S3.4). B: Annual non-hunting mortality probabilities from the best-supported model (P10, Table S3.4). Dashed lines separate the three time periods with different hunting regulations. Error bars are 95% C.I. 65

Figure 3.4 Difference in mean annual mortality probability between each 'treatment' group and the 'control' group based on estimates of model M17 (Table 3.1). The 'control' group refers to non-collared birds during period 1 (1990-1998), when hunting regulations were not yet liberalized. Error bars are the upper 95% CI. 66

CHAPITRE 4

Figure 4.1 Graphical representation of the data sampling design. The circle depicts the information available for each season, and the length of each arrow represents the relative length of each season. The timeline indicates hunting periods with the hunting regulations associated with each. 82

Figure 4.2 Seasonal survival estimates of leg-ringed adult greater snow geese between 1990 and 2019. The dotted line represents survival estimated from our best supported model (M10; Table 4.1) with its 95% confidence intervals (shading). Points represent yearly survival estimates from model M6 along with their 95% CI. 85

Figure 4.3 Relationship between spring and winter mortality estimates of adult greater snow geese between 1999 and 2018, after implementation of special hunting seasons in Canada only (spring only, 1999-2008, closed dots) and in Canada and USA (spring and winter, 2008-2019, open dots). Error bars are 95% C.I. of annual survival estimates computed as 1-survival from model M6 (Table 4.1). The black line represents the mean bootstrapped slope estimated from 10 000 simulations (see methods; β [95%CI] = -0.58 [-1.19, 0.02]). The gray shading represents the central 95% of the bootstrapped relationships..... 86

Figure 4.4 Annual survival estimates of leg-ringed adult greater snow geese between 1990 and 2019. Annual values were reconstructed from seasonal survival presented in Fig. 4.2 (see methods). The dotted line represents survival estimates calculated from our best supported model (M10; Table 4.1) with its 95% confidence intervals (shaded area). Points represent yearly survival estimates calculated from model M6 along with their 95% CI. 87

CHAPITRE 5

Figure 5.1 Annual survival probability estimated for adult (orange) and juvenile (blue) greater snow geese marked on Bylot Island between 1991 and 2018. Error bars are 95% credible intervals. 107

Figure 5.2 Relationship between annual survival of juvenile greater snow geese and the mismatch between hatching date and date of peak plant quality (A and C), or the annual date of peak plant quality (day of the year), an index of spring phenology (B and D). The black lines represent mean model predictions with their 95% credible interval (shaded area) over the range of observed mismatch or spring phenology values with all other

covariates held constant. A positive mismatch indicates that goslings hatch after the peak in plant quality. Dots represent mean annual survival estimates along with their 95% credible intervals (error bars) plotted against the mean annual value of the environmental covariate in that year. In (A) and (B), mean annual survival predictions are obtained with all covariates included in the model whereas in (C) and (D), the predictions are obtained by holding the date of peak plant quality and the mismatch constant, respectively. 109

Figure 5.3 Relationship between annual survival of juvenile greater snow geese and mismatch between hatching date and date of peak plant quality, and spring phenology (date of peak plant quality; day of the year) simultaneously. The surface represents the model prediction for annual survival based on the mismatch and spring phenology covariates only. Red dots are annual survival estimates and black dots are predictions from the model for the corresponding values of annual mismatch and spring phenology (i.e. black dots are located on the 3D surface). Black lines link survival estimates (red) to model predictions (black). 110

ANNEXE S1

Figure S1.1 Period for which body condition data were available between 1979 and 2020. Each dot represents a day when geese were captured (i.e. one cannon-netting event). The line shows the time period between the first and the last goose captures every year. 153

Figure S1.2 Body mass adjusted for skeletal size in relation with day of year in greater snow geese weighed between 1979 and 2020. Points represent individual body masses corrected for skeletal size. The line represents the prediction of the best polynomial regression of mass on day of year..... 154

Figure S1.3 Spring weather data from three meteorological stations located in the staging area used by greater snow geese in southern Québec for 2010-2020. Years 2019 and 2020 are highlighted in green and orange, respectively. Horizontal dotted lines represent the 10-year mean. A: Annual variation in snowmelt date for three cities located along the staging area used by geese between 2010 and 2020. B: Annual variation in mean monthly temperatures of three cities located along the staging area used by geese for March, April and May. Source: https://climate.weather.gc.ca/historical_data/search_historic_data_e.html 155

Figure S1.4 Effect of hunting pressure on goose spring body condition using number of active spring hunters. A: Annual numbers of active greater snow goose hunters in spring from 1999 to 2020. Error bars represent 95% confidence intervals. Colored bars represent years for which data on body condition is available. B: Spring body condition of geese at the end of the staging period in relation to annual number of active hunters in spring. Values at 0 active hunters (white violin) correspond to years without a spring Conservation Harvest (before 1999). The black line represents the mean model predictions based on individual data points with its 95% CI (shaded; regression slope [95%CI]: -0.05 g/active hunter [-0.07, -0.03], n = 3460). Black dots and error bars are the mean body mass with its 95% CI for each number of active hunter level and color shading represents the density distribution of individual data points. Source of hunting statistics: Smith and Gendron 2020. 156

Figure S1.5 Effect of hunting pressure on goose spring body condition using number of spring hunting days. A: Annual numbers of greater snow goose hunting days in spring from 1999 to 2020. Error bars represent 95% confidence intervals. Colored bars represent years for which data on body condition is available. B: Spring body condition of geese at the end of the staging period in relation to annual number of spring hunting days. Values at 0 hunting days (white violin) correspond to years without a spring Conservation Harvest (before 1999). The black line represents the mean model predictions based on individual data points with its 95% CI (shaded; regression slope [95%CI]: -0.010[-0.014, -0.007] g/hunting day, n = 3460). Black dots and error bars are the mean body mass with its 95% CI for each number of hunting days level and color shading represents the density distribution of individual data points. Source of hunting statistics: Smith and Gendron 2020. 157

Figure S1.6 Average daily proportion of locations recorded in fields by GPS-marked geese in 2019 (*n*=10) and 2020 (*n*=5) near the end of the staging period. Error bars are 95% CI and colored shading represents the density distribution of data points. 158

Figure S1.7 Abdominal profile scores of greater snow geese in relation with day of year during spring staging in southern Québec in 2020. Profile score increased exponentially with days (Poisson regression; day-effect

estimate [95%CI] = 1.012 [1.010, 1.014]) going from an average score of 2 in early April to an average score of 3.5 in early May. 159

ANNEXE S2

Figure S2.1 Dates when goose body condition data are available each year between 2007 and 2022. Points represent days when goose captures occurred at Île-aux-Oies, Québec, Canada. The line represents the period covered by goose captures every year. 161

Figure S2.2 Relationship between average annual body condition of greater snow geese captured at the end of staging and yearly harvest by hunters between 1979 and 2022. Points are the average yearly condition estimates with their 95% C.I. The line represents the mean bootstrapped slope estimated from 10,000 simulations. The gray shading represents the central 95% of the bootstrapped relationships. Slope: -0.008 [-0.010, -0.006], R^2 = 0.68 [0.51, 0,83]. See above text for details on calculation of the slope value, coefficient of determination (R^2) and their respective 95% C.I. Values at 0 on the X axis correspond to years without spring hunting, before 1999. 162

ANNEXE S3

Figure S3.1 Point estimates of encounter probabilities (physical recaptures) of non-collared adult female greater snow geese marked between 1990 and 2016 and encountered from 1991 to 2017 on Bylot Island, Nunavut. Error bars are 95% C.I. Estimates were obtained from model M14 (Table 3.1)..... 172

Figure S3.2 Point estimates of encounter probabilities (physical recaptures and resighting) of adult female greater snow geese marked with collars between 1990 and 2016 and encountered from 1991 to 2017 on Bylot Island, Nunavut. Error bars are 95% C.I. Estimates were obtained from model M14 (Table 3.1)..... 173

Figure S3.3 Point estimates of hunting recovery probabilities of adult female greater snow geese marked between 1990 and 2016 on Bylot Island, Nunavut and recovered from 1990 to 2017. Error bars are 95% C.I. Estimates were obtained from model M14 (Table 3.1). 174

ANNEXE S4

Figure S4.1 Comparison of the distribution of greater snow goose encounters in the real and simulated datasets according to week of the year. Annual distribution of A: observations of birds marked with neck collars between 1990 and 2019, B: observation of collared birds from simulated datasets, C: recoveries of birds shot between 1990 and 2019, D: recoveries from simulated datasets. Yellow is used for encounters occurring during the summer seasons, orange during the fall, blue during winter and green during spring..... 187

Figure S4.2 Frequency distribution of bias in average seasonal survival estimated for 200 datasets simulated and subsequently analyzed with E-Surge for summer, fall, winter, and spring. Bias is the difference between estimated survival in each simulation and the 'true' survival used to generate simulated datasets. The dashed lines are the mean bias over all simulations for each season..... 188

Figure S4.3 Seasonal live encounter estimates of collared greater snow geese for highly- and weakly-observable groups between 1990 and 2019 from model M10 (Table 4.1). Summer live encounters pool physical recaptures and observations while only observations are available in the other seasons. Points represent annual estimates with their 95% confidence intervals (error bars)..... 194

Figure S4.4 Summer live encounter estimates (physical recapture) of male and female leg-ringed-only greater snow geese for highly- and weakly-observable groups between 1990 and 2019 from model M10 (Table 4.1). Points represent annual estimates with their 95% confidence intervals (error bars)..... 195

Figure S4.5 Seasonal recovery estimates of leg-ringed only and collared greater snow geese between 1990 and 2019 from model M10 (Table 4.1). Points represent annual estimates with their 95% confidence intervals (vertical bars)..... 196

Figure S4.6 Seasonal survival estimates of greater snow geese between 1990 and 2019 from model M6, Table 4.1 (yellow: leg-ringed-only males and females, blue: collared females; pink: both groups combined). The shaded area represents the 95% C.I. of survival estimates from the most parsimonious model, where survival is constrained equal for time periods with similar hunting regulations (model M10, Table 4.1). Points represent annual survival estimates with their 95% confidence intervals (error bars)..... 197

Figure S4.7 Comparison of annual survival estimates of leg-ringed-only adult greater snow geese obtained from the annual dataset (red; from LeTourneux et al., 2022) and reconstructed from the seasonal estimates (blue; this study, see Fig. 4.4). Points represent annual survival estimates with their 95% confidence intervals (red: model M14 in Table 3.1 (Chapter 3); blue: model M6 in Table 4.1, this study). The shaded area represents the 95% C.I. of survival estimates for models where survival is constrained equal for time periods with similar hunting regulations (red: model M17, Table 3.1 (Chapter 3); blue: model M5, Table 4.1, this study). 198

Figure S4.8 Relationship between winter and fall mortality estimates of adult greater snow geese between 1999 and 2018, after implementation of special hunting seasons in Canada only (spring, 1999-2008, closed dots) and in Canada and USA (spring and winter, 2008-2019, open dots). Error bars are 95% C.I. of seasonal survival estimates computed as 1-survival from model M6 (Table 4.1). The dashed line represents the mean bootstrapped slope estimated from 10 000 simulations (see methods; β [95%CI] = -0.03 [-0.27, 0.21]). The gray shading represents the central 95% of the bootstrapped relationships..... 199

Figure S4.9 Relationship between spring and fall mortality estimates of adult greater snow geese between 1999 and 2018, after implementation of special hunting seasons in Canada only (spring, 1999-2008, closed dots) and in Canada and USA (spring and winter, 2008-2019, open dots). Error bars are 95% C.I. of seasonal survival estimates computed as 1-survival from model M6 (Table 4.1). The dashed line represents the mean bootstrapped slope estimated from 10 000 simulations (see methods; β [95%CI] = -0.05 [-0.41, 0.31]). The gray shading represents the central 95% of the bootstrapped relationships..... 200

Figure S4.10 Relationship between annual survival probability estimates and harvest rate of adult greater snow geese between 1999 and 2018, after implementation of special hunting seasons in Canada only (spring, 1999-2008, closed dots) and in Canada and USA (spring and winter, 2008-2019, open dots). Error bars are 95% C.I. of annual survival estimates computed from seasonal estimates of model M6 (Table 4.1). The dashed line represents the mean bootstrapped slope estimated from 10,000 simulations (see text above; β [95%CI] = 0.4 [-0.6, 1.5]). The gray shading represents the central 95% of the bootstrapped relationships. 201

ANNEXE S5

Figure S5.1 Annual live encounter probability estimates for highly capturable (circles) and weakly capturable (triangles) male (green) and female (yellow) adult greater snow geese captured in banding drives at the end of the breeding season on Bylot Island between 1991 and 2019. Error bars are 95% credible intervals. 206

Figure S5.2 Annual recovery probability estimates of adult (orange) and juvenile (blue) greater snow geese marked on Bylot Island between 1990 and 2018. 207

Figure S5.3 Probability estimates of adult and juvenile male and female greater snow geese marked on Bylot Island between 1990 and 2018 to belong to different states. Points are mean model estimates and error bars are 95% credible intervals. A: Probability of belonging to the state Adult Alive and highly-capturable. Details in Appendix S5.1. B: Probability of transition to the state 'Adult Alive Emigrated' from other alive states (i.e., permanent emigration)..... 208

Figure S5.4 Relationship between hatching date of greater snow geese and plant phenology on Bylot Island between 1990 and 2019. Figure updated from Doiron et al. (2015). A: Time series of median hatching date (open dots) and date of peak plant quality derived from NDVI data ($NDVI_{50}$ date, see text; closed dots). B: Relationship between annual median hatching date and date of peak plant quality (blue line, relationship: predicted hatching date = 143 + 0.26*$NDVI_{50}$ date, R^2 = 0.29) and its 95% C.I. (shading). The dotted line represents a 1:1 relationship. 209

Figure S5.5 Relationship between individual mismatch values (difference between individual hatching date and annual date of peak plant quality) and annual date of peak plant quality for known-age, juvenile greater snow geese recaptured at the end of brood rearing on Bylot Island (Nunavut) between 1991 and 2019. Colors are used to differentiate years. A small jitter was used to better appreciate the distribution of mismatch values for every date of spring phenology. 210

Figure S5.6 Trace plots (left, A to N) and density plots (right, O to AB) of parameters linked to heterogeneity in live encounter probability from the analysis of the simulated dataset (see text). The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot. The red dashed lines represent input parameter values. 212

Figure S5.7 Simulated (red) and estimated (black) values of annual survival for adults (circles) and juvenile (triangles) from the analysis of the simulated dataset (see text). Error bars are the 95% credible intervals... 216

Figure S5.8 Relationship between annual survival probability and the mismatch (differences between hatching date and date of peak plant quality) from the analysis of the simulated dataset (see text). The black line represents mean model predictions along with its 95% credible interval (gray shading). The red dotted line represents the simulated relationship between annual survival and the trophic mismatch. 217

Figure S5.9 Trace plots (left, A to D) and density plots (right, E to H) of model parameters for the age estimation model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot. 218

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot. 219

Cette thèse est dédiée à 7 personnes sans qui les étoiles ne se seraient jamais enlignées pour que je chemine jusqu'ici.

Terry Wheeler et Chris Buddle,
qui m'ont mis l'Arctique en tête,

James Junda et David Bird,
qui m'ont transmis leur obsession des oiseaux,

Murray Humphries et Chris Solomon,
qui m'ont inspiré leur passion de la science et de l'étude de la faune,

et Louise, ma mère,
qui m'a encouragé et soutenu dans mes choix de cheminement depuis le premier jour.

« Je viens souvent ici pour essayer de voir où se trouvent les plus fortes densités d'oies dans 'Goose Paradise' et la plaine adjacente avant d'y descendre pour lire des colliers. Je m'assois toujours sur cette grosse roche plate, foncée, légèrement inclinée vers le sud. À la fin des après-midis ensoleillés elle est toujours surprenamment chaude dans la Toundra si froide.

J'aime bien cet endroit.

Une mousse verte, presque fluorescente, s'étend à nos pieds en contrebas et tente de s'approprier doucement le gris lit de la rivière.

Les graminées dorées s'étendent vers l'Ouest à perte de vue et forment un tapis fébrile qui vibre au gré des bourrasques.

Au Sud au pied du plateau s'avancent les vastes marais de Goose Paradise, parsemés d'oies qui ornent les polygones de petits picots blancs.

À l'horizon, les plateaux de Baffin glacés, étincelants, semblent crouler sous le poids du ciel qu'ils tiennent en respect depuis les temps immémoriaux.

J'aime bien cet endroit. Le temps s'y arrête.

Quand je quitte, j'en viens toujours à envier ma roche qui reste ici se faire griller au soleil tous les après-midis. Je crois que je pourrais me satisfaire… De rester ici et contempler ce spectacle éternel.

C'est sans doute la dernière fois que je m'assois sur cette roche. Mais j'ai espoir qu'en griffonnant ces quelques lignes, j'arrive à continuer de venir m'assoir ici, de temps en temps. »

– Carnet de terrain 2022, Frédéric LeTourneux

Remerciements

Un doctorat c'est le résultat du travail acharné d'une personne, mais aussi du soutien qu'elle reçoit des gens qui l'entourent et l'épaulent durant son parcours. Je trouve qu'une thèse, la mienne en tout cas, représente bien cela. Quand je feuillette ma thèse, je vois le temps et l'effort que j'y ai mis, je me souviens des longues heures passées à relire un article avant de l'envoyer à l'édition, à éplucher les forums statistiques pour décider de la meilleure méthode pour faire une analyse, à trouver le bon mot pour décrire le fond de ma pensée. Mais sur quasiment chacune des 225 pages de ce document, je trouve aussi toujours un indice de la contribution de mon entourage à mon doctorat. Une bonne tournure de phrase suggérée par un·e co-auteur·e, une analyse de plus proposée par un·e collègue qui vient donner tout leur sens aux autres résultats, une manière de construire un graphique conseillée par un·e ami·e pour mieux visualiser ce qu'il y a à montrer. Ma thèse est le résultat de contributions de beaucoup de gens.

Je me permets un dernier aparté avant d'entrer dans les remerciements. Un doctorat c'est beaucoup plus que 200 pages de science. C'est 5, 6, 7 ans d'une vie. Sept années durant lesquelles tant de choses se passent qu'il est difficile de se remémorer c'était comment la vie avant. Il se passe des joies, des peines, des moments excitants, des déceptions. Certaines choses liées à notre projet, d'autres pas du tout, mais c'est un peu à cause de ce projet qu'on est rendu là où on est et qu'on vit ces moments. J'encourage tous ceux qui liront ceci à se rappeler de profiter de ces moments, et de cette liberté qu'on peut se permettre au doctorat, même si des fois on a très hâte de passer à autre chose.

Les gens qui nous épaulent à travers ces moments forts, surtout les plus difficiles font aussi partie de ceux qui contribuent au succès d'une thèse.

Gilles. Gillos, Guilles, D-Dgilles, le parrain de l'Arctique. Je perds le compte des surnoms qu'on t'a donnés après toutes ces années, mais je voulais les écrire ici pour en avoir une trace écrite. Il y a 8 ans dans la toundra entre deux hélicos, tu m'as offert de faire un projet de maîtrise sous ta supervision alors que c'était seulement la deuxième fois que je te rencontrais. Je n'avais pas de réelle intention de poursuivre en science (je ne pensais pas vraiment en avoir les capacités) et ça m'est tombé dessus comme une tonne de briques. Sept années, quelques articles scientifiques, un paquet de présentations et une thèse plus tard, je commence finalement à croire en mes capacités de chercheur. Du haut de tes *quelques* années d'expérience, tu as su jauger quand j'avais besoin d'encadrement mais surtout quand il valait mieux me laisser cheminer par moi-même. Cela m'a permis d'accomplir de grands pans de ma thèse presqu'exclusivement par moi-même, apprendre à faire des modèles de capture-recapture, apprendre à faire des statistiques tout court. Je regarde en arrière et je suis fier de ce que j'ai accompli, mais je ne pense pas que j'y serais arrivé sans ton soutien aux moments clé. Je ne crois pas que j'aurais eu le courage d'avancer ainsi sans savoir que tu étais derrière moi et prêt à réagir au besoin.

Et besoin j'ai eu! C'était impressionnant de voir comment tu avais toujours le bon conseil, la bonne tournure de phrase, la bonne prochaine étape pour avancer. J'ai été vraiment fortuné d'avoir un chercheur de ta carrure comme soutien tout au long de mon projet. Je ne répèterai pas tout ce que j'ai écrit dans ton livre de retraite, mais merci d'avoir géré Bylot comme tu l'as fait. Cette immersion en Arctique, loin de tout, avec les autres Bylotiens, relativement maîtres de nos destins (malgré les 2 jours de réunions pré-Bylot, les 50 pages de consignes de fonctionnement de la station et les 200 pages de protocoles scientifiques lol) a permis de tisser des liens entre les gens qui dureront toute une vie. Je n'ai pas vécu d'autre expérience semblable, merci pour ça. Finalement, merci pour ton dévouement, à la science mais surtout à tes étudiants. On regarde autour de nous et au labo, on s'est tous comptés vraiment chanceux d'avoir un directeur comme toi.

Roger! Le gourou de la capture-recapture. J'ai tellement apprécié notre collaboration. Tu es la seule personne avec qui je pouvais discuter de capture-recapture, de modélisation, de bayésien, de Nimble, sans avoir à m'expliquer 3 fois avant que tu comprennes le fond de ma pensée. Même si je travaillais avec des modèles extrêmement complexes, ça ne te prenait jamais plus que 2 minutes pour comprendre ce que j'essayais de t'exposer et on pouvait ensuite entrer dans le vif du sujet. Ton apport à ma thèse et à mes connaissances statistiques a été considérable et je te remercie du temps que tu as pris pour cheminer avec moi.

Les deux MC! Marie-Christine, Marie-Claude, on vous le répète tout le temps, mais c'est comme si vous ne voulez pas l'entendre. Ce labo ne serait jamais ce qu'il est sans vous! Marie-Christine, tel Atlas, tu portes sur tes épaules la base de données des oies (et autres bibittes qu'on retrouve à Bylot) que tu tiens à jour religieusement (ou presque) à chaque année. Mais au contraire d'Atlas qui ne porte que la Terre sur son dos, tu portes également sur tes épaules toute la coordination du terrain à Bylot, celle du labo, et celle de tous les autres labos! Et maintenant on peut rajouter Pierrot… Sans ton aide le parcours des étudiants du labo serait pas mal plus laborieux. Merci pour tout Marie-Christine, on a passé des bons moments! Les colleux de genoux au baguage, les rires de l'hélico quand on se plante en courant après les oies, les vidanges de trappe à graisse et de la chapelle, les différents horaires qui se croisent à 5h du matin dans la cuisine du camp... merci!

Pas de Marie-Claude, pas d'Île-aux-oies. Merci pour ta gestion de terrain à l'IAO. On a eu tellement de plaisir tout en travaillant fort, c'est vraiment le meilleur des mondes! Ah non attends c'est vrai, toi tu faisais rien de tes journées, t'étais en vacances ;) . Merci pour tous tes enseignements, tant culinaires que terrain. Merci pour tes encouragements continuels et merci pour les belles journées. Mais surtout, merci pour cette belle amitié!

Josée Lefebvre. On n'a pas élevé les poules ensemble, mais on en a bagué des oies par exemple, pis c'est encore mieux! Merci de m'avoir montré tous les rouages du baguage d'oies. Si je me sens à l'aise aujourd'hui de partir mon propre programme de baguage, c'est en grande partie grâce à toi. Merci pour ton soutien et tes retours rapides chaque fois que j'avais besoin des données du SCF. Tu es aussi un important pilier de mon doc,

tu as la mémoire institutionnelle de tout ce qui s'est passé avec les oies et les différents acteurs depuis 20 ans. J'ai bien apprécié collaborer avec toi et j'espère qu'on en aura l'occasion à nouveau dans le futur.

Olivier Gimenez. Merci pour ton accueil chaleureux dans ta super équipe à Montpellier. J'ai eu la chance durant ma thèse de côtoyer plusieurs chercheurs qui ont comme priorité le bien-être de leur équipe et de leurs étudiants, et tu en fais définitivement partie. J'ai été impressionné par ta philosophie de la science, de ton partage de tes connaissances et de tout ton travail pour les rendre le plus accessible possible. Tu es un chercheur inspirant et j'espère que ta manière de procéder deviendra la règle plutôt que l'exception dans le futur. Merci pour ça!

La gang de Montpel. Val, Seb, Maud, Oksana, Gilles, Julie, merci pour votre accueil au labo (et à la Roqueturière!) à Montpellier. Je me suis senti comme si j'avais toujours travaillé dans votre équipe dès le départ, et on s'est bien marrés. Merci pour les cafés, le birding, les soirées, la manière de vivre méditerranéenne.

Les sept années de ma thèse ont été un long parcours d'apprentissage de statistiques, auxquelles je ne connaissais rien au départ. Plusieurs personnes ont contribué à cet apprentissage et sans elles je n'aurais pas les connaissances assez poussées que j'ai réussi à acquérir dans les dernières années. Merci d'abord à Rémi Choquet pour ton soutien avec E-Surge et R2Esurge. Tu as répondu à tellement de courriels avec des questions de formulation, de fonctionnement du programme, de déboggage, sans ton aide je ne pense pas que j'aurais pu continuer à utiliser ce programme.

Thanks to the CrossValidated community, and in particular to Ben Bolker for your active presence on this forum. I have spent countless hours on CV looking for information on how to perform proper statistical tests. I was always relieved when Ben Bolker had posted an answer as they were always clear, straight to the point and they were pieces of information I knew I could rely on. You have unknowingly supported me through long evenings of decision-making on how to best analyze certain datasets and interpret the results from mixed models, so thanks for that.

Thanks to the Nimble development team (Perry deValpine, Chris Paciorek, Daniel Turek and the others from the Nimble community) for their instantaneous support on the Nimble users forum. Your support to every user with a question in debugging nimble code and in statistical and modelling decision-making makes Nimble a great tool that will undoubtedly become widely used in the future. Thank you for your dedication to the community, you made my fifth chapter possible.

Mon cheminement statistique aurait été (encore) plus compliqué et ardu sans l'aide de Marc Mazerolle et Sandra Hamel. Même si vous n'aviez aucune responsabilité envers moi, vous avez tous les deux pris du temps à plusieurs reprises ces 7 dernières années pour répondre à mes questionnements statistiques, des fois justifiés, des fois loufoques, mais vous avez été un support disponible à tout moment et j'ai vraiment apprécié nos

discussions stats, sur ce en quoi on peut ou on peut moins avoir confiance. Vous avez été mon plan de contingence, les gens de confiance sur qui je pouvais compter pour me ré-enligner sur mes stats quand j'étais perdu dans un dédale de questions-réponses sur CrossValidated. Ces petits meetings de 15-20-30 minutes (1h?) auront vraiment fait une différence. Marc, merci aussi pour tes cours limpides d'introduction aux stats en écologie. Ces deux cours ont été la pierre angulaire de mon apprentissage des stats.

Cynthia Reséndiz-Infante. I don't know what you have seen in me in that interview back in 2015 but thank you for having picked me as your field assistant for Bylot. Sometimes small innocent decisions create ripples that can change the course of a life, and this was definitely the case for me. I would not be here today if not for you. Thank you for teaching me the ropes of goose nest monitoring and making me discover Bylot, and to have prepared me for what was awaiting me with E-Surge.

La famille du Winneux Lab. Je dis famille parce que c'est vraiment comme ça que je me sens. Merci pour ces années incroyables, pour les innombrables fous rires et pour la meilleure ambiance de labo qu'un étudiant gradué puisse espérer. Mathilde, ma co-, on s'est suivis depuis le jour 1 et ça a été sept ans de bons moments. Ta bonne humeur inépuisable et ton rire facile font de toi une personne qu'on a toujours envie d'avoir pas loin. La légèreté avec laquelle tu gères l'adversité m'a toujours impressionné et j'essaie d'apprendre de ça. Dom Fauteux, tu m'as appris qu'un doctorant ça pouvait aussi avoir du fun, notamment durant nos 5 jours de festival de métal sur un bateau de croisière dans les Caraïbes (what?). Rock on brother. Marianne Valcourt (mais pas trop vite!), meilleure aide de terrain ever, ta joie de vivre et ton bonheur contagieux ont été un chaud rayon de soleil dans le frette Arctique. Tout le reste de la famille, vous avez contribué à un moment ou à un autre dans mon parcours, scientifiquement, socialement, émotionnellement, ou les trois! Merci à Thierry Grandmont (T-BIRD) pour toutes nos sorties de bro-birding et pour avoir été willing de littéralement toute, tout le temps; Ilona Grentzmann pour nos longues conversations sur la vie, la mort, et ce qui est vraiment important au final; Myriam Trottier-Paquet, David Bolduc, Maëliss Hoarau, Matthieu Weiss-Blais (Visse-Blette), Guillaume Slevan-Tremblay, Maëlle Colin et Florian Houy. Les 5 à 7, les lab meetings déglingués, les bières de pandémie à -25 dans le jardin communautaire, les conférences, les soupers chez Gilles, les jasettes de coin de table qui tournent en conversations d'un après midi. Vous avez grandement contribué à faire des sept dernières années une période de ma vie où j'ai été heureux. C'est ça qui compte au final non?

Downtown Partyeurs, le 881, Bourlamaque, les Bernaches, … finalement quasiment toute la vie sociale de la Ville de Québec. Merci pour le support moral, les activités à plus finir et votre énergie débordante!

I want to thank the Mittimatalik community (Pond Inlet) for welcoming us in the North every year. In particular, I want to thank Adrian Ootoova for his friendship and the fun times spent on Bylot, in the community and out on the land. I want to thank Jonas Arreak for welcoming us in Pond Inlet and his happiness to share stories and a

good time. I want to thank the community for generously sharing this incredible land that they live off of, we are extremely lucky and thankful to be able to spend time up there.

Merci à tou·te·s les Bylotien·ne·s que j'ai cotoyé·e·s à travers les années. On a vécu des moments inoubliables dans des endroits époustouflants et magiques. J'ai passé plus d'un an cumulé à coup de périodes de 3 mois en votre compagnie mais avec la proximité qu'on a là-haut, on se connaît comme si ça faisait des dizaines d'années qu'on se côtoyait. Merci pour les beaux moments à plus finir, les discussions scientifiques fertiles et l'émerveillement du monde qui nous entoure. Merci Yannick et JF d'avoir été des chefs de camp inspirants. Merci à tous ceux avec qui j'ai vécu ces épopées. Aurélie, Flo, Clément, Veillette, Claire-Céclie, Mimi, Matthieu (les 3!), Justine, Ben, Jojo, Lilou, Dédé, Tété, Dondon, Jeanne, Alexis, Kamil, Charles, Marylou, Andra, Madeleine, Jacob, Karine, Gab, Thomas, Vincent, Louis, Arianne, Sylvia, pour n'en nommer 'que' quelques-uns; il m'en manque tant mais vous avez été si nomberux! Vous resterez bien ancrés dans ma mémoire.

Merci aux équipes de l'Île-aux-Oies avec qui j'ai vécu un terrain pas comme les autres. Farniente à plus finir suivi de rush débile quand on a soudain 200 oies à baguer à 19h, et qu'on s'attelle jusqu'à l'aube pour traiter tout ça. Quelle équipe incroyable. Merci pour votre dévouement et ces moments inoubliables. Merci à Alex de chez Scott pour les délicieux plats préparés qui nous ont tenu en forme durant ces longues nuits de baguage. Merci également à Marc Séguin et André Desmarais de nous avoir accueilli gracieusement dans leur petit coin de paradis.

On y est presque!

Je veux remercier ma famille : Loulou, JP, Clapon. Vous avez été derrière moi du début à la fin et avez trippé à m'écouter raconter mes histoires de l'Arctique et d'écologie. Vous avez été un support moral et financier inestimable et vous avez continué à m'encourager même si des fois vous étiez pas trop certains d'où je m'en allais avec ce projet. J'ai ressenti votre soutien inconditionnel malgré la distance (surtout ma sœur!) et je vous en serai toujours très reconnaissant.

Pierrot. C'tait 2 gars ben éméchés : un chercheur un peu perdu et le fils de Gilles qui s'assoient dans le coffre d'un char… on connaît la suite. Sans toi, mon doc aurait sans doute été pas mal moins intéressant et diversifié, mais ça tu le sais! Avec ton obsession et ton acharnement d'aller capturer des oies pendant la COVID, on a finalement fait de la science vraiment cool. Merci de m'avoir épaulé et d'avoir été ce drôle de mélange dans ma vie. Tu as été mon poteau, mais aussi un mentor de science et de vie. J'ai apprécié ta contribution scientifique à ma thèse, mais surtout, j'ai apprécié chaque minute passée en ta compagnie. T'es complètement fou et t'as des idées et des plans complètement cons, mais on finit toujours par en tirer du bon. Finalement, merci d'avoir réuni au sein d'un même labo une gang de winneux tous plus fous les uns que les autres.

Fred. Mon frère. Je manque de mots pour souligner tout ce que tu as représenté dans ma vie ces sept dernières années. Depuis la première fois qu'on s'est rencontrés ça a tout de suite cliqué. On est devenus colocs, puis amis, puis on a fini par se faire appeler 'les Freds' par tout le monde autour de nous. Tu as été mon confident, mon opinion de dernier recours quand j'avais besoin de me faire confirmer une opinion ou une décision. Tu m'as aidé à relativiser et dédramatiser les moments où j'avais l'impression d'avoir pris des mauvaises décisions. Tu as été co-auteur de mes deux premiers chapitres de doc, mais tu as été un peu co-auteur de ce long chapitre de ma vie. Tu m'as ouvert les yeux sur tellement d'enjeux du Québec dans lequel on vit et j'ai un grand respect pour ta manière d'amener les gens à se questionner et à réfléchir à leurs points de vue. Tu m'as aidé à tenir la barre et maintenir le cap dans les tempêtes. On a vécu tellement d'aventures que je ne peux pas commencer à les énumérer ici. Mais merci d'avoir été là du premier jour jusqu'à la fin. J'ai hâte à la suite!

Et finalement, merci à Maria. Maria ma partner, ma collaboratrice de tous les jours, mon phare dans la brume, la mère de ma fille. La femme qui m'a épaulé à travers la houle comme à travers les moments plats, qui m'a soutenu (et c'est pas peu dire) dans mes insécurités, qui a partagé mes victoires, mes échecs. Tu as été présente à tous les jours depuis plusieurs années et tu m'as aidé à cheminer à travers les moments difficiles. Tu as été mon ancre, la partie de ma vie qui me poussait à continuer d'avancer. Merci d'avoir été là pour moi, ton soutien et ta présence ont grandement facilité mon parcours et l'achèvement de cette thèse.

Avant-propos

Cette thèse est composée de 7 sections dont une introduction et une conclusion générales rédigées en langue française. Les 5 chapitres principaux sont quant à eux publiés (ou en voie de l'être) dans des revues scientifiques révisées par les pairs, et sont conséquemment rédigés en anglais. L'introduction consiste en une revue de la littérature scientifique sur laquelle se basent les hypothèses et questions de recherche qui sont abordées tout au long de ma thèse. Dans la conclusion générale, je présente brièvement les principaux résultats des chapitres de ma thèse, et j'explique comment ceux-ci se complètent pour offrir une synthèse de l'impact de la chasse et de ses changements réglementaires des 30 dernières années sur une population aviaire migratrice longévive. J'aborde également dans cette section les limites principales dans l'interprétation des résultats de mon projet et je termine avec de brèves recommandations quant à la gestion de la population de la grande oie des neiges. Les chapitres 1 à 3 sont déjà publiés dans des revues scientifiques et la version présentée est identique à la version publiée. Le chapitre 4 a récemment été soumis à une revue scientifique avec comité de révision, tandis que le chapitre 5 est en préparation pour être soumis à une telle revue dans les mois à venir. La documentation supplémentaire pour chaque chapitre est annexée à la fin de la thèse.

Le chapitre 1 est intitulé « COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species » et a été publié dans la revue *Biological Conservation* en janvier 2021. Cet article a été conçu et rédigé avec l'aide de plusieurs co-auteurs dont Frédéric Dulude-de Broin, Thierry Grandmont, Gilles Gauthier et Pierre Legagneux en sont les principaux. Marie-Claude Martin, Akiko Kato, Josée Lefebvre et Joël Bêty ont également contribué à cet article à titre de co-auteurs.

Le chapitre 2 est intitulé « Additional data confirms the impact of the COVID19 lockdown on the behavior and fattening of migratory snow geese » et a été publié dans la revue *Biological Conservation* en septembre 2023. Frédéric Dulude-de Broin, Thierry Grandmont, Marie-Claude Martin, Joël Bêty, Gilles Gauthier et Pierre Legagneux ont contribué à cet article à titre de co-auteurs.

Le chapitre 3 est intitulé « Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species » et a été publié dans la revue *Journal of Applied Ecology* en novembre 2022. Cet article a été conçu et rédigé avec l'aide de Gilles Gauthier et Roger Pradel qui en sont les principaux co-auteurs. Josée Lefebvre et Pierre Legagneux ont également contribué à cet article à titre de co-auteurs.

Le chapitre 4 est intitulé « Evidence for seasonal compensation of hunting mortalities in a long-lived migratory bird » et a été publié dans la revue *Journal of Applied Ecology* en août 2024. Cet article a été conçu et rédigé avec l'aide de Gilles Gauthier et Roger Pradel qui en sont les principaux co-auteurs. Josée Lefebvre et Pierre Legagneux ont également contribué à cet article à titre de co-auteurs.

Le chapitre 5 est intitulé « Environmental conditions outweigh the effect of hunting on juvenile survival in greater snow geese » et est en préparation pour soumission à une revue scientifique. Cet article a été conçu et rédigé avec l'aide de Gilles Gauthier et Roger Pradel qui en sont les principaux co-auteurs. Josée Lefebvre et Maria Belke-Brea ont également contribué à cet article à titre de co-autrices.

En tant que premier auteur de tous ces articles, j'ai contribué à la collecte des données dans les années récentes même si j'ai bénéficié de jeux de données à long terme récoltés depuis plusieurs décennies. J'ai dirigé toutes les autres étapes pour en arriver à l'obtention de manuscrits scientifiques pour chaque chapitre, sous la supervision de Gilles Gauthier, mon directeur de recherche. La conception des questions de recherches s'est faite en collaboration avec Gilles Gauthier (Chapitres 2 à 5), Pierre Legagneux (Chapitres 1 à 4) et Frédéric Dulude-de Broin (Chapitres 1 et 2). Les analyses statistiques sont le résultat de proches collaborations avec Frédéric Dulude-de Broin (Chapitres 1 et 2), Roger Pradel (Chapitres 3 à 5), Gilles Gauthier (Chapitres 3 et 4) et Maria Belke-Brea (Chapitre 5). La conception des figures a été faite en collaboration avec Thierry Grandmont (Chapitre 1), Frédéric Dulude-de Broin (Chapitres 1 et 2) et Maria Belke-Brea (Chapitre 5). Outre ces principales contributions, tous les co-auteurs de chacun des chapitres ont contribué à ma thèse soit en fournissant des commentaires constructifs sur les différentes versions des manuscrits, en participant aux analyses statistiques, ou encore en fournissant une aide importante à la collecte des données.

Durant ma thèse, j'ai également contribué en tant que co-auteur aux six articles scientifiques suivants :

Setash C, Behney A, Gammonley J, Overton C, Casazza M, LeTourneux F, Buderman F, Schummer M, Luukkonen B, Huck N, Beatty K, Legagneux P, Koons D. 2024. Can waterfowl buffer the mortality risk induced by GPS tags? A cautionary tale for applied inference across species. Anim. Biotelemetry 12: 26.

Weiss-Blais M, Bolduc D, Corbeil-Robitaille MZ, Dulude-de Broin F, Grandmont T, LeTourneux F, Poirier M, Sarrazin D, Legagneux P. 2024. Worth the dip? Polar bear predation on swimming flightless greater snow geese and estimation of energetic efficiency. Arctic Science 10: 233-239.

Bates AE, Primack RB, Biggar BS, Bird TJ, Clinton ME, Command RJ, Richards C, Shellard M, Geraldi NR, Vergara V, […], LeTourneux F, et al., 2021. Global COVID-19 lockdown highlights humans as both threats and custodians of the environment. Biol. Conserv. 263, 109175.

Hoarau M, Dulude-de Broin F, LeTourneux F, Angelier F, Gauthier-Bouchard M, Martin M-C, Kato A, Lefebvre J, Thomas P, Williams CK, Bêty J, Legagneux P, *In press.* Bird migration on the edge: experimental manipulation of corticosterone advances migration departure dates. Ecology.

Grentzmann I, Gauthier G, Angelier F, Bêty J, LeTourneux F, Legagneux P. *In press.* Manipulating individual state during migration: carry-over effects of cumulative stress on survival. Ecol. Evol.

Grandmont T, Dulude-de Broin F, LeTourneux F, Gauthier G, Bêty J, Legagneux P. In prep. Adjusting migration and breeding phenology under climate change: can greater snow geese "wind the clock"?

Introduction

Un consensus scientifique incontestable est que les impacts négatifs des populations humaines sur les écosystèmes et la faune sont en constante augmentation (Steffen et al., 2011). L'étalement urbain et la transformation des écosystèmes en terres agricoles confinent la faune à des habitats toujours plus restreints (Newbold et al., 2015). Le réchauffement global du climat et la fréquence des évènements météorologiques extrêmes exercent une forte pression sur les délicates interactions biotiques et abiotiques déjà fragilisées par la multitude de pressions que les humains exercent sur leur environnement (Descamps et al., 2017; Dueñas et al., 2021; Mantyka-pringle et al., 2012). Paradoxalement, certains des impacts négatifs les plus importants de l'homme sur les écosystèmes naturels ont été causés en facilitant l'établissement de nouvelles espèces dans des écosystèmes où elles étaient initialement absentes (Bellard et al., 2016). Certaines de ces espèces dites invasives prolifèrent sans contraintes grâce à l'absence de prédateurs ou de compétiteurs, et réussissent à accaparer une partie importante des ressources disponibles qu'elles consomment aux dépens des espèces indigènes. Ce fléau est la cause principale de l'extinction de nombreuses espèces animales et végétales à travers le monde (Vitousek et al., 1996). De manière similaire, certaines espèces indigènes profitent aussi des transformations de l'environnement par l'humain et deviennent surabondantes (e.g., Côté et al., 2004; Coulson, 2007; Jefferies and Rockwell, 2002). Ces espèces peuvent causer des changements importants dans les écosystèmes qui les abritent et sont régulièrement la cause de conflits avec les humains (e.g., Bradbeer et al., 2017; Côté et al., 2004; Tombre et al., 2013; Wagner and Seal, 1992; Witmer, 2022).

La gestion des espèces invasives et surabondantes représente un défi car les solutions disponibles peuvent entraîner des coûts importants (Diagne et al., 2021) ou encore faire l'objet de contestations sociales (e.g., Shields, 2021). Lorsque c'est une option, la chasse sportive peut être un bon outil de gestion pour diminuer la taille des populations surabondantes. Dans le cas d'espèces traditionnellement chassées, cette méthode de gestion nécessite peu d'investissements en temps et financiers de la part des organismes de gestion de la faune car les chasseurs sont équipés pour cette activité et la pratiquent déjà. Cependant, il faut bien comprendre la dynamique d'une population et comment la chasse peut l'affecter pour qu'un programme de gestion par la chasse aie les effets escomptés.

Dynamique des populations

Lorsqu'on étudie une population animale, la taille de la population, soit le nombre d'individus qui la compose, est une quantité fondamentale (Lebreton et al., 1992). C'est l'information de base qui nous permet de juger de son état : les petites populations courent un risque d'extinction plus élevé que les grosses populations (Caughley, 1994). L'étude de la dynamique d'une population est l'étude des changements temporels dans sa

taille. À la base, le changement dans la taille d'une population entre un temps *t* et *t +1* ($N_{t \to t+1}$) est régit par 4 paramètres : la mortalité, la natalité, l'immigration et l'émigration (Eq.1)

$$N_{t+1} = N_t + B - D + I - E, \quad \text{(Eq.1)}$$

où *B* représente les natalités (births), *D* les mortalités (deaths), *I* l'immigration et *E* l'émigration. Pour une population isolée géographiquement (sans immigration ou émigration), l'équation 1 peut être écrite sous une forme où les mortalités et natalités sont fonction du nombre d'individus présent dans la population au temps *t* :

$$N_{t+1} = (F_t + S_t) \times N_t, \quad \text{(Eq.2)}$$

où S_t représente le taux de survie des individus et F_t la fécondité, soit le nombre d'individus produits par individu ayant survécu à l'intervalle entre *t* et *t +1*. Il existe un continuum de stratégies qui permettent aux individus d'une espèce de produire le plus de jeunes possibles au cours de leur existence. Sans entrer dans les détails de la théorie des traits d'histoire de vie (voir l'excellente synthèse de Reznick et al., 2002), on retrouve à une extrémité de ce continuum les espèces qui maximisent la fécondité (dites *r*-sélectionnées, ou '*fast species*') alors qu'à l'autre extrémité les espèces maximisent la survie des adultes (dites *K*-sélectionnées, ou '*slow species*'). Les espèces qui ont des caractéristiques *r* se reproduisent souvent plusieurs fois par année, et investissent un maximum de ressources pour produire le plus grand nombre de jeunes rapidement. Elles sont généralement caractérisées par de courts cycles de vies, une importante fécondité, un taux de survie faible et variable et une petite taille (e.g., insectes, micromammifères). De l'autre côté, les espèces avec des caractéristiques *K* ont plutôt tendance à réduire leur investissement reproducteur ou même sauter un évènement de reproduction lors de périodes difficiles afin de maximiser leurs chances de survivre et d'avoir l'opportunité de se reproduire à plusieurs occasions par la suite (Ferraz, 2020). Les espèces caractérisées par l'une ou l'autre de ces grandes stratégies maximisent un paramètre différent de l'équation 2, soit la fécondité pour les espèces plutôt *r*-sélectionnées et la survie des adultes dans le cas des espèces plutôt *K*-sélectionnées.

Importance de la reproduction et déterminants de la survie juvénile

Peu importe qu'une espèce ait des caractéristiques *r*- ou *K*-, la reproduction et le recrutement de juvéniles dans la population adulte demeure une condition fondamentale au maintien d'une population animale dans le temps. Même une population avec un taux de survie adulte élevé est vouée à l'extinction sans reproduction. D'ailleurs, chez une espèce caractérisée par une survie adulte élevée et peu variable, les paramètres qui contribuent le plus aux fluctuations réalisées de la taille de population à travers le temps sont souvent liés à la reproduction ou à la mortalité des juvéniles (e.g., Gaillard et al., 2000). En effet, lorsque la survie adulte ne varie pas ou peu, ce sont les variations dans la production de jeunes et leur survie jusqu'à l'âge adulte qui vont éventuellement induire des variations du taux de croissance d'une population.

Pour la plupart des espèces animales, les conditions durant le développement des juvéniles ont un impact sur leur qualité et affectent leur fitness (Lindström, 1999; Madsen and Shine, 2008; Marquis et al., 2008; Hamel et al., 2009). Des conditions favorables durant les premières semaines de vie mènent généralement à une meilleure croissance des jeunes ce qui leur confère plusieurs avantages comme de meilleures chances de survie, une taille adulte plus importante, et un meilleur potentiel de reproduction (Haywood and Perrins, 1992; Lindström, 1999; Saino et al., 2012). Puisque l'abondance et la qualité des ressources alimentaires varient généralement dans le temps, la synchronie entre la naissance des jeunes et les périodes où les ressources sont abondantes permet une croissance rapide avec les avantages qui s'ensuivent. Il est donc logique qu'on observe une synchronie serrée entre le moment de la reproduction et la disponibilité des ressources alimentaires chez de nombreuses espèces d'oiseaux (e.g., Gwinner, 1996). Cependant, la phénologie des ressources alimentaires comme les insectes ou les plantes dont se nourrissent de nombreuses espèces aviaires dépend souvent de la température. Conséquemment, le réchauffement climatique a généralement comme effet de devancer la croissance des plantes et la reproduction des espèces (Forchhammer et al., 1998; Post and Stenseth, 1999; Stenseth et al., 2002). Cependant, on a de plus en plus d'indices que l'écologie de plusieurs espèces migratrices ne leur permet pas d'ajuster le moment de la reproduction suffisamment pour conserver cette synchronie serrée entre l'éclosion des jeunes et les périodes où les ressources alimentaires sont les plus favorables (Møller et al., 2008). En effet, les espèces migratrices ne peuvent se baser que sur les conditions locales pour entamer la migration, mais celles-ci ne sont pas nécessairement représentatives des conditions sur leurs aires de reproduction à des milliers de kilomètres (Reséndiz-Infante and Gauthier, 2024; Tombre et al., 2008). Ce phénomène est exacerbé pour les espèces qui se reproduisent en Arctique car cet écosystème se réchauffe plus rapidement que le reste de la planète (Rantanen et al., 2022). L'asynchronie entre le pic d'abondance ou de qualité des ressources alimentaires et la phénologie de reproduction des oiseaux est donc un phénomène de plus en plus présent globalement et peut affecter l'investissement reproducteur, la croissance des juvéniles, leur survie, et même leur qualité sur le long terme (Knudsen et al., 2011; Visser and Gienapp, 2019).

Canalisation des traits **d'histoire de vie** et considérations pour la gestion

Chez les espèces longévives, un compromis peut être fait sur la reproduction lors d'une année donnée afin de maximiser les chances de survie d'un individu (Bêty et al., 2003; Erikstad et al., 1998). Cela se traduit par un investissement reproducteur soit faible ou variable dans le temps, et une survie élevée et peu variable dans le temps pour les adultes (e.g., Weimerskirch et al., 1987). On dit de ce trait démographique qu'il est canalisé, soit que des mécanismes permettant de réduire sa variabilité ont été sélectionnés (Gibson and Wagner, 2000; Wagner et al., 1997). Pfister (1998) a montré que les traits exhibant le moins de variabilité (i.e., les plus canalisés) sont ceux qui ont le plus fort potentiel d'induire des changements dans le taux de croissance d'une population. Dans le cas d'une espèce dont la reproduction varie grandement d'une année à l'autre mais dont le

taux de survie des adultes est élevé (e.g., > 0.8) et peu variable, une proportion importante des adultes survit d'une année à l'autre et ce sont eux qui composent la majeure partie de la population. Par contre, si un événement ponctuel survient et diminue le taux de survie adulte, on a alors un effet direct et immédiat sur la taille de la population qui peut difficilement être compensé par un accroissement de la reproduction ou du recrutement des juvéniles car ces taux sont relativement faibles et variables d'une année à l'autre. Autrement dit, un petit changement de paramètres très canalisés peut avoir un effet important sur la taille de la population l'année suivante. Conséquemment, pour contrôler le taux de croissance d'une population, il devrait être plus payant d'agir sur les traits les plus canalisés que sur ceux qui le sont moins selon la théorie. Par exemple, si on veut gérer la population d'une espèce longévive surabondante, des mesures agissant sur la survie des adultes devraient être les plus efficaces pour affecter sa croissance et contrôler la taille de sa population (Gauthier and Brault, 1998).

Gestion des populations par la chasse sportive

Toute population animale est affectée par plusieurs sources de mortalité qui peuvent parfois interagir entre elles. Une bonne connaissance des sources de mortalité et de leurs interactions possibles est donc importante afin de bien comprendre les facteurs qui contrôlent la croissance d'une population. Pour cette raison, les concepts de mortalité à la chasse additive et compensatoire sont au cœur de la gestion des populations exploitées. Pour gérer une population exploitée, on regroupe souvent les sources de mortalité en deux catégories : la mortalité causée par la chasse, et la mortalité dite 'naturelle', qui englobe toutes les autres sources de mortalités. Anderson et Burnham (1976) sont les premiers à avoir formellement énoncé l'hypothèse que la mortalité à la chasse pouvait être additive ou compensatoire à la mortalité naturelle, et ces concepts ont depuis fait l'objet de plusieurs synthèses et débats (Boyce et al., 1999; Cooch et al., 2014; Lebreton, 2005; Riecke et al., 2022).

Mortalité compensatoire et additive

Dans une population, la mortalité à la chasse est dite compensatoire lorsqu'elle n'a pas d'effet sur le taux de survie annuel parce qu'elle est compensée par la réduction d'une autre source de mortalité à un moment ultérieur du cycle annuel (Boyce et al., 1999; Lebreton, 2005). Par exemple, cela peut se produire lorsque la mortalité à la chasse réduit la mortalité due aux effets dépendants de la densité, ou encore s'il y a une hétérogénéité importante dans la qualité des individus et leur vulnérabilité à différentes sources de mortalité. On assume donc en quelque sorte qu'il y a une portion de la population qui est condamnée à mourir peu importe la cause, que ce soit par la chasse, la prédation, ou la compétition avec leurs congénères pour les ressources disponibles (le fameux 'doomed surplus'; Errington, 1945). Évidemment, la mortalité à la chasse doit être inférieure à la somme de la mortalité qui pourrait être causée par d'autres sources pour qu'on observe de la compensation. Au-delà de cette valeur, la mortalité à la chasse ne peut plus être compensée et devient additive.

On parle de mortalité additive lorsque la mortalité à la chasse a un effet négatif direct sur le taux de survie d'une population (Lebreton, 2005). Cela se produit lorsqu'il n'y a pas de processus par lequel la mortalité à la chasse peut être compensée par la mortalité naturelle, ces deux sources de mortalité agissent alors de manière indépendante sur la population. C'est le cas lorsque la mortalité naturelle est très faible, en l'absence de mécanismes dépendants de la densité, ou encore lorsque la mortalité à la chasse surpasse la mortalité naturelle. Celle-ci ne peut alors pas être réduite, ou du moins pas suffisamment pour compenser la mortalité à la chasse. La distinction entre ces concepts est importante parce que la mortalité à la chasse doit être additive à la mortalité naturelle si on souhaite contrôler une population surabondante à l'aide de la chasse sportive. À l'inverse, en présence d'une relation compensatoire, l'augmentation de la mortalité à la chasse n'aura que peu d'effet sur la croissance de la population (e.g., Koons et al., 2014).

Généralement, la mortalité à la chasse a plus de chances d'être compensatoire chez les espèces *r*-sélectionnées car la forte mortalité naturelle qui caractérise ces populations permet davantage une compensation de la mortalité à la chasse (e.g., Riecke et al., 2022). À l'opposé, la mortalité à la chasse tend plutôt à s'additionner à la mortalité naturelle pour les espèces exploitées qui sont plus longévives (i.e., les espèces *K*-sélectionnées) car leur taux de mortalité naturelle plus faible ne permet pas (ou très peu) de compenser la mortalité à la chasse (e.g., Gauthier et al., 2001; Hamel et al., 2006; Rexstad, 1992).

Mécanismes de compensation

Les processus saisonniers par lesquels les facteurs dépendants de la densité et l'hétérogénéité individuelle permettent la compensation entre différentes sources de mortalité sont assez intuitifs mais agissent différemment. D'une part, la réduction de la densité d'une population par la chasse peut entraîner une réduction des effets négatifs des facteurs dépendant de la densité (e.g., moins de compétition pour les ressources au moment où elles sont le plus limitantes, car moins d'individus) et donc une diminution de la mortalité naturelle qui compense la mortalité à la chasse. D'autre part, une hétérogénéité individuelle importante dans la vulnérabilité aux facteurs de mortalité dans une population pourrait aussi causer de la compensation (Guillemain et al., 2007; Lebreton, 2005; Lindberg et al., 2013). Par exemple, si la mortalité à la chasse affecte principalement les individus les plus vulnérables aux facteurs de mortalité naturelle, la mortalité à la chasse pourrait alors se substituer à cette dernière et n'avoir que peu d'impact sur les individus présentant une faible vulnérabilité aux facteurs de mortalité naturelle. Dans les deux cas, le résultat est similaire: le taux de survie annuel ne varie pas en fonction de la mortalité à la chasse.

Jusqu'à présent, les phénomènes de compensation ont été étudiés et expliqués principalement par une interaction entre deux sources de mortalité différentes, par exemple une réduction de la mortalité naturelle compensant une augmentation des mortalités à la chasse. Par contre, en présence d'une forte hétérogénéité

individuelle dans la vulnérabilité à la chasse, on peut imaginer un processus similaire au sein d'une seule source de mortalité, soit celle due à la chasse, mais à des moments distincts dans le cycle annuel. Par exemple, si la récolte à une saison réduit fortement le nombre d'individus vulnérables à la chasse, on pourrait observer une réduction de cette mortalité durant la saison suivante puisqu'il resterait moins d'individus vulnérables disponibles pour être tués à la chasse dans la population. Le potentiel pour une compensation entre la mortalité à la chasse à différentes saisons est particulièrement d'intérêt dans le cas de la sauvagine, car ces espèces migratrices parcourent de grandes distances et sont chassées dans différentes juridictions où les réglementations de chasse sont souvent différentes (Holopainen et al., 2018). Curieusement, l'hypothèse d'une compensation saisonnière de la mortalité à la chasse ne semble pas à ce jour avoir été mise de l'avant. Une difficulté pour évaluer une telle hypothèse est qu'il faut disposer de données suffisantes (nombre d'individus et nombre d'années) et de bonne qualité sur une base saisonnière. Comme la collecte exhaustive de données démographiques à différentes saisons représente un défi logistique et financier (voir section suivante), il y a peu de jeux de données qui permettent de tester une telle hypothèse. Considérant l'importance des phénomènes de compensation pour la gestion des populations exploitées (e.g., Kokko and Lindström, 1998; Kokko, 2001), cette hypothèse mérite d'être évaluée.

Effets non-létaux de la chasse

Au-delà de son impact direct sur la mortalité, la chasse peut également affecter indirectement la dynamique d'une population par le biais d'effets sur le comportement des individus. On parle alors d'effets non-létaux. Le dérangement causé par la chasse pousse les individus à modifier leur comportement de manière à échapper aux chasseurs, soit en changeant leurs patrons d'activité, ou en sélectionnant des habitats qui leur fournissent un refuge de la chasse (Casas et al., 2009; Madsen and Fox, 1995). Par exemple, durant la saison de chasse, le cerf de Virginie (*Odocoileus virginianus*) se déplace vers des refuges sans chasse lorsqu'ils sont disponibles, sélectionnent les habitats avec un couvert forestier plus dense, et sont davantage actifs durant la nuit (Kilgo et al., 1998; Rhoads et al., 2013; Sullivan et al., 2018). De tels impacts du dérangement sur la sélection d'habitat et les patrons d'activité ont également été montrés chez plusieurs espèces de canards diurnes qui s'alimentent aussi davantage de nuit durant la saison de chasse et évitent les régions où la pression de chasse est plus forte (McDuie et al., 2021; Thornburg, 1973). On peut considérer ces changements comportementaux comme un mécanisme permettant aux individus de s'adapter à un changement important de leur environnement qui représente pour eux un fort risque de prédation.

Chez les espèces migratrices, le dérangement peut perturber le comportement de prise alimentaire et augmenter les dépenses énergétiques à des moments critiques du cycle annuel comme durant les haltes migratoires, ou l'hiver lorsque les besoins énergétiques pour la thermorégulation sont élevés (Béchet et al., 2004; Madsen and Fox, 1995). Plusieurs auteurs ont émis l'hypothèse que cela devrait se répercuter sur la

condition physique des oiseaux mais peu ont réussi à en faire la démonstration (Casas et al., 2009; Jamieson et al., 2006; Sokos et al., 2013). Il faut néanmoins considérer que peu d'études ont pu tester directement l'impact du dérangement sur la condition des oiseaux, ou bien disposent de très peu d'années de données. Au printemps par contre, on dispose d'éléments montrant que le dérangement causé par la chasse ou l'effarouchement dans les terres agricoles affecte le comportement des oiseaux et a des répercussions sur leur condition physique (Béchet et al., 2004; Féret et al., 2003; Klaassen et al., 2006; Pearse et al., 2012). Durant la migration printanière, les migrateurs de longue distance sont en période de fort engraissement en préparation pour la migration et la reproduction. Les impacts du dérangement sur la condition physique sont donc plus faciles à détecter lors de cette saison. Chez les animaux se reproduisant au moins en partie sur capital comme plusieurs espèces d'oies, la dynamique d'engraissement durant la migration printanière affecte l'investissement reproducteur (Bêty et al., 2003; Gauthier et al., 2003; Klaassen et al., 2017; Sharp et al., 2013). Les impacts du dérangement par la chasse sur le comportement et la condition physique durant cette saison ont donc un fort potentiel d'affecter la dynamique de ces populations par le biais d'une réduction de la fécondité (Klaassen et al., 2006).

Estimation de la survie en condition naturelles

Estimation de la survie à partir du marquage

L'estimation à grande échelle de paramètres démographiques comme le taux de survie d'une population repose principalement sur le marquage longitudinal des individus. On nomme cette technique 'Capture-Marquage-Recapture' (CMR) et elle consiste à d'abord capturer et marquer un échantillon d'individus de la population étudiée. Ceux-ci sont marqués à l'aide d'un marqueur comportant un numéro unique, relâchés, et recapturés par la suite (Lebreton et al., 1992). Lorsqu'on recapture des individus marqués périodiquement dans le temps, on peut estimer la proportion qui a survécu entre chaque évènement de capture. Cependant, on ne peut pas assumer qu'un individu qui n'est pas recapturé est nécessairement mort. Il est donc primordial d'estimer la probabilité de détection des individus encore vivants (Kéry and Schaub, 2012; Lebreton et al., 1992). En recapturant les individus au fil du temps, on recapture éventuellement des individus qui n'avaient pas été recapturés à certaines occasions. Lorsqu'on dispose d'un grand nombre d'individus, cela permet de modéliser une probabilité de capturer un individu à chaque évènement de capture, et donc de contrôler pour la détection imparfaite des individus lors de l'estimation de la survie. Les premiers modèles statistiques de CMR pour estimer la survie ont été développés dans les années 1960 (Brownie et al., 1985; Cormack, 1964; Jolly, 1965; Seber, 1965) mais ont été continuellement raffinés depuis. Le développement de modèles pouvant combiner l'information des recaptures d'individus vivants aux observations d'individus morts ont permis d'obtenir des estimations de survie plus précises (Burnham, 1993; Lebreton et al., 1995).

Le développement des modèles de CMR dits 'multi-états' a permis plusieurs avancées importantes. Dans ces modèles, les individus sont classés selon l'état dans lequel ils se trouvent (e.g. vivant ou mort, ou encore reproducteur ou non-reproducteur), et on modélise ensuite la probabilité que les individus transitionnent entre ces états à travers le temps (Lebreton et al., 2009; Nichols et al., 1992). Cette approche permet de combiner facilement différents types de données dans le même modèle (e.g. observations d'individus vivants et récupération d'individus morts) et offre des solutions à des problèmes spécifiques comme l'estimation de la perte de marqueurs auxiliaires (Conn et al., 2004; Juillet et al., 2011). Par exemple, on peut calculer le taux de perte de ces marques en modélisant la perte comme une transition entre états (e.g. de 'vivant avec marque auxiliaire' vers 'vivant sans marque auxiliaire'). Une autre application intéressante des modèles multi-états est qu'en modélisant la mortalité de différentes sources avec des états différents (e.g. mort de causes naturelles vs. mort par la chasse), on peut estimer la probabilité de transition d'un individu vivant vers l'un ou l'autre de ces états, et donc mesurer la contribution de chacune de ces sources de mortalité à la mortalité totale (Schaub and Pradel, 2004). Sans surprises, ces modèles se sont avérés utiles pour tester les hypothèses de mortalité compensatoire et additive. En calculant la relation entre différentes sources de mortalité, on peut mesurer si la mortalité naturelle compense ou non la mortalité à la chasse (e.g., Schaub and Lebreton, 2004; Servanty et al., 2010). Finalement, le raffinement des modèles multi-états vers des modèles multi-évènements a aussi permis de tenir compte de l'incertitude dans l'assignation des états (Pradel, 2005). En dissociant le vrai état dans lequel se trouve un individu des observations, qu'on appelle ici 'évènements', on peut mieux gérer les situations où par exemple certains états sont non-observables (e.g., Souchay et al., 2014).

Avantages et inconvénients des marqueurs auxiliaires

Lorsqu'on marque des individus sauvages, ceux-ci sont idéalement identifiés avec des marqueurs discrets qui n'affectent pas leurs traits vitaux. Chez les oiseaux, on utilise de petites bagues métalliques fixées aux pattes des individus mais on peut également utiliser en plus certains marqueurs dits 'auxiliaires'. Ces marqueurs plus gros et très voyants permettent d'identifier les individus à distance sans avoir besoin de les capturer physiquement, ce qui confère plusieurs avantages. Les plus importants sont d'augmenter significativement les probabilités que les individus soient observés, et permettre la récolte d'observations à tout moment de l'année et à des sites différents du site de marquage. Ceci est particulièrement utile avec les oiseaux migrateurs qui parcourent souvent de grandes distances tout au long de l'année et visitent de nombreux sites. L'observation à distance d'individus portant des marqueurs auxiliaires permet d'obtenir des données qu'il serait difficile d'obtenir autrement, comme le mouvement d'individus entre différentes régions (Alisauskas et al., 2012; Hestbeck et al., 1991) ou encore le statut des individus (e.g., Souchay et al., 2014). La récolte d'observations à différentes saisons permet également l'estimation de la survie sur une base saisonnière et non uniquement sur une base annuelle. Cela nous donne une connaissance plus fine de la démographie d'une espèce car on peut alors cerner

les périodes du cycle annuel où la mortalité est plus importante et mieux comprendre les causes de cette mortalité.

Toutefois, à cause de leur taille et de leur visibilité, les marqueurs auxiliaires sont plus invasifs et plus susceptibles d'affecter le comportement ou les paramètres démographiques des individus (e.g., Johnsen et al., 1997; Barron et al., 2010; Saraux et al., 2011). Un cas classique est l'utilisation de colliers chez les oies, qui ont été utilisés durant de nombreuses années sur virtuellement toutes les espèces d'oies étudiées (e.g., Schmutz and Morse, 2000; Alisauskas and Lindberg, 2002; Alisauskas et al., 2006; Fox et al., 2014). Cependant, chez presque toutes ces espèces, on a éventuellement trouvé des effets négatifs des colliers sur différents paramètres comme le comportement, la reproduction et même la survie, ce qui a mené à l'arrêt de leur utilisation dans beaucoup de cas (Caswell et al., 2012 et références s'y trouvant). Pour des raisons éthiques évidentes mais également pour s'assurer d'obtenir des données non-biaisées, il est essentiel de bien cerner l'impact des marqueurs utilisés pour s'assurer qu'ils n'ont pas d'effet sur les paramètres étudiés. Dans le cas d'études à long terme, il est important d'être vigilant et de tester régulièrement l'effet des marqueurs utilisés car il est possible que des impacts apparaissent ou changent avec le temps.

Le cas de la grande oie des neiges

Considérations **biologiques et traits d'histoire de vie**

L'oie des neiges (*Anser caerulescens*) est une espèce migratrice d'une grande valeur socio-économique. Les oies sont chassées historiquement en Amérique du Nord depuis des centaines d'années, et sont également la source d'importantes retombées économiques liées à l'écotourisme pour l'observation des oies durant la migration (Bélanger et al., 2007). La grande oie des neiges (*A. caerulescens atlanticus*) est une sous-espèce d'oie des neiges qui hiverne sur la côte est des États-Unis, se reproduit dans l'est du haut-Arctique canadien et fait une halte migratoire de plusieurs semaines au Québec dans les basses terres du Saint-Laurent au printemps et à l'automne (Mowbray et al., 2020). Particulièrement au printemps, la halte migratoire est une étape critique de leur cycle annuel car les oies accumulent des réserves endogènes pour la migration et la reproduction (Gauthier et al., 2003, 1992). Les conditions en vigueur lors de la halte migratoire ont donc un fort potentiel d'affecter l'investissement reproducteur des oies. On a une excellente connaissance de l'écologie de cette espèce principalement grâce à un programme de suivi de la reproduction et de marquage établi en 1990 à l'Île Bylot, Nunavut, un site abritant la plus importante colonie de nidification de cette sous-espèce connue à ce jour (Cadieux, 2023; Reed et al., 1998).

La grande oie des neiges est une espèce relativement longévive. Les adultes ont un taux de survie élevé (~0.80) relativement stable (Gauthier et al., 2001), vivent en moyenne 5 à 6 ans (Gauthier and Lebreton, 2004), mais peuvent survivre jusqu'à plus de 20 ans en conditions naturelles (LeTourneux, données non-publiées).

L'investissement dans la reproduction est fortement influencé par la condition physique des femelles, et celles-ci peuvent même sauter un évènement de reproduction si leur condition est trop faible, ce qui leur octroie de meilleurs chances de survie et donc de pouvoir se reproduire à nouveau par la suite (Bêty et al., 2003; Souchay et al., 2014). L'espèce niche en Arctique, un milieu caractérisé par une forte stochasticité environnementale, ce qui a des répercussions sur sa démographie (Reed et al., 2004). Par exemple, les conditions environnementales durant la période de croissance des jeunes affectent leur taille à l'envol, au moment de quitter l'aire de reproduction (Doiron et al., 2015). Cela se produit notamment lorsqu'il y a un fort décalage entre la date du pic de qualité nutritive des plantes dont ils se nourrissent et la date d'éclosion des oisons (Lepage et al., 1998; Doiron et al., 2015). Les conditions environnementales pourraient alors avoir un impact important sur la survie des jeunes de 1^{e} année et expliquer pourquoi ce paramètre varie fortement entre les années (0.1-0.7; Lepage et al., 2000; Menu et al., 2005; Calvert and Gauthier, 2005). La dynamique de population des oies est donc caractérisée par un taux de survie adulte élevé et peu variable, et un investissement reproducteur modulé en fonction de leur condition physique pour maximiser leur survie (Bêty et al., 2003; Gauthier et al., 2001). Ces caractéristiques en font une espèce avec une stratégie d'histoire de vie similaire aux espèces décrites comme *K*-sélectionnées. Conséquemment, selon la théorie des traits d'histoire de vie, le trait de cette espèce qui est le plus canalisé et a le plus fort potentiel d'affecter la croissance de sa population est la survie des adultes (Gauthier and Brault, 1998).

Démographie de la grande oie des neiges au XXe siècle

À l'instar de plusieurs espèces d'oies en Amérique du Nord, la grande oie des neiges a connu des fluctuations de population importantes au cours du dernier siècle, principalement en réponse aux activités humaines (Gauthier et al., 2005; Lefebvre et al., 2017). Au début des années 1900, la taille de la population était estimée entre 2000 et 3000 individus (White and Lewis, 1937), un faible nombre probablement dû à la pression de chasse trop élevée au cours du XIXe siècle. La population de la grande oie des neiges a ensuite augmenté lentement durant la première moitié du XXe siècle suite à une protection stricte de l'espèce (interdiction de chasse aux États-Unis et saison d'automne très limitée au Canada; White and Lewis, 1937) après la signature de la Convention sur les oiseaux Migrateurs en Amérique du Nord (Anonymous, 1917). Le nombre de grandes oies des neiges a d'abord atteint environ 40 000 individus à la fin des années 1960 pour ensuite croître plus rapidement et atteindre 150 000 individus au milieu des années 1970 (Menu et al., 2002; Reed et al., 1998). Suite à cette reprise, la réouverture d'une saison de chasse aux États-Unis en 1975 a doublé la récolte et induit une stabilisation de la population jusqu'en 1985 (Gauthier et al., 2005).

Au début des années 1980, les oies ont commencé à se nourrir de façon significative dans les champs agricoles (maïs, céréales) qui sont devenus une partie importante du paysage américain et québécois. Cela a mené à des changements majeurs dans leur distribution et leur route migratoire (Gauthier et al., 2005), leur a permis

d'éviter en partie certains secteurs avec une forte pression de chasse (Calvert et al., 2005) et a ultimement mené à une seconde phase de croissance de la population (Fig. 0.1; Gauthier et al., 2005). À ce moment, les oies ont presque complètement délaissé les marais naturels où elles s'alimentaient au début du siècle pour se nourrir presqu'exclusivement dans les milieux agricoles en hiver et au printemps, ce qui est suggéré par plusieurs auteurs comme la principale cause de la taille inégalée de nombreuses populations d'oies à l'aube du XXIe siècle, incluant l'oie des neiges (Fox and Abraham, 2017; Fox and Madsen, 2017; Gauthier et al., 2005; Lefebvre et al., 2017). À ce moment, la population de la grande oie des neiges se chiffrait aux alentours d'un million d'individus (Fig. 0.1).

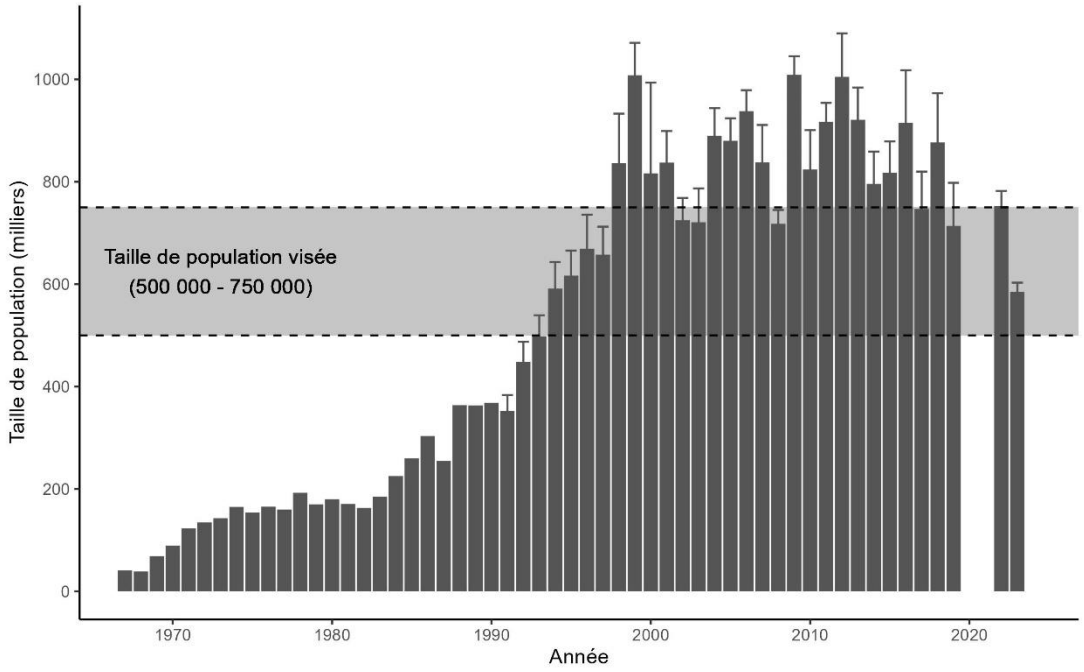

Figure 0.1 Taille de population de la grande oie des neiges au printemps entre 1967 et 2023. Les estimations sont fournies par le Service Canadien de la Faune et sont obtenues par survol aérien (détails dans l'Appendice S3.2).

Rôle écologique **de l'oie des neiges**

La grande oie des neiges occupe un rôle central dans les écosystèmes arctiques où elle se reproduit, notamment à cause de son influence sur les interactions trophiques. Leur abondance et leur grégarité font de cet herbivore une ressource alimentaire importante durant l'été pour plusieurs prédateurs comme les labbes (*Stercorarius spp.*), les goélands (*Larus spp.*) et surtout les renards arctiques (*Vulpes lagopus*; Gauthier et al., 2004). La présence des oies permet de tamponner les fortes variations interannuelles dans les ressources disponibles pour ces prédateurs induites par les fluctuations cycliques des populations de lemmings (Gauthier et al., 2004; Giroux et al., 2012), leur proie principale (Schmidt et al., 2012; Therrien et al., 2014).

Les populations d'oies surabondantes peuvent également avoir des impacts négatifs importants sur les écosystèmes qu'elles utilisent (Gauthier et al., 2006). En Arctique par exemple, on a montré que l'intensité du broutement par les oies affecte les communautés végétales en favorisant la dominance de certaines espèces (Nishizawa et al., 2021). Le broutement par les oies réduit également significativement la biomasse aérienne et l'accumulation de litière végétale (Gauthier et al., 1995; Valéry et al., 2010), ce qui peut même affecter la vitesse de formation du pergélisol (Deschamps et al., 2023). Dans certains cas extrêmes comme pour la petite oie des neiges (*Anser caerulescens caerulescens*) dont la population a atteint plusieurs millions d'individus (Alisauskas et al., 2022), les impacts du surbroutement de la végétation arctique peuvent être dévastateurs et mener à une dégradation sévère des habitats qu'elles utilisent (Abraham et al., 2005; Handa et al., 2002; Srivastava and Jefferies, 1996). Cela a également des répercussions pour les autres espèces abritées par ces écosystèmes (e.g. Samelius and Alisauskas, 2009; Peterson et al., 2014; Flemming et al., 2019). Dans le cas de la grande oie des neiges, on a également montré qu'elle peut nuire à des espèces avec lesquelles elle partage les mêmes prédateurs en permettant à ces derniers de maintenir des tailles de populations élevées malgré les fluctuations importantes dans la disponibilité des autres ressources alimentaires (Beardsell et al., 2023; Duchesne et al., 2021; Lamarre et al., 2017).

Mesures de gestion pour contrôler la surabondance des oies des neiges

Considérant l'important rôle tant socio-économique qu'écologique de la grande oie des neiges, il était primordial de gérer cette population de manière à conserver une taille de population raisonnable, tout en évitant les forts impacts négatifs potentiels liés à la surabondance (Jefferies et al., 2003). Ce constat a motivé une évaluation de la situation par un conseil d'experts en 1998 et a mené à des recommandations pour arrêter la croissance de cette population pendant que c'était encore possible (Batt, 1998). Les mesures proposées visaient à éviter une dégradation irréversible des écosystèmes arctiques et des milieux humides utilisés par les oies lors de la migration. Le Service Canadien de la Faune et le U.S. Fish & Wildlife Service ont donc collaboré pour instaurer des mesures de gestion exceptionnelles à la fin du XX^{e} siècle visant à stabiliser la population entre 500 000 et 750 000 oiseaux (Lefebvre et al., 2017). Ces organismes ont conjointement libéralisé les règlements de chasse dans leurs juridictions respectives, notamment en augmentant les limites de prises et de possession lors des saisons de chasse régulières, et en permettant l'utilisation de techniques prohibées jusqu'alors comme l'appâtage et l'utilisation d'appeaux électroniques (Lefebvre et al., 2017). Les mesures les plus importantes ont cependant été d'établir de nouvelles saisons de chasse spéciales. Une saison de chasse spéciale légalement appelée 'Spring Conservation Harvest' a donc été instaurée au printemps en 1999 au Canada. Aux États-Unis, on a subséquemment instauré le 'Conservation Order', une saison de chasse spéciale à partir du milieu de l'hiver et s'étendant jusqu'au départ des oies en migration au printemps. Cependant, cette mesure n'a été appliquée qu'à partir de 2009, car des contestations juridiques par des groupes de protection des animaux ont

repoussé son instauration d'une décennie (Lefebvre et al., 2017). Ces deux dernières mesures étaient sans précédent et de loin les plus audacieuses puisque la récolte de tout oiseau migrateur entre le 10 mars et le 1er septembre était auparavant prohibée depuis la signature de la Convention des oiseaux migrateurs en 1918 (Anonymous, 1917).

Effet à court terme des mesures de gestion

Une première évaluation de l'impact des mesures spéciales au Canada sur différents paramètres démographiques des oies a eu lieu dans les premières années suivant leur instauration. L'effet le plus évident a été une diminution du taux de survie des adultes, ce qui était l'objectif principal découlant des recommandations émises dans le rapport de 1998 (Batt, 1998; Calvert and Gauthier, 2005). Par contre, cette mesure ne semble pas avoir affecté le taux de survie des juvéniles de première année (Calvert and Gauthier, 2005). De plus, on a trouvé plusieurs impacts du dérangement par la chasse sur la dynamique d'engraissement et la condition prénuptiale des oies durant la halte migratoire printanière. En effet, Béchet et al. (2004) ont montré que la chasse intense dans les terres agricoles au printemps a mené à une diminution de l'utilisation de ces habitats au profit des milieux humides, malgré que les champs procurent une source de nourriture plus profitable en termes d'engraissement au printemps (Bédard and Gauthier, 1989). De plus, le dérangement constant dans ces milieux a forcé les oies à voler sur de plus grandes distances pour trouver des sites d'alimentation, ce qui a eu un impact double sur leur dynamique d'engraissement puisqu'elles dépensent alors plus d'énergie en vol, et passent moins de temps à s'alimenter (Béchet et al., 2004). Finalement, Féret et al. (2003) ont montré que la condition physique des oies avant le départ pour la migration était plus faible après l'instauration de la chasse printanière. Comme une partie des ressources accumulées sur la halte migratoire sont investies dans la reproduction, cette mesure a également eu des répercussions néfastes sur la productivité de la population (Mainguy et al., 2002; Morrissette et al., 2010). Globalement, ces mesures ont atteint leur objectif initial de réduire le taux de survie des adultes, le paramètre avec le plus fort potentiel d'affecter la croissance de cette population (Calvert and Gauthier, 2005; Gauthier and Brault, 1998). Cela a en partie eu l'effet escompté puisqu'elles ont mené à un arrêt de la croissance de la population qui s'est depuis maintenue entre 700 000 et 1 000 000 d'individus (Fig. 0.1; Lefebvre et al., 2017).

Effets à long-terme des mesures de gestion

Bien que les mesures de gestion par la chasse aient globalement eu les effets escomptés sur la population de la grande oie des neiges, notre compréhension des impacts de la chasse sur la démographie des oies demeure rudimentaire. D'abord, les évaluations dont on dispose des effets de ces mesures sur les paramètres démographiques des oies ne couvrent que les 5 premières années après leur instauration au Canada et nous ignorons si ces effets ont perduré dans le temps. Compte tenu de la capacité d'adaptation des oiseaux aux

changements dans leur environnement (voir plus haut), il est possible qu'elles aient modifié leur comportement afin d'atténuer les impacts négatifs de la chasse sur leur traits vitaux. De plus, aucune évaluation de l'impact de l'ajout des mesures spéciale aux États-Unis en 2009 n'a été faite. Il était attendu, compte tenu de la théorie et de notre connaissance de l'espèce, que cette mesure permettrait de réduire la taille de la population qui s'était stabilisée depuis 1999, mais ce n'est pas ce qu'on observe (Fig. 0.1; Lefebvre et al., 2017). Les raisons de cette contradiction demeurent inconnues pour l'instant.

Force est donc de constater que la théorie et les connaissances actuelles ne concordent pas complètement avec l'information dont on dispose. Plusieurs questions restent sans réponses et motivent les travaux de ma thèse. Premièrement, on ne sait pas si les impacts de la chasse de printemps sur la dynamique d'engraissement et la condition physique des oies sont toujours présents aujourd'hui. Les communautés de chasseurs sont unanimes sur le fait que les oies sont beaucoup plus difficiles à chasser aujourd'hui qu'il y a 20 ans, car elles ont appris à reconnaître les dispositifs de chasse (e.g., appelants dans les champs). Il est donc logique de penser que les oies pourraient s'être habituées à cette mesure après y avoir été exposées pendant 20 ans.

Ensuite, on a une compréhension limitée de l'impact relatif des mesures instaurées au Canada et aux États-Unis sur la survie des oies. En effet, plusieurs mécanismes pourraient expliquer qu'on n'observe pas de changements majeurs dans la taille de population des oies depuis 25 ans malgré les mesures de gestion spéciales implantées aux États-Unis en 2009. Il est possible que ces mesures de gestion n'aient pas eu l'impact escompté sur la survie ou encore que l'effet de ces mesures ait été compensé par une diminution de l'efficacité des mesures au Canada. Pour répondre à ces questionnements, il est nécessaire de quantifier la contribution relative de chacune de ces mesures aux variations du taux de survie des adultes de cette population et donc de déterminer de manière fiable la survie des oies sur une base saisonnière.

L'estimation de la survie des oies par saison tout au long de l'année ne peut se faire que par l'observation d'individus portant des marqueurs auxiliaires, en l'occurrence les fameux colliers observables à distance. Aucun impact de ces marqueurs n'a été décelé auparavant sur la survie de la grande oie des neiges (Menu et al., 2000; Reed et al., 2005) même si des impacts négatifs sur la condition physique et l'investissement reproducteur ont été rapportés (Legagneux et al., 2013; Reed et al., 2005). Il était néanmoins important de valider l'absence continue d'un impact des colliers sur la survie des individus au fil du temps dans cette étude, en particulier avec la forte augmentation de la pression de chasse induite par la libéralisation des règlements depuis 20 ans.

Finalement, il était important de déterminer si la survie des juvéniles a été affectée ou non par les changements réglementaires de la chasse. Comme ce paramètre est très variable dans le temps, il est possible qu'un tel effet ne puisse être détecté qu'avec plusieurs années de données, ce qui n'était pas disponible dans les études précédentes (e.g. Calvert and Gauthier, 2005). De plus, compte tenu du fort impact des conditions

environnementales et en particulier du décalage trophique sur la croissance des juvéniles (Dickey et al., 2008; Doiron et al., 2015), il était intéressant de déterminer comment ce phénomène affecte ultimement le taux de survie des juvéniles en combinaison avec les changements de règlements de chasse.

Objectifs de la thèse

Cette thèse a comme objectif principal d'améliorer notre compréhension des impacts de la chasse à différents moments du cycle annuel sur les paramètres démographiques (survie, reproduction) et leurs déterminants chez une espèce aviaire migratrice et longévive, la grande oie des neiges. Notamment, je tente de comprendre l'effet de la chasse sur la survie annuelle et saisonnière des adultes, ainsi que sur leur condition physique précédant le départ en migration vers les aires de reproduction, un déterminant important de l'investissement reproducteur (Bêty et al., 2003). Puisque les connaissances disponibles indiquent que les conditions environnementales estivales en Arctique seraient le déterminant principal de la survie des juvéniles (Menu et al., 2005), je tente également de comprendre comment l'effet de la chasse diffère en fonction de l'âge. Pour atteindre cet objectif au sein d'une population naturelle, je bénéficie d'une étude à long-terme sur 30 ans et surtout d'une situation quasi-expérimentale, soit l'instauration d'une saison de chasse spéciale de printemps au Canada après 10 ans de suivi (en 1999) et d'une saison de chasse spéciale à l'hiver aux États-Unis 10 ans plus tard (à partir de 2009). Ces modifications de la pression de chasse à 10 ans d'intervalle peuvent être vues comme une manipulation à grande échelle de la population.

Le premier chapitre de cette thèse a pour but de déterminer si l'impact de la saison de chasse spéciale printanière établie au Canada en 1999 a eu un effet soutenu sur la condition physique et l'utilisation d'habitat des femelles adultes durant la halte migratoire. Puisque la chasse de printemps est en place depuis plus de 20 ans, l'absence d'années récentes sans chasse printanière auxquelles comparer la condition des oies était problématique. Cependant, nous avons bénéficié du confinement lié à la COVID-19 qui a causé une réduction importante de la pression de chasse au printemps 2020. Cette année récente avec une intensité de chasse très réduite a permis de comparer les dynamiques d'engraissement actuelles avant et pendant cette année particulière, minimisant ainsi de potentiels effets confondants liés à des changements environnementaux à long-terme.

Le second chapitre a pour objectif de confirmer les résultats du premier chapitre dans une optique de réplication de résultats scientifiques. Puisque le premier chapitre s'appuie principalement sur deux années récentes, soit juste avant et pendant la COVID-19 (2019 et 2020), nous validons les résultats et interprétations du premier chapitre en incluant des données provenant de deux années supplémentaires (2021 et 2022) post-COVID.

L'objectif du troisième chapitre est d'évaluer la présence d'une interaction possible entre l'impact du port d'un marqueur auxiliaire, en l'occurrence un collier, et de la libéralisation des règlementations de chasse au fil du temps sur la survie annuelle des oies. Je teste l'hypothèse que la combinaison de ces deux sources de stress résulte en un impact synergique sur la probabilité de survie des oies. Le développement du modèle d'analyse statistique sur une base annuelle dans ce chapitre et la présence d'un effet potentiel du marqueur auxiliaire ont servi de fondation pour le développement du modèle saisonnier utilisé pour mon chapitre suivant.

Le quatrième chapitre a pour objectif de déterminer l'impact relatif des deux modifications majeures aux règlements de chasse sur la survie des oies aux saisons auxquelles ces mesures ont été mises en place. Ces mesures sont la saison de chasse spéciale de printemps établie au Canada en 1999 ainsi que la saison de chasse spéciale instaurée à l'hiver aux États-Unis en 2009. Un second objectif de ce chapitre est de tester l'hypothèse d'une compensation saisonnière entre les mortalités à la chasse à l'hiver et au printemps après l'instauration de la saison de chasse spéciale en hiver.

Finalement, le cinquième et dernier chapitre de cette thèse a pour objectif d'identifier les principaux déterminants de la survie des juvéniles de première année. J'examine la contribution relative de l'impact d'un décalage trophique entre la date d'éclosion des oisons et le pic de qualité nutritive des plantes et de l'impact des changements de règlements de chasse sur leur survie annuelle. Je teste l'hypothèse que les conditions environnementales estivales sur les aires de reproduction seront le principal déterminant de la survie des juvéniles de première année. Cela permet de déterminer si la chasse affecte différemment les adultes et les juvéniles.

En répondant à ces questions, ma thèse permettra de brosser un tableau plus complet de l'état des facteurs qui affectent la dynamique de cette population. Ultimement, cela nous offrira une meilleure compréhension des effets que peuvent avoir la chasse à différentes saisons sur la dynamique de population d'une espèce aviaire migratrice et longévive.

Chapitre 1 – COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species

Capture d'oies à l'Île-aux-Oies, Québec, durant le confinement du printemps 2020

Référence de la publication :

LeTourneux, F., Grandmont, T., Dulude-de Broin, F., Martin, M.-C., Lefebvre, J., Kato, A., Bêty, J., Gauthier, G., Legagneux, P., 2021. COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species. Biol. Conserv. 255, 108968. DOI:10.1016/j.biocon.2021.108968

1.1 Résumé

Les espèces surabondantes peuvent avoir des impacts majeurs sur leurs habitats et induire des cascades trophiques au sein des écosystèmes. En Amérique du Nord, la population surabondante de la grande oie des neiges (*Anser caerulescens atlanticus*) est contrôlée par une chasse spéciale de printemps depuis 1999. La chasse est une source de mortalité mais également de dérangement, ce qui affecte le comportement et la dynamique d'engraissement des oies durant la halte migratoire. En 2020, le confinement imposé par la pandémie de COVID19 a réduit l'intensité de la chasse au Québec durant la halte migratoire printanière d'au moins 31%. Cela a fourni une opportunité unique d'évaluer les effets d'une réduction subite du dérangement causé par la chasse sur les oies. Nous avons utilisé des données à long terme de condition physique des oies combinées à des données sur le mouvement des oies suivies par GPS en 2019 et en 2020 pour déterminer les effets du confinement de 2020 sur leur condition physique et leur comportement au printemps. La condition physique des oies était plus élevée en 2020 que durant toutes les autres années depuis l'instauration de la chasse de printemps sauf 2019. Cependant, en 2020 les oies on atteint leur condition physique maximale plus tôt au printemps que durant toutes les autres années, et elles ont réduit de moitié leur temps passé à s'alimenter dans les champs agricoles, des habitats hautement profitables mais risqués, par rapport à 2019. Bien que notre étude n'ait pas été conçue pour évaluer les impacts du confinement, la réduction du dérangement en 2020 supporte l'hypothèse que celui-ci affecte négativement la dynamique d'engraissement et la condition physique des oies. Puisque la condition physique printanière est liée au succès reproducteur, le confinement pourrait avoir augmenté la productivité de cette population surabondante.

Mots clés: Confinement COVID19 · Chasse · Dérangement · Condition physique · Oie des neiges · Utilisation d'habitat

1.2 Abstract

Overabundant species can have major impacts on their habitat and induce trophic cascades within ecosystems. In North America, the overabundant greater snow goose (*Anser caerulescens atlanticus*) has been successfully controlled through special spring hunting regulations since 1999. Hunting is a source of mortality but also of disturbance, which affects the behavior and nutrient storage dynamics of staging snow geese. In 2020, the lockdown imposed by the COVID19 pandemic reduced hunting activity during their migratory stopover in Québec by at least 31%. This provided a unique opportunity to assess the effects of a sudden reduction in hunting disturbance on geese. We used long-term data on body mass combined with movement data from GPS-tracked birds in 2019 and 2020 to assess the effects of the 2020 lockdown on the spring body condition and behavior of greater snow geese. Body condition was higher in 2020 than in all years since the inception of spring hunting in 1999, except for 2019. However, in 2020 geese reached maximal body condition earlier during the staging period than in any other year and reduced by half time spent feeding in highly profitable but risky agricultural habitat in late spring compared to 2019. Although our study was not designed to evaluate the effects of the lockdown, the associated reduction in disturbance in 2020 supports the hypothesis that hunting-related disturbance negatively affects foraging efficiency and body condition in geese. Since spring body condition is related to subsequent breeding success, the lockdown could increase productivity in this overabundant population.

Keywords: COVID19 lockdown · Hunting · Disturbance · Body condition · Snow geese · Habitat use

1.3 Introduction

Predictable anthropogenic food subsidies, such as agriculture, livestock, fishing or waste, can be responsible for major changes in natural communities and ecosystem functioning (Oro et al., 2013). Exploitation of subsidies by wildlife is thought to have largely contributed to the demographic explosion of many species (Castro et al., 2005; Fox and Abraham, 2017; Oro et al., 2013; Rotem et al., 2011). Overabundant species that depend on those subsidies can have major impacts on their habitat and induce trophic cascades within ecosystems (Allombert et al., 2005; Flemming et al., 2019; Jefferies et al., 2004; Lamarre et al., 2017). The onset of industrial agricultural practices in North America provides a prime example as it was a key component in the unprecedented increase of many goose populations, and led to severe overgrazing of some tundra ecosystems (Abraham et al., 2005; Gauthier et al., 2005; Jefferies et al., 2004).

Hunting can be an effective tool to manage overabundant populations because it impacts survival and its effect is easily controlled through regulations (Cromsigt et al., 2013). The greater snow goose (*Anser caerulescens atlanticus*), a migratory species breeding in the Canadian Arctic, was declared overabundant after it underwent radical population growth and increased from ~25 000 to over 1 000 000 individuals between 1965 and 1999 (Gauthier et al., 2005, Lefebvre et al., 2017). In 1998, wildlife management authorities liberalized hunting regulations for this species to stop population growth and prevent the potentially devastating impacts that such numbers of geese could have on tundra plant communities (Batt, 1998; Reed and Calvert, 2007). The most significant measure implemented was a special spring hunting season (legally referred to as the Conservation Harvest) introduced in 1999 in the Québec province, followed by a new extended winter hunting season with very liberal hunting regulations (the Conservation Order) introduced in winter 2009 in Eastern USA. These management actions were a success as the population stopped growing and has been oscillating between 750 000 and 1 000 000 individuals since 1999 (Lefebvre et al., 2017). From 1999 onwards, snow geese were hunted almost year-round: from their arrival on the Québec staging grounds in early fall until their departure from the same staging grounds to the Arctic in the following spring. This dramatic increase in hunting pressure induced a reduction in population growth primarily through a decrease in adult survival, which declined from 83.0% in 1990-1998 to 72.5% in 1999-2002, the first years of the Conservation Harvest (Calvert and Gauthier, 2005).

Because overabundant geese also cause damage to farmlands (Filion et al., 1998), the Québec agricultural producers' union has been conducting organized scaring activities to limit depredation since 1999. People are hired to patrol agricultural areas and drive geese away from fields in a coordinated effort. Disturbance caused by hunting and scaring activities can have major impacts on several waterfowl species (Bélanger and Bédard, 1990; Madsen, 1995; Madsen and Fox, 1995). In greater snow geese, such disturbances during staging increase energy expenditure and reduce nutrient storage and overall body condition prior to the spring migration to the Arctic (Béchet et al., 2004; Féret et al., 2003). A reduction in body condition during a critical part of the annual

cycle when geese are fattening has been shown to negatively affect breeding (Bêty et al., 2003; Legagneux et al., 2012). Indeed, in the first two years following the implementation of the Conservation Harvest, body condition of nesting geese was reduced by 28%, breeding propensity was dramatically reduced, laying date was delayed by 2-7 days and clutch size was reduced by 1.5 eggs (Mainguy et al., 2002). The recruitment rate of females into the breeding population and the proportion of young in the fall flock also declined after implementation of the Conservation Harvest (Juillet et al., 2012; Morrissette et al., 2010).

In spring 2020, the lockdown imposed in response to the COVID19 pandemic provided an unprecedented opportunity to document how wildlife responds to large-scale reductions in human activities (Bates et al., 2020; Corlett et al., 2020; Manenti et al., 2020; Rutz et al., 2020). In Québec, the government declared a generalized lockdown on March 16th, 2020, which was fully enforced by March 23rd and lasted until May 4th, after which restrictions were gradually lifted over the next 4 weeks. During the lockdown, all economic activities, except essential services such as agriculture, were stopped and people were largely confined in their homes, with movements between regions forbidden. We anticipated that the lockdown reduced hunting pressure and scaring activities on greater snow geese staging in southern Québec. Reductions in hunting and scaring disturbance on the main stopover area has a strong potential to positively affect the foraging efficiency, energy budget and spring body condition of geese, which could lead to higher reproductive output in the subsequent breeding season (Morrissette et al., 2010).

The negative impacts of the spring Conservation Harvest on goose body condition were driven by changes in movements and behavior, as documented through a before-after-impact design by Béchet et al. (2003, 2004), and Féret et al. (2003). In this study we first determine the magnitude of the reduction in hunting activity associated with the lockdown. Using data from previous studies (collected in 10 springs between 1979 and 2009), along with new data acquired in 2019 and 2020, we then assess the impact of a reduction in hunting pressure on the behavior and body condition of spring staging geese.

Agricultural fields provide a high-quality foraging habitat for geese due to the presence of nutrient-rich crops (Bédard and Gauthier, 1989; Giroux and Bergeron, 1996); however, they are a riskier habitat than marshes because geese are exposed to hunters unlike in marshes where hunting is forbidden in spring. Geese usually commute daily between roosting sites in marshes, where some feeding can also occur, to farmlands which are predominantly used for foraging. Geese foraging in fields are exposed to disturbance and threats like scaring by farmers protecting their crops and, most importantly, hunting since 1999. The Conservation Harvest disrupted goose foraging behavior in agricultural fields by shortening foraging bouts and increasing flying time, which ultimately reduced their energy intake (Béchet et al., 2004). During spring 2020, we would expect a dampening of these conditions as a reduction in disturbance should lead to longer, uninterrupted foraging bouts, less time

spent flying and an increased energy intake rate in agricultural fields, particularly in the first half of staging when the lockdown was strictest. Based on this hypothesis, we predicted that during the COVID19 lockdown, staging geese should accumulate more nutrient reserves, and reach a better body condition more rapidly compared to previous years. We also predicted that geese should spend less time in risky agricultural fields at the end of the staging period, when we were able to track their movements. Indeed, if nutrient accumulation was more rapid in 2020 than in 2019 as expected, birds in good condition near the end of the staging period should be less prone to use a riskier habitat (cropfields) where hunting could occur, than the marsh habitat where hunting was always prohibited.

1.4 Methods

1.4.1 Data acquisition

Study model and site

Greater snow geese winter along the Atlantic coast of the United States and breed in the eastern high Arctic (Fig. 1.1). In spring, they migrate north through eastern Canada and stage in southern Québec between late March and late May (Reed et al., 1998). During this stopover, geese fatten up as they accumulate the large endogenous reserves needed to complete their migration and subsequent reproduction (Gauthier et al., 1992, 2003). Traditionally, snow geese fed on *Schoenoplectus americanus* in tidal marshes, but have been increasingly relying on corn and hay in farmlands since the 1980s, a higher-quality food source (Bédard and Gauthier, 1989; Gauthier et al., 2005). Since 1999, hunting occurs from April 15th to May 31st in Québec (April 1st since 2000) and solely takes place on agricultural lands, inducing potential trade-offs between the risk of getting shot and the access to highly profitable food resources (Béchet et al., 2004).

Capture procedures

Geese were captured in spring during the migratory staging period at Île-aux-Oies (47°08N 70°29W, Fig. 1.2), a small agricultural island in the Saint-Lawrence estuary, 60 km northeast of Québec City (Canada). We used baited canon-nets placed in fields to capture geese between late April and mid-May every year between 2006 and 2009 as well as in 2019 and 2020 (see Morez et al., 2000 for details and Fig. S1.1 for timing of captures). The firing of cannon-nets (6 to 15 cannon-netting events over a 3-week period) represents a negligible source of disturbance for the goose population considering that this activity occurred over <0.01% of the area used by staging geese in spring. Adults were sexed based on cloacal examination. Females were weighed to the nearest gram with an electronic balance and culmen and tarsus were measured to the nearest 0.1mm using calipers (n= 499 in 2006, 715 in 2007, 650 in 2008, 686 in 2009, 370 in 2019 and 193 in 2020). Large adult females were equipped with GPS-GSM collars (OrniTrack-N44 - neck collar solar-powered GPS-GSM tracker, 45g,

approximately 1.5% body mass) in 2019 (n=10) and 2020 (n=5) and were tracked ever since. Collars were programmed to record location every 5 minutes from 3:00AM to 11:00PM. Geese were released together either immediately after handling when captures occurred during the day or the following morning when handling ended after dark to avoid disorientation. In 2020, special protective equipment was used when handling birds to avoid any cross-contamination between human and geese (Frederick et al., 2021). All manipulations conducted in 2019 and 2020 were approved by the Committee of Animal Protection of our institution.

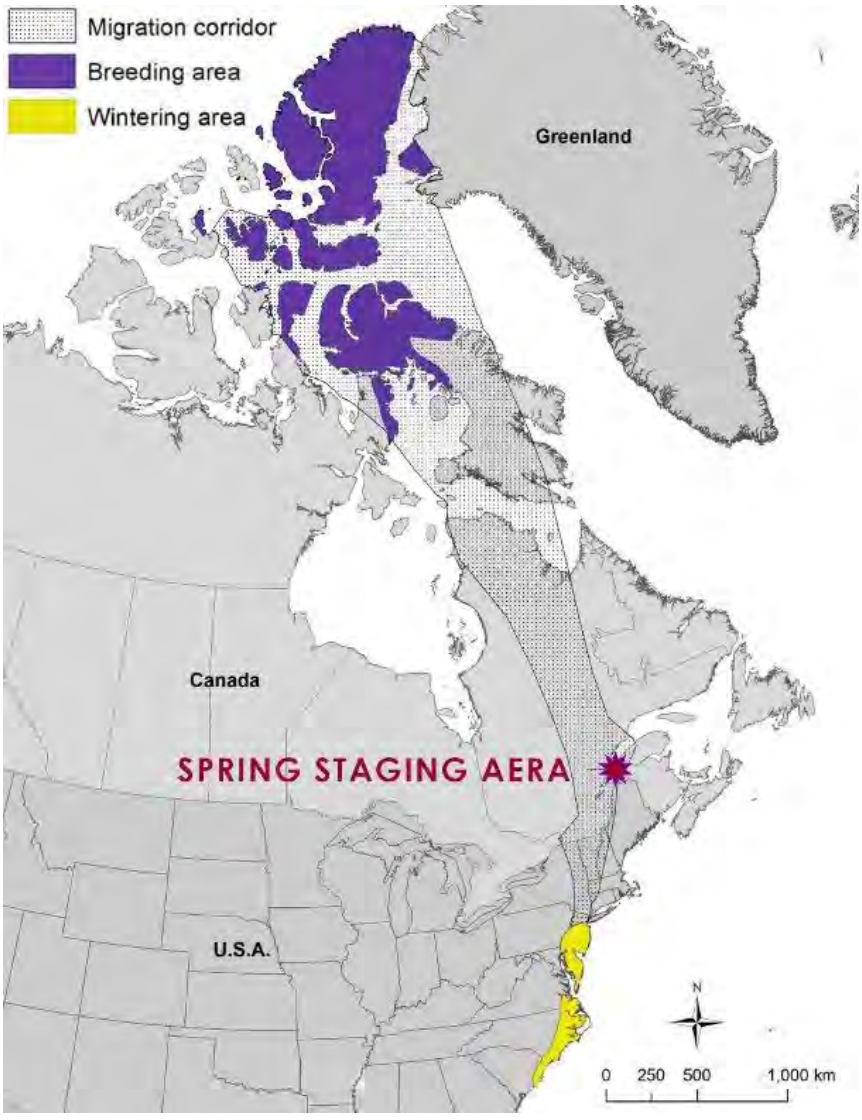

Figure 1.1 Map of the breeding (purple), wintering (yellow) and staging areas (red star) of the migratory greater snow goose population. The hatched polygon represents the migratory flyway. This map was modified from Lefebvre et al. (2017).

To compare goose body condition between years, we retrieved original data on geese collected in 1979 and 1980 by Gauthier et al. (1984), in 1989 and 1990 by Gauthier et al. (1992), and in 1999 and 2000 by Féret et al. (2003). In 1979 and 1980, geese were shot throughout the staging grounds under special scientific permit, stored frozen in plastic bags and weighed in the laboratory (*n*= 91 in 1979 and 84 in 1980). Between 1989 and 2000, geese were captured with baited canon nets at three sites along the St-Lawrence River. A random sample of females were killed by lethal injection, stored in plastic bags and frozen (*n*= 38 in 1989; 39 in 1990, 92 in 1999 and 148 in 2000). Geese were subsequently weighed to the nearest gram (except in 1990 where birds were weighed in the field, to the nearest 25g) and culmen and tarsus measurements were taken in the laboratory. Fluid loss is possible but was likely minimal because carcasses were rapidly frozen after collection and weighed before thawing. Body masses from all years are thus comparable.

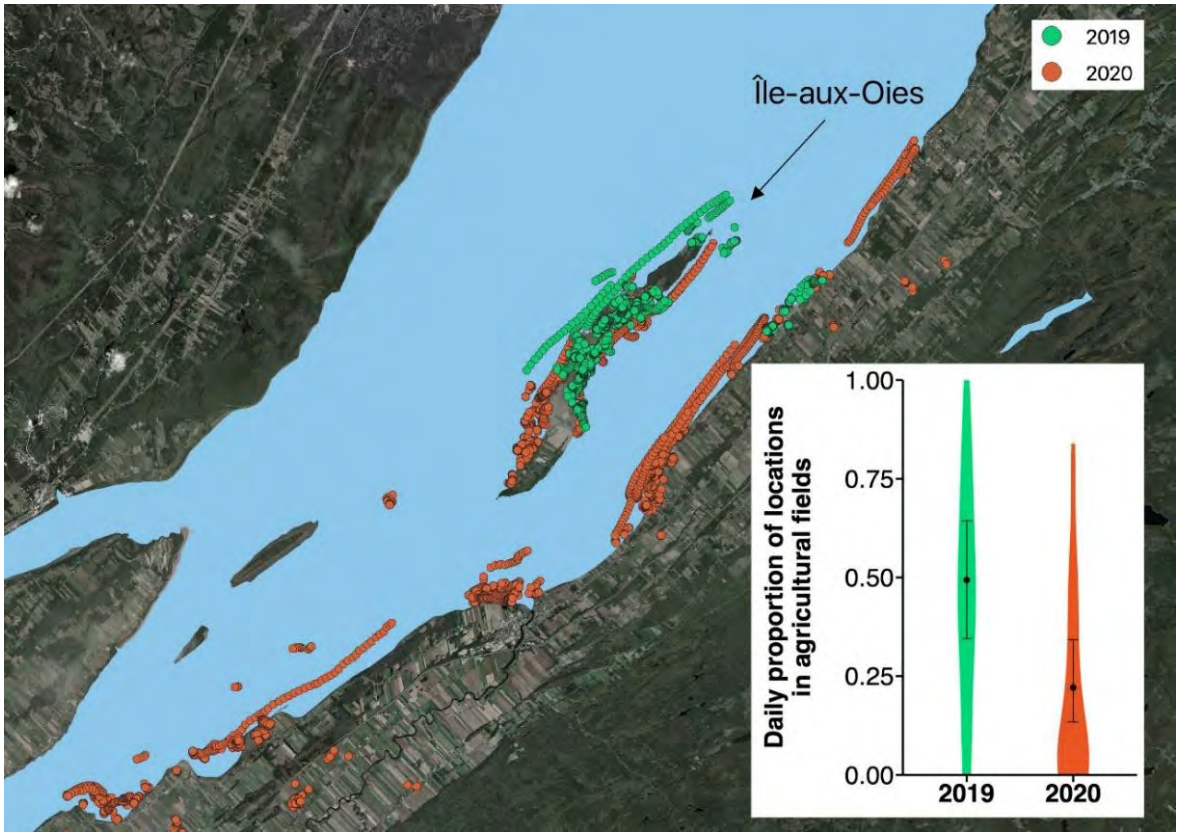

Figure 1.2 Locations of the four GPS-collared snow geese tracked near the end of the staging period from May 6th to 24th in both 2019 (green dots) and 2020 (orange dots) in the St. Lawrence estuary. All geese were captured and marked at Île-aux-Oies, which explains the larger concentration of dots there in 2019, the year of marking. Restricting the analysis to only the Île-aux-Oies area did not affect the proportion of locations in agricultural fields in either year. Window: average daily proportion of locations recorded in fields by the same individuals (*n*=4) tracked in 2019 and 2020. Error bars are 95% CI and colored shading represents the density distribution of individual data points.

1.4.2 Statistical analyses

Body condition

To compare body condition among individuals, we needed a non-invasive measure of endogenous reserves that was independent of structural size. Following the procedure described in Féret et al. (2003), we ran a principal component analysis (PCA) on two skeletal measurements (culmen and tarsus lengths) and used the resulting first principal component (PC1) as a measure of relative body size. Loadings for the two variables were above 0.5 and the first axis explained over 50% of the overall variation. We then used the residuals of the regression between individual body mass and PC1 to which we added the average mass of the population as a measure of relative mass corrected for skeletal size. We validated that this index was a reliable indicator of endogenous reserves using a dataset of 90 females randomly sacrificed during captures in 2006, 2007 and 2008 and for which fresh abdominal fat was weighed (data from Legagneux et al., 2013). Our condition index was related to fat mass values ($F_{1,88}$ = 52.9; p<0.001; adjusted R^2=0.37).

We first assessed the potential effect of a reduction in hunting-related disturbance due to the COVID19 lockdown on overall body condition. Because geese gain approximately 10g per day during spring staging, and because birds are captured on different dates in different years (Fig. S1.1), we adjusted our condition index to take this daily mass gain into account. Thus, we corrected individual condition to a single date near the end of staging (May 12th) using the average daily mass gain for all years pooled. We obtained the average daily mass gain by fitting polynomial regressions with mass adjusted for skeletal size as a response variable, day of year as a fixed effect and year as a random intercept. Candidate models were fitted up to the 5th degree, and we selected the most parsimonious of equivalent models (ΔAICc<2; see Fig. S1.2 for selected date adjustment model) using Akaike Information Criterion (AICc; Burnham and Anderson, 2002). The resulting index provides a measure of body condition independent of skeletal size and capture date. We inferred hunting disturbance using three yearly metrics of hunting pressure in spring: total number of geese harvested in a hunting season ("harvest" from here on), number of active hunters and total number of hunting days. This is determined annually by wildlife agencies who conduct standard surveys among a large sample of hunters (data provided by M. Gendron, Environment and Climate Change Canada). We examined the relationship between body mass corrected for structural size and our three metrics of hunting pressure (fixed effect) using separate linear mixed models with capture ID and year as random intercepts to account for the block structure of the data. Next, we compared overall body condition between years. We compared average body condition corrected for size and date among years using a linear mixed model with year as a fixed effect and again capture ID as random intercepts.

Because disturbance could act on the rate at which geese gain mass during spring staging, we compared the rate of condition increase in 2020 to years with hunting for which data was available over a comparable period

(2007, 2008, 2009, 2019; Fig S1.1). We fitted a linear mixed model with body condition index (mass adjusted for skeletal size only; see above) as the response variable. Year, date and their interaction were fitted as fixed effects and capture number as random intercepts. We fitted the fixed effect as a 3-level variable comparing 2020, 2019 and 2007-2009. The year 2019 was fitted as a separate level because goose body condition and weather conditions were similar to 2020 (see section 1.5.2 and Fig. S1.3) and we were thus interested in this specific contrast.

For all models described above, we tested and validated the assumptions of normality, homoscedasticity, non-collinearity among fixed effects, and independence of residuals. Linear mixed models were fitted using the `lmer` function of package `lme4` (Bates et al., 2015). All statistical analyses were conducted in the R statistical environment (version 4.0.1, R Core Team, 2020) and all estimates are reported with their 95% confidence intervals throughout.

Habitat use

We used locations of radio-marked geese at Île-aux-Oies and in the surrounding area to compare the use of the two main habitats used by geese: tidal marsh areas and agricultural fields (Fig. 1.2). We classified agricultural fields and marshes in our study area by hand using the `Esri.WorldImagery` base map from package `mapedit` (Appelhans et al., 2020) in R (R Core Team, 2020). Location data was collected during the same period in both years, from May 6th to 24th, near the end of the staging period. We only considered locations from sunrise to sunset because geese do not use farmlands at night (Gauthier et al., 1988), and hunting is only permitted during the day. In addition, because locations taken during flight may not reflect habitat use on the ground, we removed them from the analysis. We computed the speed between each pair of consecutive points (distance covered divided by time elapsed between locations) and eliminated locations for which the average speed to the next point was above 10km/h (376/10991, ~3%). We visually assessed our classification and there were few errors (~70 points, <0.7%).

We computed the proportion of locations in agricultural fields vs. in tidal marshes every day for the individuals tracked in both years (n = 4 individuals; 68 individual-days total over both years). The number of days considered ranges from 4 to 16 per individual, depending on the number of days individuals spent in the study area (Fig. 1.2) in each year. To compare the proportion of locations on land between years, we fitted a generalized linear mixed-model with a binomial distribution using Penalized Quasi-Likelihood to account for overdispersion using the `glmmPQL` function in the MASS package (Ripley et al., 2020) in R (R Core Team, 2020). The model was fitted with year and day of year (to account for potential temporal trends in habitat use) as fixed effects and bird ID as random intercepts to account for repeated measurements on individuals. Finally, we ran a second analysis with all collared individuals (n=15), but only using data from the year in which each individual was captured.

1.5 Results

1.5.1 Lockdown impacts on sources of disturbance

The travel restrictions imposed by the lockdown reduced overall hunting pressure and goose harvest in spring 2020 as we expected. Data on hunting activity showed a decrease of 54% in the number of active hunters, 32% in hunting days and 31% in geese harvested in 2020 compared to 2019 (Fig. 1.3 and Appendix S1.4). Organized scaring activities aimed at chasing goose flocks from farmlands throughout the province were also affected due to the difficulty of recruiting staff during the lockdown. The number of scaring events in spring 2020 (1501 events) was 28% lower than in 2019 (2017) and 46% lower than in 2018 (2798) (Union des producteurs agricoles du Québec, unpubl. data).

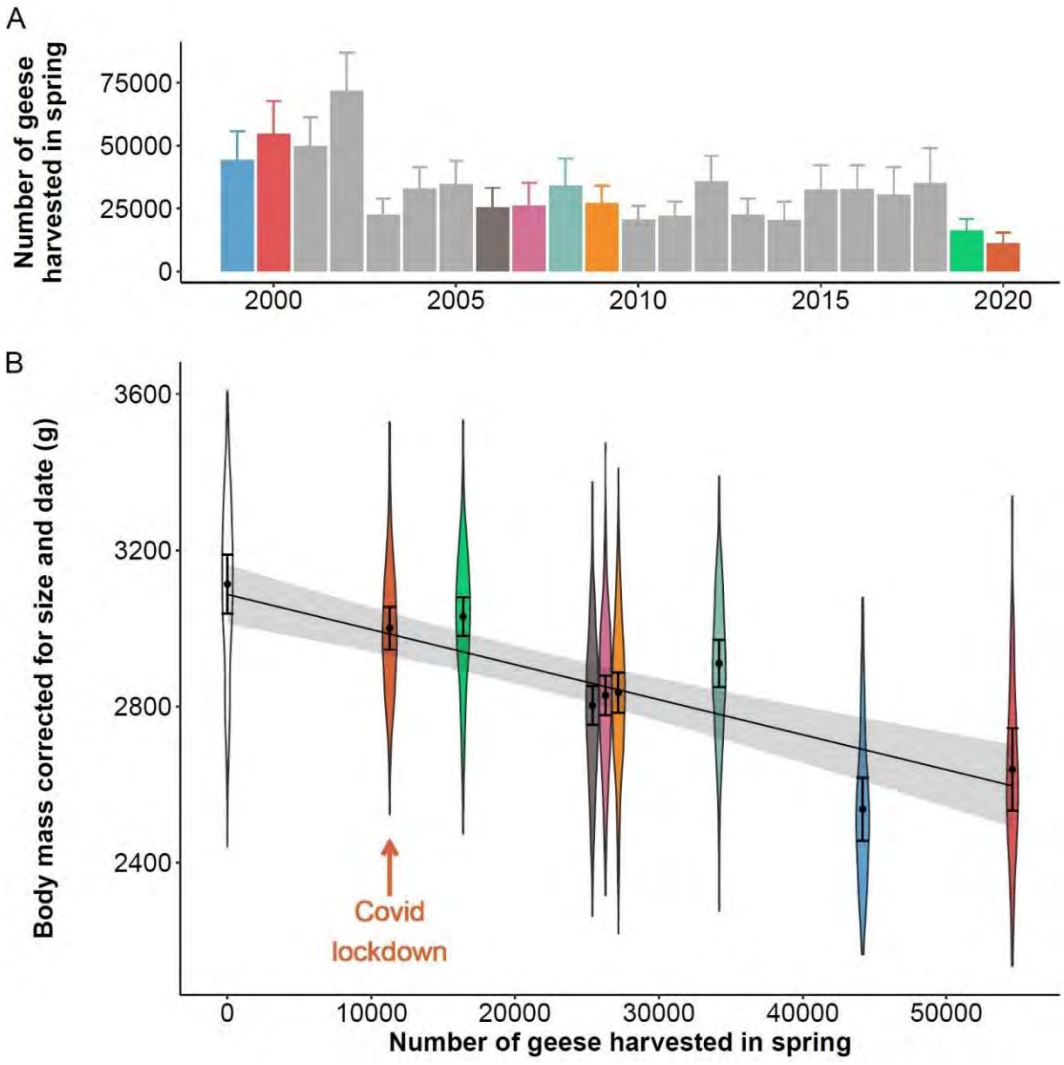

Figure 1.3 A: Annual spring harvest of greater snow goose from 1999 to 2020. Error bars represent 95% confidence intervals. Colored bars represent years for which data on body condition is available. B: Spring body condition of geese at the end of the staging period in relation to annual spring harvest. Values at 0 harvest (white

violin) correspond to years without a spring Conservation Harvest (before 1999). The black line represents the mean model predictions based on individual data points with its 95% CI (shaded; regression slope [95%CI]: -0.009 g/goose harvested [-0.012, -0.006], n = 3460). Black dots and error bars are the mean body mass with their 95% CI for each harvest level and color shading represents the density distribution of individual data points. Source of hunting statistics: Smith and Gendron 2020.

1.5.2 Body condition

The body condition index of geese adjusted to May 12th was high in all springs without hunting despite some annual variation. Average condition was highest in 1979 and 1980, before the spring Conservation Harvest was implemented, and lowest in 1999 and 2000, the first two years following its implementation (Fig 1.4). Average body condition in spring 2020 was higher than in all other years with a spring Conservation Harvest, apart from 2019 when body condition was similarly high (See Table 1.1; Fig 1.4). Overall, we found a strong inverse relationship between the body condition of birds and the intensity of the Conservation Harvest (Fig. 1.3 and Appendix S1.4). Body condition was negatively related with yearly spring harvest (Estimate = -0.009 [-0.012, -0.006] g/goose harvested).

Table 1.1 Parameter estimates of the linear mixed model comparing adjusted body mass of greater snow geese among years. *Intercept (2020)* represents the average body condition (in g) in 2020. Other estimates represent the difference (in g) in average body condition with 2020. Estimates in bold are significantly different than 2020 (n = 3460).

Year	Estimate	95% CI
Intercept (2020)	3000	2953.7, 3046.1
1979	143.9	76.8, 211.1
1980	163.4	88.8, 237.8
1989	-77.3	-191.0, 36.8
1990	4.6	-107.3, 117.2
1999	-463.5	-541.7, -384.9
2000	-361.5	-435.8, -287.9
2006	-197.9	-253.1, -142.6
2007	-172.0	-224.2, -119.2
2008	-90.2	-142.8, -38.2
2009	-164.3	-216.1, -112.5
2019	29.5	-29.1, 87.5

Daily increase in body condition index in spring 2020 differed from recent years with a spring Conservation Harvest (2007-2009, 2019; Table 1.2, Fig. 1.5). On average, goose body condition in 2019 increased by 9.8 [2.4, 17.3] g/day, a value similar to 2007-2009 (11.3 [9.2, 13.8] g/day, Table 1.2). In contrast, there was no detectable increase in body condition during the same period in 2020 (-5.5 [-14.8, 3.8] g/day), suggesting that geese had reached an optimal body condition earlier in that year.

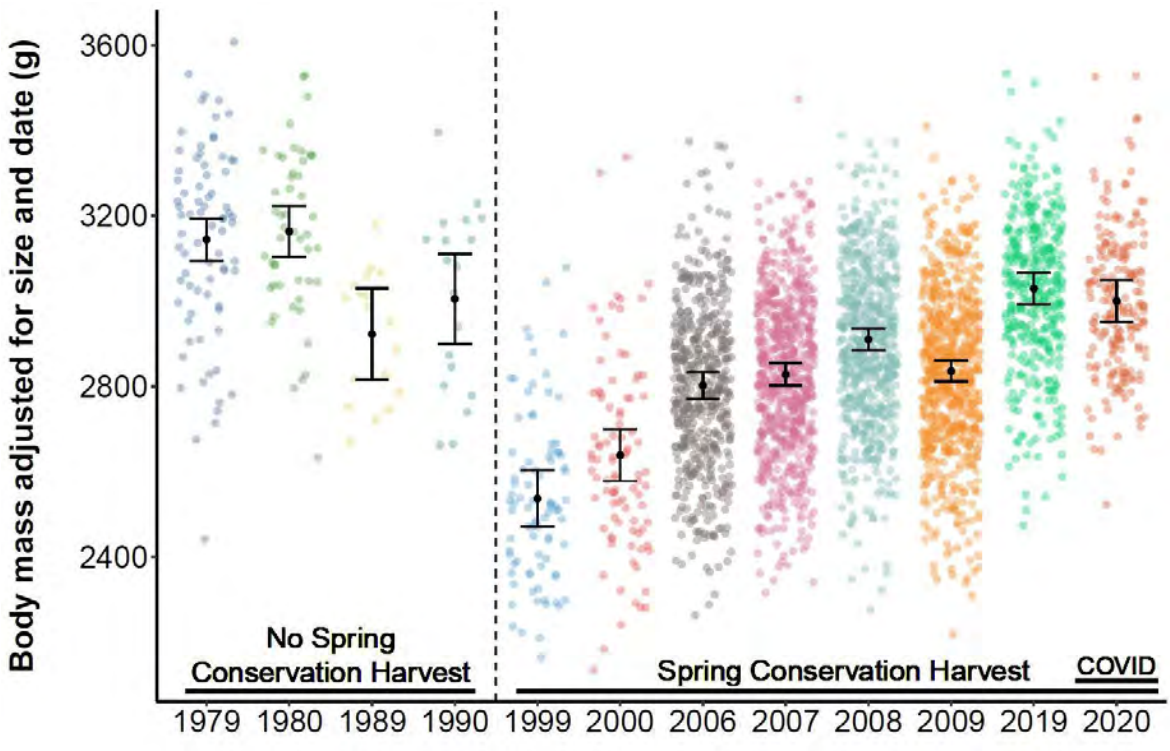

Figure 1.4 Annual variation in greater snow goose body condition index during spring migratory stopover in Québec. Points are individual body masses corrected for skeletal size and adjusted to May 12th. The black dots and error bars represent average annual body mass with their 95% confidence intervals.

Table 1.2 Parameter estimates of the linear mixed model testing the influence of year, date and their interaction on adjusted body mass of greater snow geese. *Date(2020)* is the average daily increase in body condition (g/d) in May 2020. The interactions *date*2007 – 2009* and *date*2019* represent differences in daily increase in body condition between 2020 and 2007 – 2009 or 2019, respectively. Significant effects are in bold. Model parameters other than effects of interest are in pale gray (n = 2616).

Effect	Estimate	95% CI
2020 (intercept)	3718.3	2465.6, 4970.9
2007 - 2009	-2374.5	-3680.1, -1104.5
2019	-2010.2	-3595.6, -424.7
Date (2020)	-5.5	-14.8, 3.8
Date * 2007 – 2009	16.8	7.4, 26.6
Date * 2019	15.3	3.4, 27.2

1.5.3 Habitat use

During the COVID19 lockdown, the relative use of agricultural fields by geese during the late staging period was reduced by 57% on average as the proportion of locations in this habitat decreased from 0.49 [0.35, 0.63] in 2019 to 0.21 [0.12, 0.30] in 2020 (Fig. 1.2). Geese thus spent more time in agricultural fields during daytime in the 2 to 3 weeks preceding departure for migration in 2019 compared to 2020, and conversely less time in tidal

marshes. Strikingly similar results were obtained when data from all GPS-marked individuals are analyzed (see Appendix S1.5).

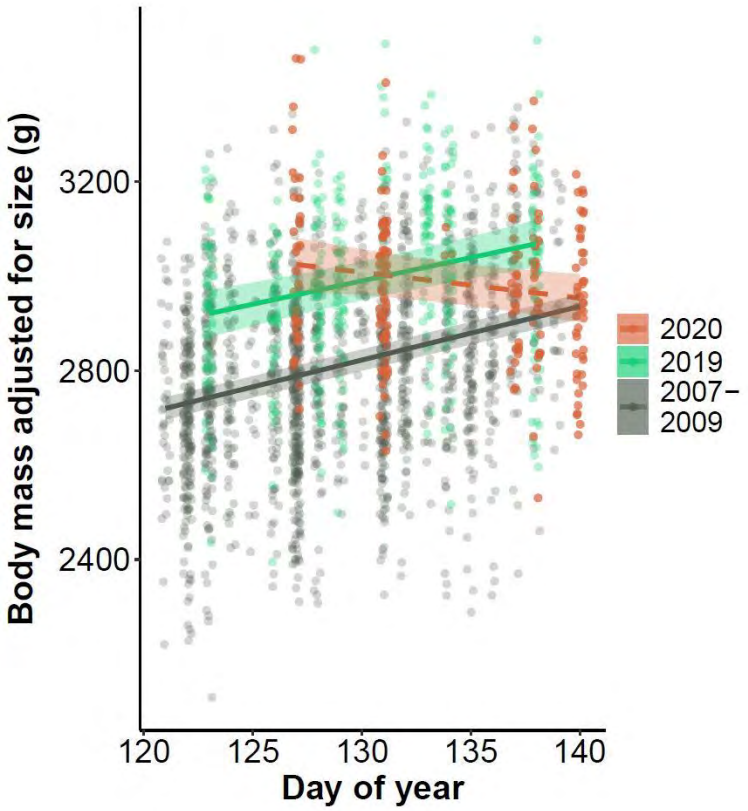

Figure 1.5 Body condition index (mass corrected for body size) of greater snow geese in relation with date for 2019 (green), 2020 (orange) and years with a spring Conservation Harvest and sampling dates comparable to 2020 (2007 – 2009; grey). Lines are the mean model predictions with their 95% CI (shading) and represent the increase in goose body condition at the end of their migratory stopover in Québec. Full lines represent significant relationships and the dashed line a non-significant relationship (2020).

1.6 Discussion

We took advantage of the unplanned COVID19 lockdown (Bates et al., 2020) and the ensuing reduction in hunting and scaring activities in southern Québec to opportunistically evaluate the impact of reduced disturbance on goose body condition and habitat use. By comparing body condition near the end of staging in 2019 and 2020 to historical information, we found that body condition in those two years was the highest since the implementation of the spring Conservation Harvest. However, our results suggest that body condition plateaued earlier in 2020 than in 2019 as it was already maximum at the onset of our captures at the beginning of May. This sets 2020 apart from 2019, where body condition was also high but increased throughout the capture period, as observed in other years. Finally, geese spent less time in agricultural fields near the end of staging in 2020 compared to 2019. Taken together, our results suggest that the reduction of hunting- and scaring-related disturbance during the COVID19 lockdown allowed geese to build fat reserves faster and reach an optimal body condition for their northward migration earlier than in previous years, which led to a change in habitat use near the end of staging.

1.6.1 Body condition

Body condition was particularly high in spring 2020, among the highest in our historical data and higher than all years with a spring Conservation Harvest, except 2019. Because of the known effect of disturbance on goose foraging behavior (Béchet et al., 2004; Klaassen et al., 2006; Nolet et al., 2016), the low hunting pressure in 2020 likely contributed to the high spring body condition of birds in that year and probably also in 2019. Indeed, even though harvest was lower in 2020 than in 2019, it was already moderate in the latter year, being 35% lower than the average harvest of the preceding decade (Fig 1.3A). Previous studies showed that geese collected on the spring staging grounds in the first two years following the implementation of the spring Conservation Harvest (1999 and 2000), when hunting pressure was at its maximum, had considerably reduced fat and protein stores compared to years without hunting (Féret et al., 2003). Our results thus further reinforce previous conclusions that spring hunting affects dynamics of nutrient storage in this species by clearly showing that the body condition of geese at the end of the staging period is affected by the intensity of the spring hunting activity. Therefore, it is not surprising that body condition in spring 2020 was comparable to that observed before the implementation of the spring Conservation Harvest.

However, other factors than hunting disturbance can also affect body condition of spring-staging geese. One factor is weather conditions during spring staging, which may affect timing of snowmelt and the onset of plant growth in farmlands. For instance, the springs of 2019 and 2020 were both cool with a late snowmelt (Fig. S1.3), conditions that generally benefit geese because plants grow more slowly and remain more nutritious (i.e. more protein and less indigestible fiber) for a longer period in spring (Bédard and Gauthier, 1989; Manseau and Gauthier, 1993). These conditions may thus also have contributed to the high body condition of geese in both 2019 and 2020. Presence of juveniles in spring may cause intra-family competition and interfere with foraging activity of their parents (Turcotte and Bédard, 1989). In spring 2019, there were very few juvenile birds in the population (2.5% of captured birds were juveniles) due to a widespread breeding failure of geese in 2018, whereas the opposite situation prevailed in spring 2020, with many juveniles in the population (22.1% of captured birds were juveniles). This factor may have facilitated fattening of geese in spring 2019 compared to 2020 and could explain why body condition at the end of the staging period was similar in both years despite a higher hunting pressure in 2019. An alternative explanation for the high condition of geese reached early in the season in 2020 could be that they arrived from the US wintering grounds already in high condition prior to the onset of the lockdown. However, observations of abdominal profiles of geese in 2020, a reliable index of goose body condition (Féret et al., 2005), allowed us to refute this explanation. Indeed, observations spanning the entire spring staging period (late-March to mid-May) revealed that geese arrived in Québec in low body condition and fattened considerably throughout the COVID19 lockdown period (Fig. S1.7), which is a typical pattern for geese in spring (Gauthier et al., 1992).

1.6.2 Habitat use

The most likely explanation for the high body condition of geese reached earlier in 2020 than in any other year is improved foraging in farmlands early in the staging period, when the lockdown restrictions were most severe. Indeed, geese were likely able to complete longer, undisturbed foraging bouts and maximize their foraging efficiency in farmlands in early spring 2020 due to reduced disturbance (Béchet et al., 2004). Farmlands are a high-quality feeding habitat for geese because they feed on spilled grain and young shoots. These are more profitable food items than rhizomes, their primary food source in tidal marshes in spring, which are difficult and costly to extract from the ground (Bédard and Gauthier, 1989; Dokter et al., 2018; Pot et al., 2019). Nonetheless, farmlands undoubtedly remained a risky habitat for geese in 2020 because, unlike tidal marshes, hunting and scaring activity still occurred there, albeit at a reduced rate. This is why we expected that, if geese were able to complete their fattening earlier during the lockdown, they should reduce their time spent feeding in farmlands and spend more time resting in the tidal marshes near the end of staging. This pattern is exactly what we observe. Indeed, contrary to 2019 when geese heavily used farmlands and continued to gain condition until the end of staging, in 2020 they reduced considerably their use of farmlands after reaching a high body condition. It is also possible that, as travel restrictions within Québec started to be lifted in May, more hunting activity took place at the end of staging than at the beginning. This could have further encouraged geese to spend less time in farmlands and more time in marshes in late spring. Unfortunately, we do not have data on the temporal pattern of hunter activity in spring to test this idea. In summary, the high body condition of birds reached early in spring 2020 may have shifted the trade-off between food acquisition in a risky habitat (agricultural fields) and safety (natural marshes) at the end of staging, leading to the observed reduction of time spent in the former habitat.

1.6.3 Limitations

The data presented in this study was not collected with the objective of comparing seasonal variations in body condition or habitat used by geese, and the effects uncovered here should therefore be interpreted cautiously. There is much inter-individual and inter-annual variation in goose body condition, likely influenced by factors such as weather conditions in winter and presence of young in the population. Because the COVID19 lockdown is a punctual event, its effect is partly confounded with year effect. Moreover, it is also possible that geese have habituated to hunting activity in spring since its implementation 20 years ago and modified their behavior accordingly. However, the clear relationship between body condition and hunting pressure observed in our results supports the conclusion that the lockdown-related reduction in hunting and scaring disturbance affected dynamics of nutrient storage in spring-staging snow geese.

Start of field work was delayed in 2020 due to the special authorizations required during the lockdown, which resulted in a reduction in the number of captures (n=6 vs. 9-15 between 2006 and 2019) and slightly later capture

dates. There was thus little overlap in dates between 2020 and some other years with body condition data (e.g. 1999, 2000 and 2006; Fig. S1.1), making the comparison between these years challenging. To account for this, we restricted the analysis on body condition increase to years with similar capture dates and we only compared overall body condition after adjusting for the effect of sampling date.

In spring 2019, tracked geese had recently been fitted with GPS-GSM collars for the period considered in our habitat use analysis. While we excluded the first day after collars were fitted from our analysis, collars may affect behavior in the first few weeks after being fitted on a bird, for example by increasing preening or head-shaking to get rid of the collar (Kölzsch et al., 2016). Still, this should have little impact on the habitat use pattern of individuals in this gregarious species because they mostly commute between marshes and farmlands in large groups. Moreover, restricting the analyses to only birds tracked in both 2019 and 2020 or using all birds yielded identical results, suggesting that our habitat use data were robust.

Data collected in the upcoming years will provide the opportunity to revisit the conclusions of this paper with a before-after impact design (Osenberg and Schmitt, 1996). According to the mechanisms proposed here, if disturbance due to hunting and scaring increases in the future relative to 2020, foraging efficiency in agricultural land should decrease and lead to a new reduction in body condition.

1.7 Conclusion

The overabundance of snow geese has been shown to negatively affect plant communities through overgrazing in several regions (Jano et al., 1998), as well as other arctic-nesting species through apparent competition (Lamarre et al., 2017). These effects played an important role in the decision of liberalizing hunting regulations to limit the growth of this population (Lefebvre et al., 2017). Moreover, goose overabundance was the source of important conflicts with farmers, who suffer depredation losses to geese in Québec. Following the establishment of a special spring hunt in 1999, production of young was reduced, and population growth stopped (Lefebvre et al., 2017). Taking advantage of a release in hunting pressure associated with the COVID19 lockdown in 2020, our results, combined with long-term data on harvest and body condition, show that spring hunting activity still negatively impacts the body condition of spring staging geese twenty years after its implementation. Our study provides useful insights for the management of this overabundant population. Indeed, the high body condition achieved by geese due in part to reduced hunting activity during the COVID19 lockdown may improve reproductive success and lead to high recruitment of young, thereby fueling additional population growth. At a broader level, our study further emphasizes that sustained human disturbance during a critical period of the life cycle, i.e., spring staging, interferes with the nutrient storage dynamics of a long-distance migrant even after being exposed to these sources of disturbance for more than two decades. This suggests no or little long-term

habituation, which may have consequences for the reproduction and ultimately the population growth of species exposed to such disturbances.

1.8 Acknowledgements

We would like to thank C. Girard, C. Geoffroy, M. Belke-Brea, G. Picard for assistance in the field, M.-C. Cadieux for managing our databases, A. Langwieder for proof-reading the manuscript, Z. Tolszczuk-Leclerc for help with figures and M. Séguin and A. Desmarais for providing fieldwork facilities. We thank A. Smith and M. Gendron from Environment and Climate Change Canada for providing data on hunting pressure and G. Charron from the Québec's agricultural producers' union for providing data on scaring activities. We acknowledge funding from the Natural Sciences and Engineering Council of Canada (RGPIN-2019-05185), Fonds de recherche du Québec Nature et Technologies (271544), Sentinelle Nord program from the Canada First Research Excellence Fund and the Network of Centre of Excellence of Canada (ArcticNET; PP12). All bird handling and fieldwork protocols were conducted according to the relevant national and institutional regulations on animal welfare and were approved by the 'Comité de Protection des Animaux de l'Université Laval' (CPAUL # 2019-304, delivered on 2020-03-02) and the Canadian Bird Banding Office (permit #10648, delivered on 2020-04-22).

1.9 Supplementary material

Annexe S1.1 – Dates of data acquisition

Annexe S1.2 – Selected model to adjust mass for the effect of date

Annexe S1.3 – Weather data

Annexe S1.4 – Hunting pressure metrics

Annexe S1.5 – Analysis of habitat use for all GPS-marked birds

Annexe S1.6 – Abdominal profile scores

1.10 Bibliography

Abraham, K.F., Jefferies, R.L., Alisauskas, R.T., 2005. The dynamics of landscape change and snow geese in mid-continent North America. Glob. Chang. Biol. 11, 841–855. https://doi.org/10.1111/j.1365-2486.2005.00943.x

Allombert, S., Stockton, S., Martin, J.-L., 2005. A Natural Experiment on the Impact of Overabundant Deer on Forest Invertebrates. Conserv. Biol. 19, 1917–1929. https://doi.org/10.1111/j.1523-1739.2005.00280.x

Appelhans, T., Russell, K., Busetto, L., O'Brien, J., Gutschlhofer, J., 2020. mapedit: Interactive editing of spatial data in R.

Bates, A.E., Primack, R.B., Moraga, P., Duarte, C.M., 2020. COVID-19 pandemic and associated lockdown as a "Global Human Confinement Experiment" to investigate biodiversity conservation. Biol. Conserv. 248, 108665. https://doi.org/10.1016/j.biocon.2020.108665

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Batt, B.D.J., 1998. The greater snow goose: report of the arctic goose habitat working group. U.S. Fish and Wildlife Service, and Canadian Wildlife Service, Washington, D.C., and Ottawa, Ontario.

Béchet, A., Giroux, J.-F., Gauthier, G., 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese: Effects of hunting on snow geese behaviour. J. Appl. Ecol. 41, 689–700. https://doi.org/10.1111/j.0021-8901.2004.00928.x

Béchet, A., Giroux, J.-F., Gauthier, G., Nichols, J.D., Hines, J.E., 2003. Spring hunting changes the regional movements of migrating greater snow geese. J. Appl. Ecol. 40, 553–564. https://doi.org/10.1046/j.1365-2664.2003.00812.x

Bédard, J., Gauthier, G., 1989. Comparative energy budgets of greater snow geese Chen caerulescens atlantica staging in two habitats in spring. Ardea 77, 3–20.

Bélanger, L., Bédard, J., 1990. Energetic cost of man-induced disturbance to staging snow geese. J. Wildl. Manag. 54, 36. https://doi.org/10.2307/3808897

Bêty, J., Gauthier, G., Giroux, J., 2003. Body condition, migration, and timing of reproduction in snow geese: A test of the condition-dependent model of optimal clutch size. Am. Nat. 162, 110–121. https://doi.org/10.1086/375680

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag, New York. https://doi.org/10.1007/b97636

Calvert, A.M., Gauthier, G., 2005. Effects of exceptional conservation measures on survival and seasonal hunting mortality in greater snow geese: Survival and hunting mortality of snow geese. J. Appl. Ecol. 42, 442–452. https://doi.org/10.1111/j.1365-2664.2005.01042.x

Castro, M., Araújo, A., Monteiro, P., 2005. Fate of discards from deep water crustacean trawl fishery off the south coast of Portugal. N. Z. J. Mar. Freshwater Res. 39, 437–446. https://doi.org/10.1080/00288330.2005.9517323

Corlett, R.T., Primack, R.B., Devictor, V., Maas, B., Goswami, V.R., Bates, A.E., Koh, L.P., Regan, T.J., Loyola, R., Pakeman, R.J., Cumming, G.S., Pidgeon, A., Johns, D., Roth, R., 2020. Impacts of the coronavirus pandemic on biodiversity conservation. Biol. Conserv. 246, 108571. https://doi.org/10.1016/j.biocon.2020.108571

Cromsigt, J.P.G.M., Kuijper, D.P.J., Adam, M., Beschta, R.L., Churski, M., Eycott, A., Kerley, G.I.H., Mysterud, A., Schmidt, K., West, K., 2013. Hunting for fear: innovating management of human–wildlife conflicts. J. Appl. Ecol. 50, 544–549. https://doi.org/10.1111/1365-2664.12076

Dokter, A.M., Fokkema, W., Ebbinge, B.S., Olff, H., Jeugd, H.P., Nolet, B.A., 2018. Agricultural pastures challenge the attractiveness of natural saltmarsh for a migratory goose. J. Appl. Ecol. 55, 2707–2718. https://doi.org/10.1111/1365-2664.13168

Féret, M., Bêty, J., Gauthier, G., Giroux, J.-F., Picard, G., 2005. Are abdominal profiles useful to assess body condition of spring staging greater snow geese? Condor 107, 694–702.

Féret, M., Gauthier, G., Bechet, A., Giroux, J.-F., Hobson, K.A., 2003. Effect of a spring hunt on nutrient storage by greater snow geese in southern Quebec. J. Wildl. Manag. 67, 796–807. https://doi.org/10.2307/3802687

Filion, B., Luszcz, D., Allard, G., 1998. Chapter 3: Impact of geese on farmlands., in: The greater snow goose: Report of the arctic goose habitat working group. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, Ontario, pp. 58–64.

Flemming, S.A., Smith, P.A., Rausch, J., Nol, E., 2019. Broad-scale changes in tundra-nesting bird abundance in response to hyperabundant geese. Ecosphere 10, 1–14. https://doi.org/10.1002/ecs2.2785

Fox, A.D., Abraham, K.F., 2017. Why geese benefit from the transition from natural vegetation to agriculture. Ambio 46, 188–197. https://doi.org/10.1007/s13280-016-0879-1

Frederick, C., Girard, C., Wong, G., Lemire, M., Martin, M.-C., Legagneux, P., 2020. Communicating with Northerners on the absence of SARS-CoV-2 in migratory snow geese. Écoscience 28, 217-223. https://doi.org/10.1080/11956860.2021.1885803

Gauthier, G., Bedard, J., Huot, J., Bedard, Y., 1984. Spring accumulation of fat by greater snow geese in two staging habitats. Condor 86, 192–199. https://doi.org/10.2307/1367040

Gauthier, G., Bedard, Y., Bedard, J., 1988. Habitat use and activity budgets of greater snow geese in spring. J. Wildl. Manag. 52, 191–201. https://doi.org/10.2307/3801222

Gauthier, G., Bêty, J., Hobson, K.A., 2003. Are greater snow geese capital breeders? New evidence from a stable-isotope model. Ecology 84, 3250–3264. https://doi.org/10.1890/02-0613

Gauthier, G., Giroux, J.-F., Bédard, J., 1992. Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. Can. J. Zool. 70, 2077–2087. https://doi.org/10.1139/z92-280

Gauthier, G., Giroux, J.-F., Reed, A., Béchet, A., Bélanger, L., 2005. Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands? Glob. Chang. Biol. 11, 856–868. https://doi.org/10.1111/j.1365-2486.2005.00944.x

Giroux, J.-F., Bergeron, R., 1996. Spring diets of sympatric greater snow geese and Canada geese in southern Quebec. Can. J. Zool. 74, 950–953. https://doi.org/10.1139/z96-107

Jano, A.P., Jefferies, R.L., Rockwell, R.F., 1998. The detection of vegetational change by multitemporal analysis of LANDSAT data: The effects of goose foraging. J. Ecol. 86, 93–99. https://doi.org/10.1046/j.1365-2745.1998.00232.x

Jefferies, R.L., Rockwell, R.F., Abraham, K.F., 2004. The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands — a continuing saga. Environ. Rev. 11, 193–232. https://doi.org/10.1139/A04-002

Juillet, C., Choquet, R., Gauthier, G., Lefebvre, J., Pradel, R., 2012. Carry-over effects of spring hunt and climate on recruitment to the natal colony in a migratory species. J. Appl. Ecol. 49, 1237–1246. https://doi.org/10.1111/j.1365-2664.2012.02199.x

Klaassen, M., Bauer, S., Madsen, J., Tombre, I., 2006. Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. J. Appl. Ecol. 43, 92–100. https://doi.org/10.1111/j.1365-2664.2005.01109.x

Kölzsch, A., Neefjes, M., Barkway, J., Müskens, G.J.D.M., van Langevelde, F., de Boer, W.F., Prins, H.H.T., Cresswell, B.H., Nolet, B.A., 2016. Neckband or backpack? Differences in tag design and their effects on GPS/accelerometer tracking results in large waterbirds. Anim. Biotelemetry 4, 1–14. https://doi.org/10.1186/s40317-016-0104-9

Lamarre, J.-F., Legagneux, P., Gauthier, G., Reed, E.T., Bêty, J., 2017. Predator-mediated negative effects of overabundant snow geese on arctic-nesting shorebirds. Ecosphere 8, 1–13. https://doi.org/10.1002/ecs2.1788

Lefebvre, J., Gauthier, G., Giroux, J.-F., Reed, A., Reed, E.T., Bélanger, L., 2017. The greater snow goose Anser caerulescens atlanticus: Managing an overabundant population. Ambio 46, 262–274. https://doi.org/10.1007/s13280-016-0887-1

Legagneux, P., Fast, P.L.F., Gauthier, G., Bêty, J., 2012. Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proc. R. Soc. Lond. B Biol. Sci. 279, 876–883. https://doi.org/10.1098/rspb.2011.1351

Legagneux, P., Simard, A.-A., Gauthier, G., Bêty, J., 2013. Effect of neck collars on the body condition of migrating greater snow geese. J. Field Ornithol. 84, 201–209. https://doi.org/10.1111/jofo.12019

Madsen, J., 1995. Impacts of disturbance on migratory waterfowl. Ibis 137, S67–S74. https://doi.org/10.1111/j.1474-919X.1995.tb08459.x

Madsen, J., Fox, A.D., 1995. Impacts of hunting disturbance on waterbirds - a review. Wildl. Biol. 1, 193–207. https://doi.org/10.2981/wlb.1995.0025

Mainguy, J., Bêty, J., Gauthier, G., Giroux, J.-F., 2002. Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? Condor 104, 156–161.

Manenti, R., Mori, E., Di Canio, V., Mercurio, S., Picone, M., Caffi, M., Brambilla, M., Ficetola, G.F., Rubolini, D., 2020. The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: Insights from the first European locked down country. Biol. Conserv. 249. https://doi.org/10.1016/j.biocon.2020.108728

Manseau, M., Gauthier, G., 1993. Interactions between greater snow geese and their rearing habitat. Ecology 74, 2045–2055. https://doi.org/10.2307/1940850

Morez, V., Gauthier, G., Reed, A., 2000. Effect of body condition on vulnerability of greater snow geese to hunting and capture. J. Wildl. Manag. 64, 875–886. https://doi.org/10.2307/3802758

Morrissette, M., Bêty, J., Gauthier, G., Reed, A., Lefebvre, J., 2010. Climate, trophic interactions, density dependence and carry-over effects on the population productivity of a migratory Arctic herbivorous bird. Oikos 119, 1181–1191. https://doi.org/10.1111/j.1600-0706.2009.18079.x

Nolet, B.A., Kölzsch, A., Elderenbosch, M., van Noordwijk, A.J., 2016. Scaring waterfowl as a management tool: how much more do geese forage after disturbance? J. Appl. Ecol. 53, 1413–1421. https://doi.org/10.1111/1365-2664.12698

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514. https://doi.org/10.1111/ele.12187

Osenberg, C.W., Schmitt, R.J., 1996. Detecting ecological impacts caused by human activities, in: Schmitt, R.J., Osenberg, C.W. (Eds.), Detecting ecological impacts. Academic Press, San Diego, pp. 3–16. https://doi.org/10.1016/B978-012627255-0/50003-3

Pot, M.T., Koning, S. de, Westerduin, C., de Boer, W.F., Shariati, M., Lameris, T.K., 2019. Wintering geese trade-off energetic gains and costs when switching from agricultural to natural habitats. Ardea 107, 183–196. https://doi.org/10.5253/arde.v107i2.a6

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reed, A., Giroux, J.-F., Gauthier, G., 1998. Population size, productivity, harvest and distribution., in: Batt, B.D.J. (Ed.), The greater snow goose: Report of the arctic goose habitat working group. Canadian Wildlife Service and U.S. Fish and Wildlife Service, Ottawa, Ontario and Washington, D.C.

Reed, E.T., Calvert, A.M., 2007. Evaluation of the special conservation measures for greater snow geese: report of the greater snow goose working group, Arctic Goose Joint Venture special publication.

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., 2020. MASS: Support functions and datasets for Venables and Ripley's MASS.

Rotem, G., Berger, H., King, R., Kutiel, P.B., Saltz, D., 2011. The effect of anthropogenic resources on the space-use patterns of golden jackals. J. Wildl. Manag. 75, 132–136. https://doi.org/10.1002/jwmg.9

Rutz, C., Loretto, M.-C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R.B., Ropert-Coudert, Y., Tucker, M.A., Wikelski, M., Cagnacci, F., 2020. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. Nat. Ecol. Evol. 4, 1156–1159. https://doi.org/10.1038/s41559-020-1237-z

Turcotte, Y., Bédard, J., 1989. Shared parental investment, parent-offspring conflict and brood size in greater snow geese. Anim. Behav. 38, 703–706. https://doi.org/10.1016/S0003-3472(89)80016-8

Chapitre 2 – Additional data confirms the impact of the COVID19 lockdown on the behavior and fattening of migratory snow geese

Envolée d'oies à l'Île-aux-Oies, Québec, 2021

Référence de la publication :

LeTourneux, F., Grandmont, T., Dulude-de Broin, F., Martin, M.-C., Bêty, J., Gauthier, G., Legagneux, P., 2023. Additional data confirms the impact of the COVID19 lockdown on the behavior and fattening of migratory snow geese. Biol. Conserv. 286, 110240. DOI:10.1016/j.biocon.2023.110240

2.1 Résumé

Le confinement imposé suite à la COVID19 a fourni une opportunité sans précédent d'étudier l'impact des activités humaines et des mesures de conservation sur la faune. Cependant, la plupart des études sur les effets du confinement étaient opportunistes et basées sur des données limitées car cette 'manipulation' à grande échelle était inattendue et de courte durée. La réplication des résultats scientifiques est la pierre angulaire de la méthode scientifique et assure que les conclusions de telles études sont robustes. Ici, nous testons les prédictions d'une étude précédente dans laquelle nous avons quantifié les impacts de la réduction du dérangement lié au confinement pour la COVID19 sur la condition physique et le comportement de la grande oie des neiges (*Anser caerulescens atlanticus*), une espèce dont une bonne gestion est cruciale pour la conservation des écosystèmes nordiques. L'analyse de deux années de données supplémentaires confirme nos prédictions. Le retour à une intensité de chasse élevée en 2021 et 2022 (post-confinement) a de nouveau réduit la condition physique des femelles comparé au printemps du confinement (2020). L'engraissement prénuptial des oies lors de ces deux printemps était similaire aux années précédant cette mesure d'urgence et différait de 2020 quand les oies ont atteint une haute condition physique plus tôt au printemps que ce qui avait été détecté jusqu'ici. Comparé à 2020, les oiseaux suivis par GPS ont passé davantage de temps en 2021 dans les champs agricoles, des habitats profitables mais hautement risqués, comme c'était aussi le cas dans l'année précédant le confinement. Cette étude fournit des résultats robustes qui confirment les effets du dérangement causé par la chasse de printemps sur la physiologie de la grande oie des neiges. Cela démontre également l'efficacité à long terme de cette mesure de conservation établie il y a deux décennies pour limiter la taille de cette population d'oies et préserver les écosystèmes arctiques du surbroutement et des impacts négatifs y étant associés pour les autres espèces aviaires de l'Arctique.

Mots clés: Mesure de conservation · Confinement COVID19 · Grande oie des neiges · Condition physique · Dérangement · Étude de réplication

2.2 Abstract

The COVID19 lockdown provided a unique opportunity to study the impact of human activities and conservation measures on wildlife. However, most lockdown studies were opportunistic and based on limited data, because this 'natural experiment' was unexpected and short-lasting. Replication of scientific results is the cornerstone of the scientific method and ensures that conclusions from such short-term studies are robust. Here, we test predictions arising from a previous study where we showed the impact of the lockdown-induced reduction in hunting disturbance on the body condition and behavior of greater snow geese (*Anser caerulescens a.)*, a species whose management is crucial for the conservation of northern ecosystems. The analysis of two additional years of data confirmed our predictions. The return to a high hunting pressure in springs 2021-2022 (post-lockdown) reduced overall goose body condition compared to the lockdown year. Goose fattening in post-lockdown springs was very similar to pre-lockdown years, differing from 2020 when a high body condition was reached earlier in spring than in any other year. Radio-tracked birds spent more time in profitable but risky agricultural lands in 2021 compared to 2020, as was the case in the pre-lockdown year. Our study provides robust evidence confirming the impacts of spring hunting on greater snow goose physiology. It demonstrates the long-lasting efficiency of the spring conservation hunt established two decades ago to limit the size of the population with the aim of preserving Arctic ecosystems from overgrazing and associated negative impacts on other arctic-nesting birds.

Keywords: Conservation measure · COVID19 lockdown · Greater snow geese · Body condition · Disturbance · Replication study

2.3 Introduction

The global lockdown induced by the COVID-19 pandemic in spring 2020 was an unprecedented opportunity to measure human impacts on wildlife. Indeed, this quasi-experimental, worldwide reduction of human activity has been extensively studied and reviewed (e.g. Bates et al., 2021; Derryberry et al., 2020) and revealed both positive and negative impacts on wildlife. Unsurprisingly, species suffering from the overbearing presence of humans were temporarily relieved from anthropogenic pressures whilst those benefitting from human presence have suffered from this hiatus in human activity (Manenti et al., 2020).

Researchers invested considerable efforts to evaluate the impacts of this unique 'Anthropause', but this has been a challenging task. First, this measure was unexpected and happened rapidly, leaving little time for designing proper protocols. Studies on the effects of the lockdown on wildlife are thus entirely opportunistic and their results are based on a few pre-lockdown years and one "experimental" (i.e. covid lockdown) period (e.g. Seress et al., 2021). Consequently, revisiting the results from these studies with post-lockdown data is essential to confirm or refute their findings. The unexpected nature of this 'manipulation' has restricted the breadth of the data scientists were able to collect, potentially weakening the robustness of their conclusions. For instance, most data on wildlife responses to the lockdown focus on changes in the presence or abundance of species (e.g. Gilby et al., 2021; Vardi et al., 2021). Still, some research teams had the opportunity to measure lockdown effects on life-history traits of wild species (Corsini et al., 2022; Hentati-Sundberg et al., 2021; Manenti et al., 2020) including our work that investigated the impact of the lockdown on physiological changes in an overabundant migratory species, the greater snow goose (*Anser caerulescens atlantica*; LeTourneux et al., 2021).

The control of overabundant goose populations is a major conservation challenge that has large implications for the preservation of Arctic ecosystems worldwide (Flemming et al., 2019, 2016; Hessen et al., 2017; Samelius and Alisauskas, 2009). Indeed, overgrazing, grubbing and fecal deposition of expanding goose populations have led to severe degradation of arctic habitats and plant communities (Abraham et al., 2005; Handa et al., 2002; Srivastava and Jefferies, 1996), disruption of nutrient cycles and plant-soil interactions (Bazely and Jefferies, 1986; Deschamps et al., 2023), and irreversible shifts of ecological communities (Jefferies and Rockwell, 2002). Eutrophication of freshwater wetlands and ponds by goose feces was shown to alter the productivity and community composition of arctic freshwater ecosystems (Hessen et al., 2017; Jensen et al., 2019). Adverse effects on Arctic species are also commonly reported for a wide range of taxa that share the same habitat and predators (invertebrates: Sherfy and Kirkpatrick, 2003, shorebirds: Duchesne et al., 2021; Flemming et al., 2016, 2019; Lamarre et al., 2017, passerines : Peterson et al., 2014, small mammals: Samelius and Alisauskas, 2009). These strong negative effects could locally exclude vulnerable species, and are often cited as a potential cause for the circumpolar decline of shorebird populations (Flemming et al., 2016, 2019).

Successful conservation of arctic ecosystems and the species they harbor depends on adequate management of overabundant goose populations in many areas, which is a challenge for conservation agencies (Fox and Madsen, 2017). The special spring conservation harvest of greater snow geese established in 1999 in Canada was an attempt to control this rapidly-growing population and limit its impacts on Arctic habitats (Lefebvre et al., 2017). This conservation measure largely contributed to maintain the population below one million individuals, partly through an indirect effect on reproductive investment (Lefebvre et al., 2017) that was mediated by a reduction of spring body condition (LeTourneux et al., 2021). Spring staging is a critical period in the annual cycle of snow geese because they need to accumulate enough resources for the 3000-km migration to their Arctic breeding grounds and for the subsequent reproduction (Gauthier et al., 2003). In LeTourneux et al. (2021), we took advantage of the COVID lockdown to confirm that the impact of spring hunting on pre-breeding body condition was still effective after 20 years. Our results suggested that this conservation measure could be switched on or off with immediate consequences on goose physiology. However, the evidence was limited by the absence of post-lockdown data, calling for follow-up studies to strengthen these conclusions.

In the current study, we revisit the results of LeTourneux et al. (2021), with additional data on hunting pressure, body condition and use of agricultural lands by staging greater snow geese in two springs following the lockdown (2021 and 2022). Based on our original results, we predicted that an increase in hunting pressure compared to 2020 should decrease goose foraging efficiency and lead to lower body condition during staging compared to the lockdown year. Furthermore, we predicted that geese in lower condition should continue accumulating body reserves later in the season and thus spend more time in agricultural lands despite the high hunting risk associated with this habitat.

2.4 Methods

2.4.1 Data acquisition

Geese were captured with baited cannon nets during spring on the staging grounds in 7 years between 2007 and 2022 (2007-2009, 2019-2022) following the procedures described in LeTourneux et al. (2021). Captures took place at Île-aux-Oies (47N 70W) in southern Quebec during the last 3 weeks of the snow goose staging period, which occurs from late March to mid May. All adult females were banded, weighed, and their tarsus and head lengths were measured. To compare the physical condition among individuals of different structural size, we obtained an index of body condition independent of size for each bird by correcting body mass with two skeletal measurements (tarsus and head lengths; details in LeTourneux et al., 2021). Geese gain mass during the migratory stopover (~10g/day) and they were not always captured on the same dates in different years even though capture periods overlapped between years (Fig. S2.1). Consequently, to compare average body condition between years, we corrected the body condition index for the capture date (details in LeTourneux et

al., 2021). Positions of geese marked with GPS radio collars during captures between 2019 and 2021 were obtained at 5-minute intervals. Females equipped with GPS devices in 2022 were part of an experiment using hormone implants and were therefore excluded from this analysis.

2.4.2 Statistical analyses

With these additional years of data (2021, 2022), we revisited the analyses performed in LeTourneux et al. (2021) for the years 2007 to 2020. First, we contrasted overall spring body condition during the COVID lockdown (2020) with that of pre- (2007-2009, 2019) and post-lockdown years (2021-2022) using a linear mixed model where body mass corrected for size and date was fitted as the response variable, year as a fixed categorical variable and capture IDs as random intercepts. Next, we compared the rate of condition gain of 2020 (lockdown year) with pre- and post-lockdown years using a linear mixed model with body mass corrected for size only as the response variable and year, day of year and their interaction as fixed effects. In this second analysis, the 'year' variable had 5 levels as 2020 (lockdown) was compared to 2021 and 2022 (post-lockdown), 2019 (pre-lockdown) and 2007-2009. We fitted 2019, 2021 and 2022 as separate levels because we were particularly interested in comparing the rate of condition gain during the pandemic to the years just before and after the lockdown. Individual years and captures were fitted as random intercepts in this analysis to account for repeated mass measurements within years and capture groups. Including individual years as random intercepts was necessary in this analysis because of repeated measurements within years in the 2007-2009 level. These analyses were conducted using the `lmer` function from the `lme4` package in `R` (Bates et al., 2015; R Core Team, 2020).

We determined the proportion of time spent in agricultural lands in 2019, 2020 and 2021 between May 6 and May 24, near the end of the staging period. This was based on the number of locations obtained in agricultural lands compared to other habitats (natural marsh and water) in radio-tracked birds. Spatial location data was treated the same way as in LeTourneux et al. (2021). Namely, we restricted locations to our capture area (Île-aux-Oies and adjacent shoreline of the St-Lawrence River), we removed locations during flight and during the night, and resampled locations at the frequency of one point every 5 minutes. The main difference with our original analysis is that we considered habitat use data from all individuals in all years (n=24). We could not restrict the analysis to only individuals present in all 3 years as in LeTourneux et al. (2021) because this would have reduced our sample to a single bird. Still, our previous study showed that analyses based on all individuals or only those seen in both years (2019 and 2020) yielded the same results (see Fig S1.6). We analyzed the daily proportion of time spent in agricultural lands with a quasi-binomial generalized linear mixed effects model where year was fitted as a categorical fixed effect and bird IDs as random intercepts to account for differences between

individuals. This was done with the `glmmPQL` function from the `MASS` package in `R` (R Core Team, 2020; Venables and Ripley, 2002).

2.5 Results

Between 29 April and 14 May 2021 and 2022, we captured, weighed and measured 452 and 249 females, respectively, for the body condition analyses. In 2021, 5 females were fitted with GPS radio-collars for habitat use analyses. As expected, hunting pressure increased in 2021 and 2022 compared to the very low value of 2020 and was also higher than in 2019 (Fig. 2.1A).

In spring 2021, body mass corrected for structural size and adjusted to 12 May was 75g [95% CI = 20g, 129g] and 104g [57, 149g] lower than in 2020 and 2019, respectively. Body mass in 2022 was comparable to 2021 (non-significant difference of 35g [-15, 86g]), and was also 110g [49, 171g] and 139g [86, 193g] lower than in 2020 and 2019, respectively. Daily mass gain did not differ significantly between 2022 (15.4g/day [6.1, 24.6g/day]), 2021 (10.3g/day [3.5, 17.0g/day]), 2019 (9.8g/day [2.7, 16.9g/day]) and 2007-2009 (11.3g/day [9.3, 13.8g/day]). However, we found strong evidence that the seasonal increase in body mass in 2022 and 2021 was higher than in 2020, where no mass gain was observed during our capture period (Fig. 2.1B). Finally, near the end of spring staging in 2021, geese spent more time in agricultural lands than in 2020 ($\beta_{2021\text{-}2020}$ = 0.70 [0.17, 1.24]) but not compared to 2019 ($\beta_{2021\text{-}2019}$ = -0.44 [-0.96, 0.09]). They spent on average 47% of the daytime in agricultural lands in 2021, 31% in 2020 and 58% in 2019 (Fig. 2.1C).

2.6 Discussion

Extending our analysis of the impacts of hunting on body condition and behaviour of spring-staging snow geese with additional post-covid data allowed us to confirm the conclusions of LeTourneux et al. (2021). More importantly, it enabled us to test the hypotheses that we had put forward to explain those results and to validate the long-lasting efficiency of spring hunting in controlling an overabundant population, a conservation measure essential for the preservation of several Arctic ecosystems.

As we predicted based on the results of LeTourneux et al. (2021), the increase in hunting pressure in spring 2021 and 2022 after the lockdown year led to a lower overall body condition of geese compared to 2020. Geese were also in lower body condition in 2021 than in 2019, probably because the hunting pressure was relatively low in 2019 compared to other recent years (Fig 2.1A). Indeed, the overall condition observed in post-lockdown years fit well with our previous evaluation of the impact of hunting pressure on pre-migratory body condition (Fig. S2.2). Also, in accordance with our predictions, we observed a gain in mass late during the staging period in 2021 and 2022 similar to other recent years, including in the year just before the lockdown. This differed from 2020 when geese seemed to have reached a plateau in body condition relatively early with no further increase

in body condition during the last two weeks prior to migratory departure. These results thus provide strong evidence that the reduction in hunting-related disturbance during the COVID lockdown allowed staging snow geese to reach a high body condition earlier than in years with high hunting pressure.

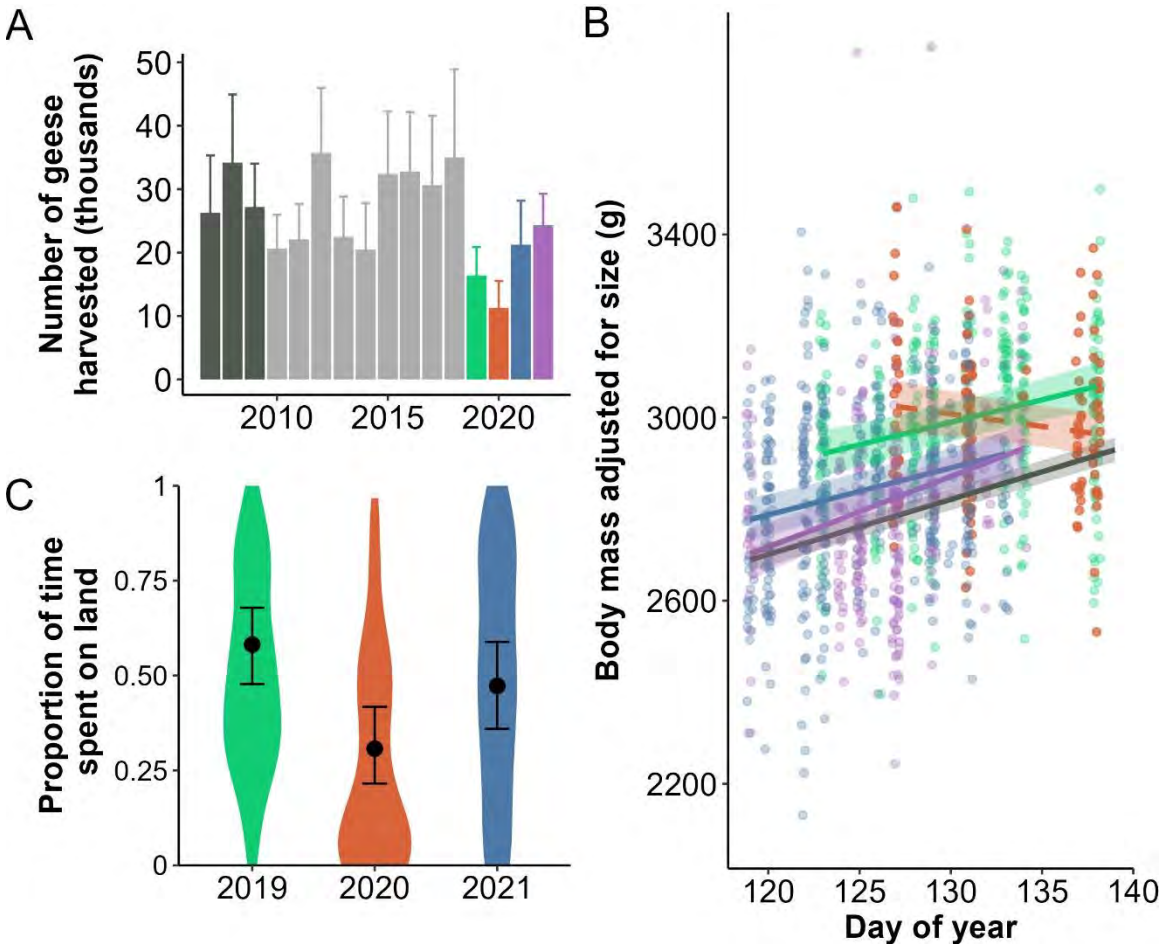

Figure 2.1 Impacts of spring hunting pressure on body condition and behavior of spring-staging greater snow geese. A: Annual spring harvest of greater snow geese. Error bars are the upper 95% confidence intervals. Data obtained from Smith and Gendron (2022). B: Relationship between body condition index of captured geese and day of the year for 2019 (green), 2020 (orange), 2021 (blue), 2022 (purple) and other years with sampling dates comparable to 2020 (2007-2009; gray). Lines are the model prediction for each year along with their 95% confidence intervals (shading). The dotted line (2020) indicates a non-significant relationship. Individual data points for 2007-2009 were omitted to reduce clutter but are presented in LeTourneux et al. (2021). Day of year 132 = 12 May. C: Daily proportion of time spent in agricultural lands near the end of spring staging determined by radio-tracking in 2019 (n=10 birds), 2020 (n=7) and 2021 (n=7). Black dots are the mean model prediction by year with their 95% CI. Violins represent the distribution of individual data points. No comparable habitat use data is available for 2022.

According to the hypothesis proposed in LeTourneux et al. (2021), geese in lower pre-migratory body condition should spend more time feeding in profitable agricultural lands compared to those in better condition. This is because agricultural lands pose a high mortality risk as goose hunting only occurs in this habitat in spring. Hence, use of this habitat in spring was hypothesized to occur mostly when the need to accumulate endogenous reserves in preparation for migration and reproduction is high (Gauthier et al., 2003; LeTourneux et al., 2021). Our results support this hypothesis as geese spent more time in agricultural lands near the end of staging in 2021 when they were still accumulating body reserves, unlike in 2020.

Based on the lower population-wide body condition of geese in 2021 compared to 2019, we could have expected geese to spend more time in agricultural lands in 2021 than in 2019, but it was not the case here. We should remember that our analysis of habitat use relies on a small sample size (24 individuals in total, 7-10 per year). Although the use of agricultural lands in our sample should reflect that of the population because snow geese are highly gregarious (Gauthier et al., 1988), individual variation in habitat use or in initial spring body condition may still affect yearly estimates. Despite these limitations, the decrease in body condition in 2021 associated with a return to pre-lockdown level of use of agricultural lands nonetheless suggests that geese faced a trade-off between safety (natural marshes) and food acquisition in a profitable but risky habitat (agricultural lands) and can adjust their behavior to mitigate this risk according to their body condition. The evidence presented here is compelling since the additional data collected in 2021 confirms the interpretations presented in LeTourneux et al. (2021).

We demonstrate that hunting disturbance during spring staging has an immediate but reversible effect on pre-breeding body condition of a migratory waterfowl population. Indeed, the steep reduction of hunting pressure in 2020, and to a lesser extent in 2019, resulted in high goose body condition in those years, while the return to pre-2019 hunting pressure in 2021 and 2022 resulted in a low body condition, comparable to data obtained in the previous decade (2007-2009). Moreover, our results indicate that geese did not habituate to disturbance from spring hunting, despite 20 years of exposure to it. Geese responded instantaneously to changes in the hunting regime, highlighting the high potential of this conservation measure to remain effective in the long run for controlling overabundant populations. In this case, the lack of habituation by geese may stem from the fact that hunting disturbance prevents access to highly profitable food resources (agricultural lands), shortens foraging bouts, and increases flying time, ultimately reducing energy intake and storage (Béchet et al., 2004). Finally, our results show that solely considering harvest mortality when assessing the impact of hunting likely underestimates its overall effect on population dynamics.

2.7 Conclusion

Studies based on limited or unplanned data sampling should be replicated to reach robust scientific conclusions. This applies to most research on the effects of COVID-related changes in human activities on wildlife because it was an unexpected and short-lasting measure, which increases the risk of obtaining spurious results due to unaccounted confounding factors. While it might not always be possible to replicate a natural experiment, researchers can still make predictions based on their results and test them with additional data. Here, the collection and analysis of additional years of data allowed us to confirm the conclusions of LeTourneux et al. (2021) and provide compelling evidence of the effects of spring hunting activity on the physiology of a wild species. To our knowledge, this is the first study on the impacts of the COVID lockdown on wildlife that has tested the interpretations and hypotheses stemming from their results with additional data.

2.8 Acknowledgements

We would like to thank all Île-aux-Oies team members for assistance in the field, M.-C. Cadieux for managing our databases, and M. Séguin and A. Desmarais for providing fieldwork facilities. We thank A. Smith and M. Gendron from Environment and Climate Change Canada for providing data on hunting pressure. We acknowledge funding from the Natural Sciences and Engineering Council of Canada (RGPIN-2019-05185), Fonds de recherche du Québec Nature et Technologies (271544), Sentinelle Nord program from the Canada First Research Excellence Fund and the Network of Centre of Excellence of Canada (ArcticNET; PP12). This research was conducted according to the relevant national and institutional regulations on animal welfare and was approved by the 'Comité de Protection des Animaux de l'Université Laval' (CPAUL # 2019-304) and the Canadian Bird Banding Office (permit #10648).

2.9 Supplementary material

Annexe S2.1 – Supplementary figures

Annexe S2.2 – Calculation of hunting effect on average annual body condition

2.10 Bibliograpy

Abraham, K.F., Jefferies, R.L., Alisauskas, R.T., 2005. The dynamics of landscape change and snow geese in mid-continent North America. Glob. Chang. Biol. 11, 841–855. https://doi.org/10.1111/j.1365-2486.2005.00943.x

Bates, A.E., Primack, R.B., Biggar, B.S., Bird, T.J., Clinton, M.E., Command, R.J., Richards, C., Shellard, M., Geraldi, N.R., Vergara, V., et al., 2021. Global COVID-19 lockdown highlights humans as both threats and custodians of the environment. Biol. Conserv. 263, 109175. https://doi.org/10.1016/j.biocon.2021.109175

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Soft. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Bazely, D.R., Jefferies, R.L., 1986. Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. J. Ecol. 74, 693. https://doi.org/10.2307/2260392

Béchet, A., Giroux, J.-F., Gauthier, G., 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese: Effects of hunting on snow geese behaviour. J. Appl. Ecol. 41, 689–700. https://doi.org/10.1111/j.0021-8901.2004.00928.x

Corsini, M., Jagiello, Z., Walesiak, M., Redlisiak, M., Stadnicki, I., Mierzejewska, E., Szulkin, M., 2022. Breeding in the pandemic: short-term lockdown restrictions in a European capital city did not alter the life-history traits of two urban adapters. Urban Ecosyst. https://doi.org/10.1007/s11252-022-01309-5

Derryberry, E.P., Phillips, J.N., Derryberry, G.E., Blum, M.J., Luther, D., 2020. Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. Science 370, 575–579. https://doi.org/10.1126/science.abd5777

Deschamps, L., Maire, V., Chen, L., Fortier, D., Gauthier, G., Morneault, A., Hardy-Lachance, E., Dalcher-Gosselin, I., Tanguay, F., Gignac, C., McKenzie, J.M., Rochefort, L., Lévesque, E., 2023. Increased nutrient availability speeds up permafrost development, while goose grazing slows it down in a Canadian High Arctic wetland. J. Ecol. 111, 449–463. https://doi.org/10.1111/1365-2745.14037

Duchesne, É., Lamarre, J., Gauthier, G., Berteaux, D., Gravel, D., Bêty, J., 2021. Variable strength of predator-mediated effects on species occurrence in an arctic terrestrial vertebrate community. Ecography 44, 1236–1248. https://doi.org/10.1111/ecog.05760

Flemming, S.A., Calvert, A., Nol, E., Smith, P.A., 2016. Do hyperabundant Arctic-nesting geese pose a problem for sympatric species? Environ. Rev. 24, 393–402. https://doi.org/10.1139/er-2016-0007

Flemming, S.A., Smith, P.A., Rausch, J., Nol, E., 2019. Broad-scale changes in tundra-nesting bird abundance in response to hyperabundant geese. Ecosphere 10. https://doi.org/10.1002/ecs2.2785

Fox, A.D., Madsen, J., 2017. Threatened species to super-abundance: The unexpected international implications of successful goose conservation. Ambio 46, 179–187. https://doi.org/10.1007/s13280-016-0878-2

Gauthier, G., Bedard, Y., Bedard, J., 1988. Habitat use and activity budgets of greater snow geese in spring. J. Wildl. Manage. 52, 191–201. https://doi.org/10.2307/3801222

Gauthier, G., Bêty, J., Hobson, K.A., 2003. Are greater snow geese capital breeders? New evidence from a stable-isotope model. Ecology 84, 3250–3264. https://doi.org/10.1890/02-0613

Gilby, B.L., Henderson, C.J., Olds, A.D., Ballantyne, J.A., Bingham, E.L., Elliott, B.B., Jones, T.R., Kimber, O., Mosman, J.D., Schlacher, T.A., 2021. Potentially negative ecological consequences of animal redistribution on beaches during COVID-19 lockdown. Biol. Conserv. 253, 108926. https://doi.org/10.1016/j.biocon.2020.108926

Handa, I.T., Harmsen, R., Jefferies, R.L., 2002. Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. J. Ecol. 90, 86–99.

Hentati-Sundberg, J., Berglund, P.-A., Hejdström, A., Olsson, O., 2021. COVID-19 lockdown reveals tourists as seabird guardians. Biol. Conserv. 254, 108950. https://doi.org/10.1016/j.biocon.2021.108950

Hessen, D.O., Tombre, I.M., van Geest, G., Alfsnes, K., 2017. Global change and ecosystem connectivity: How geese link fields of central Europe to eutrophication of Arctic freshwaters. Ambio 46, 40–47. https://doi.org/10.1007/s13280-016-0802-9

Jefferies, R.L., Rockwell, R.F., 2002. Foraging geese, vegetation loss and soil degradation in an arctic salt marsh. Appl. Veg. Sci. 5, 7–16.

Jensen, T.C., Walseng, B., Hessen, D.O., Dimante-Deimantovica, I., Novichkova, A.A., Chertoprud, E.S., Chertoprud, M.V., Sakharova, E.G., Krylov, A.V., Frisch, D., Christoffersen, K.S., 2019. Changes in trophic state and aquatic communities in high Arctic ponds in response to increasing goose populations. Freshw. Biol. 64, 1241–1254. https://doi.org/10.1111/fwb.13299

Lamarre, J.-F., Legagneux, P., Gauthier, G., Reed, E.T., Bêty, J., 2017. Predator-mediated negative effects of overabundant snow geese on arctic-nesting shorebirds. Ecosphere 8, 1–13. https://doi.org/10.1002/ecs2.1788

Lefebvre, J., Gauthier, G., Giroux, J.-F., Reed, A., Reed, E.T., Bélanger, L., 2017. The greater snow goose Anser caerulescens atlanticus: Managing an overabundant population. Ambio 46, 262–274. https://doi.org/10.1007/s13280-016-0887-1

LeTourneux, F., Grandmont, T., Dulude-de Broin, F., Martin, M.-C., Lefebvre, J., Kato, A., Bêty, J., Gauthier, G., Legagneux, P., 2021. COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species. Biol. Conserv. 255, 108968. https://doi.org/10.1016/j.biocon.2021.108968

Manenti, R., Mori, E., Di Canio, V., Mercurio, S., Picone, M., Caffi, M., Brambilla, M., Ficetola, G.F., Rubolini, D., 2020. The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: Insights from the first European locked down country. Biol. Conserv. 249. https://doi.org/10.1016/j.biocon.2020.108728

Peterson, S.L., Rockwell, R.F., Witte, C.R., Koons, D.N., 2014. Legacy effects of habitat degradation by Lesser Snow Geese on nesting Savannah Sparrows. Condor 116, 527–537. https://doi.org/10.1650/CONDOR-14-45.1

R Core Team, 2020. R: A language and environment for statistical computing.

Samelius, G., Alisauskas, R.T., 2009. Habitat alteration by geese at a large arctic goose colony: consequences for lemmings and voles. Can. J. Zool. 87, 95–101. https://doi.org/10.1139/Z08-140

Seress, G., Sándor, K., Vincze, E., Pipoly, I., Bukor, B., Ágh, N., Liker, A., 2021. Contrasting effects of the COVID-19 lockdown on urban birds' reproductive success in two cities. Sci. Rep. 11, 17649. https://doi.org/10.1038/s41598-021-96858-8

Sherfy, M.H., Kirkpatrick, R.L., 2003. Invertebrate response to snow goose herbivory on moist-soil vegetation. Wetlands 23, 236–249. https://doi.org/10.1672/3-20

Smith, A.C., Gendron, M., 2022. Spring snow goose hunt in eastern Canada. Unpublished annual reports (1999-2022). National Wildlife Research Centre, Canadian Wildlife Service, Environment and Climate Change Canada.

Srivastava, D.S., Jefferies, R.L., 1996. A positive feedback: Herbivory, plant growth, salinity, and the desertification of an arctic salt-marsh. J. Ecol. 84, 31–42. https://doi.org/10.2307/2261697

Vardi, R., Berger-Tal, O., Roll, U., 2021. iNaturalist insights illuminate COVID-19 effects on large mammals in urban centers. Biol. Conserv. 254, 108953. https://doi.org/10.1016/j.biocon.2021.108953

Venables, W.N., Ripley, B.D., 2002. Modern applied statistics with S, 4th ed. ed, Statistics and computing. Springer, New York.

Chapitre 3 – Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species

Femelles recapturées marquées à l'aide de colliers à la station de baguage de l'Île Bylot, Nunavut.

Référence de la publication :

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 59: 2705-2715. DOI: 10.1111/1365-2664.14268

3.1 Résumé

Les effets non-additifs découlant de l'interaction de plusieurs sources de stress peuvent avoir des impacts imprévisibles sur la faune. Même si certains facteurs de stress ont initialement peu d'impacts, ils peuvent devenir sévères s'ils agissent en synergie avec de nouvelles sources de stress. Les marqueurs individuels sont fréquemment utilisés dans les études sur la faune mais peuvent causer un stress physiologique pour les animaux. Leurs impacts sur les traits vitaux peuvent changer au fil du temps, particulièrement lorsque des variations environnementales imposent de nouveaux stress. Dans cette étude, nous évaluons les changements temporels de l'impact combiné de deux sources de stress, une constante (marquage avec des colliers) et l'autre variable dans le temps (intensité de la pression de chasse), chez la grande oie des neiges (*Anser caerulescens atlanticus*). Sur une période de 30 ans (1990-2019), les règlements de chasse pour cette espèce ont été libéralisées à deux reprises, en 1999 et en 2009, avec l'instauration de saisons de chasse spéciales au printemps et à l'hiver. Nous avons évalué l'effet du marqueur sur la survie des oies en lien avec les changements de la pression de chasse. Nous avons comparé la survie de plus de 20,000 femelles adultes marquées avec et sans collier à l'aide de modèles de capture-recapture multi-évènements et avons partitionné la mortalité provenant de la chasse et d'autres sources. La survie des oies avec et sans collier était similaire entre 1990 et 1998, avant que la chasse ne soit libéralisée (survie annuelle moyenne [95% C.I.]: 0.87 [0.84, 0.89]). Par contre, la survie absolue des oies avec un collier était inférieure de 0.05 [0.03, 0.07] comparé aux oiseaux sans collier entre 1999 et 2008, et de 0.12 [0.09, 0.15] après 2009, lorsque les réglementations ont été libéralisées davantage. Les taux de mortalité à la chasse et naturelle étaient tous deux plus élevés chez les oies à collier comparé aux oies portant uniquement une bague. L'interaction entre les effets du collier et de la chasse était synergique puisque les colliers ont affecté la survie de manière mesurable uniquement après que la pression de chasse eut augmenté de manière importante. Le cumul de ces sources de stress a probablement réduit la condition physique des oies suffisamment pour augmenter leur vulnérabilité à différentes sources de mortalité. Les chercheurs utilisant des programmes de marquage à long terme devraient ré-évaluer l'effet des marqueurs périodiquement et non uniquement dans les premières années de ces programmes. En effet, des interactions potentielles entre les marqueurs et des changements environnementaux pourraient éventuellement affecter les conclusions d'études basées sur des individus marqués. Ici, nous fournissons une démonstration peu commune dans un système naturel qu'une combinaison de facteurs de stress peut pousser certaines espèces au-delà d'un seuil où leurs traits vitaux sont affectés, même si un de ces facteurs appliqué seul n'avait initialement pas d'impact détectable.

Mots clés: Stresseurs cumulés · Expérience en milieu naturel · Design avant-après-contrôle-impact · Effets indirects de la chasse · Grande oie des neiges · Marqueurs auxiliaires · Modèles de capture-recapture multi-évènement · Taux de survie · Stress chronique

3.2 Abstract

Non-additive effects from multiple interacting stressors can have unpredictable outcomes on wildlife. Stressors that initially have negligible impacts may become significant if they act in synergy with novel stressors. Wildlife markers can be a source of physiological stress for animals and are ubiquitous in ecological studies. Their potential impacts on vital rates may vary over time, particularly when changing environments impose new stressors. In this study, we evaluated the temporal changes in the combined impact of two stressors, one constant (collar-marking) and another one variable over time (hunting intensity), in greater snow geese (*Anser caerulescens atlanticus*). Over a 30-year period (1990-2019), hunting regulations were liberalized twice, in 1999 and 2009, with the instauration of special spring and winter hunting seasons, respectively. We evaluated the effect of collars on goose survival through this period of changing hunting regulations. We compared annual survival of >20,000 adult females marked with and without neck collars using multievent capture-recapture models, and partitioned hunting from non-hunting mortality. Survival of geese marked with or without collars was similar in 1990-1998, before hunting regulations were liberalized (average survival[95% C.I.]: 0.87[0.86, 0.89]). However, absolute survival of collared geese was 0.05[0.03, 0.07] lower than that of non-collared geese between 1999 and 2009, and 0.12[0.09, 0.15] lower after hunting regulations were liberalized further in 2009. Hunting and non-hunting mortality probabilities were both higher in collared birds compared to those without collars. The interaction between the effects of collars and hunting was synergistic because collars affected survival only after the hunting pressure increased significantly. These cumulated stresses probably reduced goose body condition sufficiently to increase their vulnerability to multiple sources of mortality. Researchers relying on long-term marking programs should evaluate the effect of markers periodically rather than solely in the beginning, as interactions with changing environmental conditions may eventually affect conclusions of studies based on marked animals. Here, we provide a rare demonstration in a natural setting that a combination of stressors can push animals beyond a threshold where vital rates are affected, even when one stressor applied alone initially had no detectable impact.

Keywords: Cumulative stressors · Natural experiment · Before-after-control-impact design · Indirect hunting impact · Greater snow geese · Neck collars · Multievent capture-recapture modeling · Survival rates · Chronic stress

3.3 Introduction

In a world dominated by ever-increasing human populations, adverse effects on ecosystems arising from human activities are growing (Steffen et al., 2011). There is ample evidence that multiple stressors can interact with one another, with the resulting impact being seldom the simple addition of individual effects (Darling and Côté, 2008). We define stressors as any factors that push a system, whether it is an ecosystem or an organism, away from its equilibrium state (or allostasis) and alter its integrity (McEwen and Wingfield, 2003). Non-additive interactions between stressors are considered antagonistic or synergistic when their overall effect is, respectively, lower or greater than the arithmetic sum of individual effects (Folt et al., 1999). Novel synergies and antagonisms are particularly problematic because their unpredictability hinders our ability to properly anticipate the outcome of our actions, which can lead to poor management decisions, ill-oriented conservation efforts (Carrier-Belleau et al., 2021; Paine et al., 1998), or flawed scientific interpretations (Côté et al., 2016). Scientists must therefore be attentive to signs of these phenomena in ecological studies. One area where potential cumulative impacts between multiple stressors have been largely neglected is between environmental stressors and markers used to identify and track wildlife.

Using marking techniques that do not affect the vital rates of the animals we are studying is paramount for ethical and scientific reasons. Ethically, scientists should work to minimize any negative impact of markers on individuals. It is also important that vital rates are not compromised to reach valid scientific conclusions based on marked animals (Barron et al., 2010). There are numerous potential adverse effects of markers on wildlife fitness components. For instance, simple colour rings can interfere with mating success (Johnsen et al., 1997). Harnesses and neck-collars may restrict movement, increase energy requirements and ultimately hamper survival or reproduction (Barron et al., 2010). Although biologists have invested much effort in quantifying and reducing the negative impacts of markers, these effects are rarely considered in the context of multiple stressors imposed by changing human activities.

Long-term marking programs increase the potential for new interactions between the physiological stress induced by markers on animals and changing environmental conditions, particularly those arising from human activity such as hunting. Detecting small chronic effects or those which may be partially hidden by favorable, short-term environmental conditions may require large sample sizes over multiple years. However, because many studies evaluating the impact of markers on animals are short term, such interactions are likely to go undetected. We are aware of only one study that evaluated the impact of markers in combination to other environmental stressors that changed over time, where flipper-banded king penguins (*Aptenodytes patagonicus*) had reduced survival and breeding success in years with unfavourable environmental conditions (Saraux et al., 2011).

Neck collars are large markers that have been used in geese for a long time. A considerable advantage is that collared birds can be identified individually from afar without the need to be physically handled, which greatly increases encounter probability and allows estimating vital rates more precisely (Alisauskas and Lindberg, 2002; Juillet et al., 2012; Souchay et al., 2014). However, neck collars were found to negatively affect survival in several goose species (Alisauskas and Lindberg, 2002 and references therein) and their use was discontinued in those situations. Several mechanisms could reduce survival in collared birds. Natural causes like collar icing or reduced body condition due to aerodynamic drag could lead to increased predation risk or exhaustion during migration (Legagneux et al., 2013; Pennycuick et al., 2012; Zicus et al., 1983). Alternately, collars could increase hunting mortality if hunters preferentially target collared birds, which are regarded as hunting trophies (Caswell et al., 2012). Still, neck collars continue to be used in species where studies failed to find negative effects of these markers (Clausen and Madsen, 2014; Fox et al., 2014), or when the investigated parameters remain unaffected by collars (Yparraguirre et al., 2020). This includes greater snow geese, a species for which two previous studies found no negative effect of neck collars on survival based on large sample sizes (Menu et al., 2000; Reed et al., 2005).

Greater snow geese have been exposed to several environmental changes over the past three decades. Habitat use shifted towards increased use of agricultural fields, which induced changes to the migration corridor and contributed to a dramatic increase in population size (Gauthier et al., 2005). Most importantly, hunting regulations were liberalized to control their unprecedented population growth and limit grazing impact on the vegetation of its arctic breeding grounds (Lefebvre et al., 2017). A special hunting season (legally referred to as the Conservation Harvest) was opened in farmlands during their spring staging in Canada, followed 10 years later by a special winter hunting season in the USA (referred to as the Conservation Order). Apart from directly reducing survival, increased hunting of greater snow geese intensified disturbance during spring, which affected foraging behavior, reduced pre-migratory fattening (Béchet et al., 2004; LeTourneux et al., 2021), and ultimately impacted reproduction decisions and investment (Bêty et al., 2003; Mainguy et al., 2002). Therefore, these changes in hunting regulations can be considered a major source of chronic physiological stress for geese.

Our long-term study of the greater snow goose demography (since 1990) constitutes an ideal, quasi-experimental design to evaluate potential temporal changes in the cumulative impacts of two stressors, one that remained constant (collar marking) and one that changed in a controlled manner over time (hunting pressure). Before 1999, geese were hunted only during fall staging in Canada and early winter in the USA. From 1999 to 2008, bag and possession limits were increased, and geese were also hunted during the 2-month long spring staging period in Canada. Finally, from 2009 onward, hunting was allowed during a special late-winter season in the USA and hunting methods and quotas were liberalized (Lefebvre et al., 2017).

In this study, we use a 30-year marking program to evaluate the effect of neck collars on greater snow goose survival during a period of temporal changes in hunting regulations. We aimed to determine whether there could be an interaction between these two physiological stressors leading to cumulative impacts on survival. We hypothesized that the impact of neck collars on survival could have changed over time as the birds were exposed to an ever-increasing hunting pressure that eventually extended over the whole non-breeding season. We also examined if any reduction in survival in neck-collared birds could result from increases in either natural mortality, hunting mortality, or both. Chronic stress is known to affect physiological processes in animals and to reduce body condition (Kleist et al., 2018; Romero and Wingfield, 2016). Therefore, natural mortality of neck-collared birds could increase if chronic stress reduces their body condition and increases predation or exhaustion risks. Alternately, hunting mortality could increase if geese in lower condition become more vulnerable to hunting (Fowler et al., 2019, but see Morez et al., 2000).

3.4 Methods

3.4.1 Data collection

Greater Snow Geese breed across the eastern Canadian Arctic, winter along the Atlantic coast of the USA and stage in southern Quebec during their fall and spring migrations (Lefebvre et al., 2017). Goose banding took place on Bylot Island (73N, 80W), the largest known greater snow goose colony (~15% of the nesting population). Geese were marked from 1990 to 2019 during mass ringing drives at the end of the brood-rearing period (August) when adults are molting and flightless (see Menu et al., 2000 for details). All geese were sexed by cloacal eversion and both adults and young were fitted with a USGS Bird Banding Laboratory metal ring. Around 2/3 of adult females were also fitted with a unique alphanumeric-coded yellow plastic neck collar. All birds caught were checked for the presence of rings or collars put in previous years. Up until 2009, collars were 55-mm diameter × 48-mm high and weighed 19g. After 2009, new smaller and lighter collars (42-mm high, 15g) gradually replaced their older counterparts over a 5-year period. No difference in survival was detected between birds wearing either collar type (LeTourneux et al., unpubl. data). Young and adult males are not marked with neck collars and were excluded from our analysis. This research was conducted according to the relevant national and institutional regulations on animal welfare and was approved by the Comité de Protection des Animaux de l'Université Laval (CPAUL # 2019-228), the Canadian Bird Banding Office (permit #10648). Fieldwork on the Bylot Island Migratory Bird Sanctuary was approved by the Mittimatalik Hunter and Trapper Organization and Parks Canada (permit # SIR-2018-28081).

Encounters of marked birds occurred in one of three ways: physical recaptures, collar re-sightings or ring recoveries from hunter-shot birds. Birds marked with a metal leg ring only ('non-collared birds' from now on) could only be encountered alive when recaptured during the summer ringing drives. Collared females could also

be re-sighted during the whole breeding season, and these observations were pooled with their physical recaptures. To satisfy the assumption of discrete live-encounter occasions of our model, re-sightings made away from the breeding grounds were ignored in this analysis. Finally, ring recoveries from hunter-shot birds were compiled and sent to us by the Bird Banding Laboratory.

3.4.2 Data analysis

We estimated annual survival probability using a joint live-encounter and dead-recovery model in a multi-event framework (Burnham, 1993; Pradel, 2005). We conducted two separate analyses. We first modeled annual survival probability of collared and non-collared geese. Then, to assess whether any collar effect was mediated through hunting, natural, or both sources of mortality, we used a second parameterization which allowed partitioning survival into hunting and natural mortality. We tested specific hypotheses by comparing models with parameter constraints representing biological processes of interest. Analyses were conducted using program E-Surge (Choquet, Rouan, et al., 2009) and models were compared using Akaike's Information Criterion corrected for overdispersion (QAIC), retaining the most parsimonious of equivalent models (ΔQAIC<2; Burnham and Anderson, 2002).

Collars can be lost, and we accounted for this in our modelling approach. Since collared birds are also fitted with metal rings that are virtually never lost, we can determine if a bird has lost its collar upon being recaptured (see Juillet et al., 2011 for details). This is easily implemented in a multi-event modelling scheme by having two different states (i.e., 'Alive with collar and ring' and 'Alive with ring only') and modelling collar loss as a transition between these states (details in Appendix S3.1).

Overall survival estimation

We estimated annual survival (*S*), collar loss (*C*), live-encounter (*p*), and recovery (Seber's *r*; Gauthier and Lebreton, 2008) probabilities using a parameterization analogous to that used in Juillet et al. (2011; details in Appendix S3.1). This parameterization allows incorporating heterogeneity in ring reporting with respect to collar loss even if we have no information from hunters regarding the presence or absence of collars when birds are recovered. We slightly modified this parametrization to incorporate heterogeneity in live-encounter probabilities detected by the goodness-of-fit tests (see below). We first tested constraints on encounter and collar loss probabilities (e.g. reduced time-dependence) before selecting constraints on survival, as advocated by Lebreton et al. (2009).

Live-encounter probabilities (*p*) were estimated separately for collared and non-collared birds because in the former case it included both re-sightings and physical recaptures. Dead encounters are registered when hunters report rings of shot birds. The recovery probability (Seber's *r*) is the probability, for a goose dying between year

i and *i+1*, that hunting was the cause of death, that it was retrieved by the hunter, and that its ring was reported. Because recoveries occur continuously throughout the year, they are coded at the next capture occasion (i.e., year *i+1*). We tested whether dead recovery probabilities differed between collared and non-collared birds, possibly due to different reporting probabilities by hunters. We also tested whether there could be a different collar loss rate in the first few years, up to 7 years after marking.

We started from a model with full time effect in interaction with collar effect on survival. Next, we reduced the *time* × *collar* interaction to our three periods with different hunting regulations (1990-1998; 1999-2008; 2009-2019) to assess whether the effect of collars on survival varied between periods. To determine whether any collar effect on survival could be affected by changes in targeting of collared birds by hunters over the course of our study, we also tested for possible effects of collars in interaction with time periods on recovery probability in our top-ranking models. Because the number of recaptures and recoveries is low for birds marked in the last few years of a CMR dataset, the estimated survival for these years is often imprecise. For this reason, survival estimates of the last two occasions were not included in the estimation of the collar effect in all analyses. Two years is a good compromise between loss of precision at the end of a dataset and maximizing the information used to estimate the collar effect.

Hunting and natural mortality estimation

In a second analysis, we partitioned mortality into mortality from hunting and from natural causes by decomposing the survival process into two transition matrices, one for each process (see Appendix S3.1). We followed the parameterization developed by vanOudenhove et al. (2014), but slightly modified to include heterogeneity in live-encounter probability and in recovery rate with respect to auxiliary mark loss. Because our dataset alone contained no information on mortality sources other than hunting, we applied an external covariate (annual harvest rate, HR) on hunting mortality probability to improve identifiability in the estimation of mortality probability from each source. Annual harvest rate was obtained by dividing the estimated number of adult geese harvested by hunters each year by the estimated fall population size. Total harvest is estimated through yearly surveys sent to hunters by national wildlife agencies in Canada and the USA. The fall population size is estimated from an aerial photographic survey of the whole population conducted in spring, when all greater snow geese are on the staging grounds in the St-Lawrence lowlands and adjusted for mortality between spring and fall (details in Appendix S3.2).

Model parameters are the same as in the previous analysis except for recovery probability. Here, *r* is conditional on the cause of death being hunting because this process is modelled by the hunting mortality probability. Consequently, *r* is analogous to a reporting rate in this parametrization as it includes only the probability that a shot bird that died is retrieved, and its ring reported. We tested whether an effect of collars was present on

hunting, natural or both sources of mortality and whether these effects differed between periods of stable hunting regulations (i.e. *collar* × *hunting period* interaction).

Goodness-of-fit tests

We used the goodness-of-fit tests for multistate capture-recapture data developed by Pradel et al. (2003) and implemented in U-CARE (Choquet, Lebreton, et al., 2009) to assess the fit of our most general model. We detected overdispersion in our data (tests 3G and M highly significant, see Table S3.1) likely due to heterogeneity in live-encounter probabilities, which can be explained by the biology of our study species and our sampling design. We therefore modified our original model structure to correct for heterogeneity in live-encounter probabilities and used a c-hat value of 1.256 to account for the remaining overdispersion (details in Appendices S3.1 and S3.3).

Interaction between stressors

To determine the presence of any interaction (synergistic or antagonistic) between our two stressors (A and B), we compared the observed combined effect of hunting and collars to an additive model (expected combined additive effect of A and B = (A + B) - (A × B); Sih et al., 1998). This additive model represents the null hypothesis of no interaction between A and B. The '- (A × B)' part of the equation ensures that the combined effect of A and B does not exceed 100%. This must be accounted for when investigating competing sources of mortality because individuals killed by one stressor cannot also die from another stressor. The combined effect of our stressors was considered additive if it was not statistically different than the expected additive effect, and non-additive otherwise (Côté et al., 2016). To evaluate the effect of each stressor alone and in combination, we compared mean mortality (i.e. 1 – survival) of collared and non-collared birds over the three periods defined by stable hunting regulations. The effect of hunting regulations alone can be defined as the difference in mortality between periods 2 (or 3) and period 1 for non-collared birds. Although there is still some hunting going on in the first period, we are comparing our stress 'treatments' to the least stressful situation (i.e. period 1, with the most conservative hunting regulations). The effect of collars alone can be defined as the difference in mortality between collared and non-collared birds in the first period (1990-1998). The observed combined effect of collars and hunting regulations is defined as the difference in mortality between collared birds in periods 2 (or 3) and non-collared birds in period 1 (our 'control'). The 95% confidence intervals around the null model estimate were obtained by bootstrapping.

3.5 Results

Between 1990 and 2018, we marked 22 599 adult females of which 15 725 were also fitted with neck-collars. We physically recaptured 1296 non-collared birds (1 to 4 times each) and 3634 neck-collared females were encountered (2703 resighted, 417 physically recaptured and 514 both) at least once but up to 9 times. Finally, 4892 marked geese were shot and had their rings reported.

3.5.1 Encounter and collar loss probabilities

Our best-supported model retained full time dependence on all encounter probabilities (Figs. S3.1 to S3.3, Appendix S3.4). A constant difference (additive effect) between high- and low-encounter groups was retained for live-encounter probabilities (M4 vs. M3 or M2, Table 3.1). Encounter probability of the highly observable group was 5.8 and 3.9 times higher than in the weakly observable one for rings and collars, respectively (Figs. S3.1 and S3.2). An interaction between collar and time period (i.e. hunting regulation changes) was also retained on recovery probability (M14 vs. M13, Table 3.1). Recovery probability was 1.3 times higher in collared than non-collared birds in period 1, 1.7 times in period 2 and again 1.3 times in period 3 (Fig. S3.3).

Our best model retained an effect of time since ringing (i.e., age) on collar loss probability over a model without any age effect (M6 vs. M5) or a with a fully age-dependent collar loss rate up to 4 years after marking (M6 vs. M4, Table 3.1). Collar loss was moderate in the first year following marking (probability [95%CI]: 0.10 [0.06, 0.18]/year), low in the two following years (0.04 [0.03, 0.07]/year) and higher for the subsequent years (0.12 [0.10, 0.15]/year).

3.5.2 Collar effect

Annual survival

Our best-supported model retained an interaction between presence of a neck collar and time periods on survival probabilities (M14 vs. M13 and M8, Table 3.1, see Appendix S3.5 for model implementation in E-Surge). We found a clear negative effect of collars on survival in the second and third periods but not in the first period. Indeed, average annual survival during the first period was 0.87 [0.85, 0.89] for collared birds and 0.88 [0.84, 0.90] for non-collared birds (M17, Table 3.1). during period 3 ($\beta_{col\,(d3)}$ [95% CI] = -0.71 [-0.86, -0.56]) when hunting regulations were liberalized in both Canada and the USA, than in period 2 ($\beta_{col\,(d2)}$ = -0.25 [-0.41, -0.10]; Fig. 3.1) when this occurred only in Canada. Inclusion of a *collar* × *time period* interaction on recovery probability (M14 vs M13, Table 3.1) had virtually no effect on annual survival probabilities or on collar effect on survival.

Table 3.1 Results of model selection for the analysis of collar loss, survival, and live and dead encounter in adult female greater snow geese marked between 1990 and 2018. For each model, deviance, number of estimated parameters (NP) and difference in QAIC (ΔQAIC) with the most parsimonious model (M14) are provided. The complete model selection is provided in Table S3.3.

Name	Collar loss	Survival	Encounter			NP	Deviance	**ΔQAIC**
			Ringed	Collared	Dead			
M14	$a_{1,2:3,4}$	$t + d_{2,3}$. *col*	$t + g$	$t + g$	$t + col$. d	129	118268.54	0.00
M15	$a_{1,2:3,4}$	$t + d$. *col*	$t + g$	$t + g$	$t + col$. d	130	118266.82	0.63
M13	$a_{1,2:3,4}$	$t + d_{2,3}$. *col*	$t + g$	$t + g$	$t + col$	127	118280.80	5.75
M9	$a_{1,2:3,4}$	$t + d$. *col*	$t + g$	$t + g$	$t + col$	128	118279.72	6.90
M11	$a_{1,2:3,4}$	$t + d_{2:3}$. *col*	$t + g$	$t + g$	$t + col$	126	118295.74	15.65
M16	$a_{1,2:3,4}$	$t + col$	$t + g$	$t + g$	$t + col$. d	128	118295.31	21.31
M8	$a_{1,2:3,4}$	$t + col$	$t + g$	$t + g$	$t + col$	126	118307.25	24.82
M18	$a_{1,2:3,4}$	$d_1 + d_{2,3}$. *col*	$t + g$	$t + g$	$t + col$. d	105	118360.23	25.00
M6	$a_{1,2:3,4}$	t . *col*	$t + g$	$t + g$	$t + col$	154	118237.77	25.50
M17	$a_{1,2:3,4}$	d . *col*	$t + g$	$t + g$	$t + col$. d	106	118360.19	26.97
M4	a	t . *col*	$t + g$	$t + g$	$t + col$	156	118237.61	27.37
M10	$a_{1,2:3,4}$	$t + d_3$. *col*	$t + g$	$t + g$	$t + col$	126	118311.04	27.83
M12	$a_{1,2:3,4}$	d . *col*	$t + g$	$t + g$	$t + col$	104	118371.72	32.15
M5	i	t . *col*	$t + g$	$t + g$	$t + col$	152	118267.49	45.16
M3	a	t . *col*	$t + g$	t . g	$t + col$	183	118193.30	48.09
M2	a	t . *col*	t . g	t . g	$t + col$	210	118161.02	76.39
M7	$a_{1,2:3,4}$	t	$t + g$	$t + g$	$t + col$	125	118388.79	87.74
M1	a	t . *col*	t . g	t . g	t . *col*	237	118119.73	97.52

Note: a, age effect; *t*, time effect; *d,* time effect reduced to three periods (1: before special hunting regulations; 2: special hunting regulations in Canada only; 3: special hunting regulations in Canada and the USA); *col*, collar effect; *g*, heterogeneity in encounter probability (groups with high and low encounter probability); *i*, constant; '+', additive effect; '.', interaction. Notation for indices: ':' denotes a parameter constrained equal for two periods or age classes; ',' denotes a parameter varying between periods or age classes.

Hunting and natural mortality

Hunting mortality probability was related to annual harvest rate although the effect was not significant (β_{HR} = 0.13 [-0.13, 0.39]). Based on our most parsimonious model, hunting mortality was higher in collared birds than in those without collars ($\beta_{col\ (d2\ \&\ d3)}$ = 0.47 [0.27, 0.67]) during the last two periods and the effect was the same during both periods (Table S3.4, Fig. 3.2). In contrast, non-hunting mortality was similar between collared and non-collared birds during the first two periods but higher in the former group during the third period ($\beta_{col\ (d3)}$ = 0.81 [0.49, 1.13]; Fig. 3.3). Based on the slope parameters, the effect was stronger on non-hunting than hunting mortality.

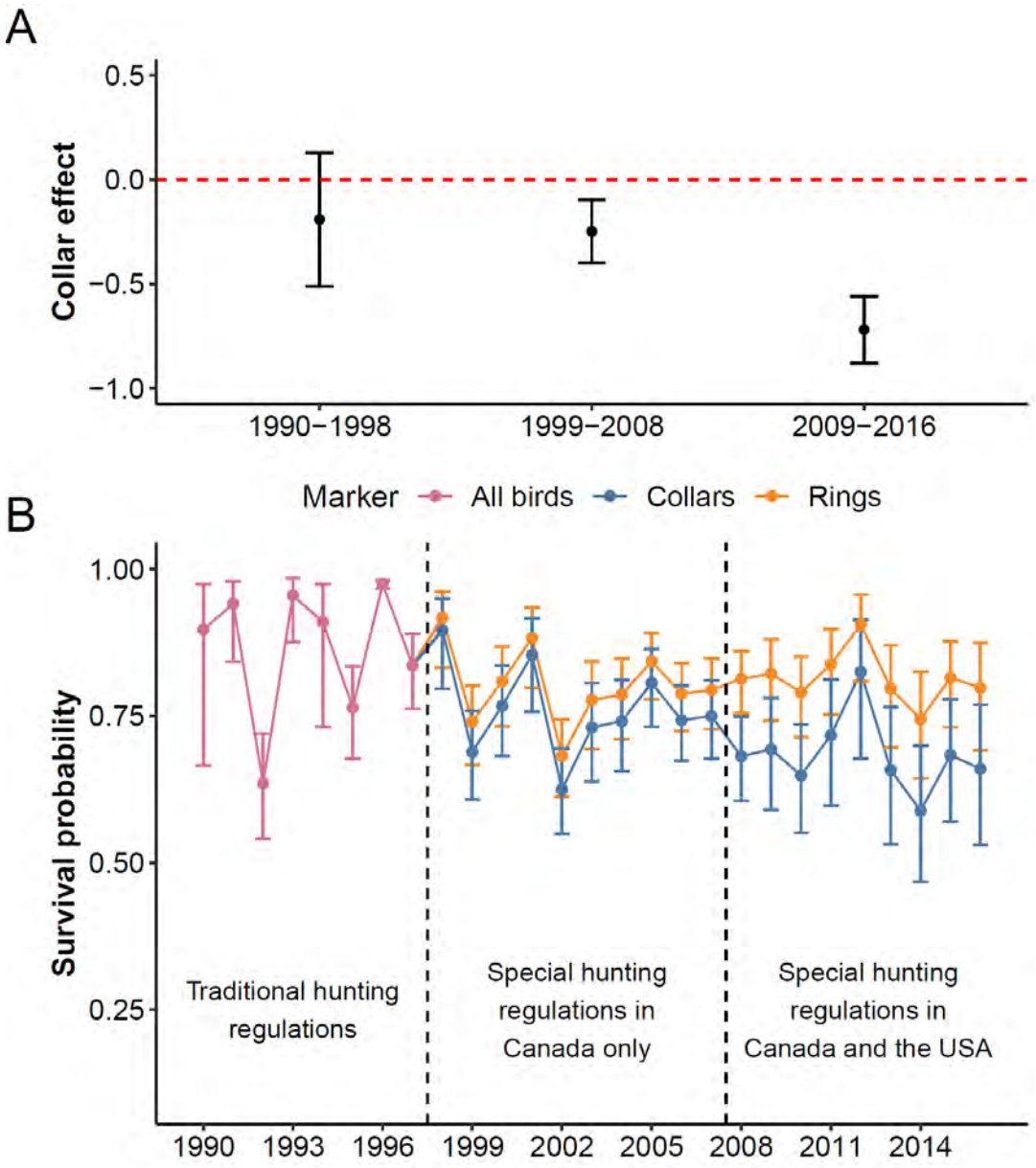

Figure 3.1 Effect of neck collars on survival probability of adult female greater snow geese marked between 1990 and 2016. A: Effect of collar on survival probability for three periods defined by different hunting regulations. Points represent the coefficient of the collar effect (β_{col}) estimated by model M15 (Table 3.1). B: Annual survival probabilities from the best-supported model (M14, Table 3.1). Dashed lines separate the three time periods with different hunting regulations. Error bars are 95% C.I.

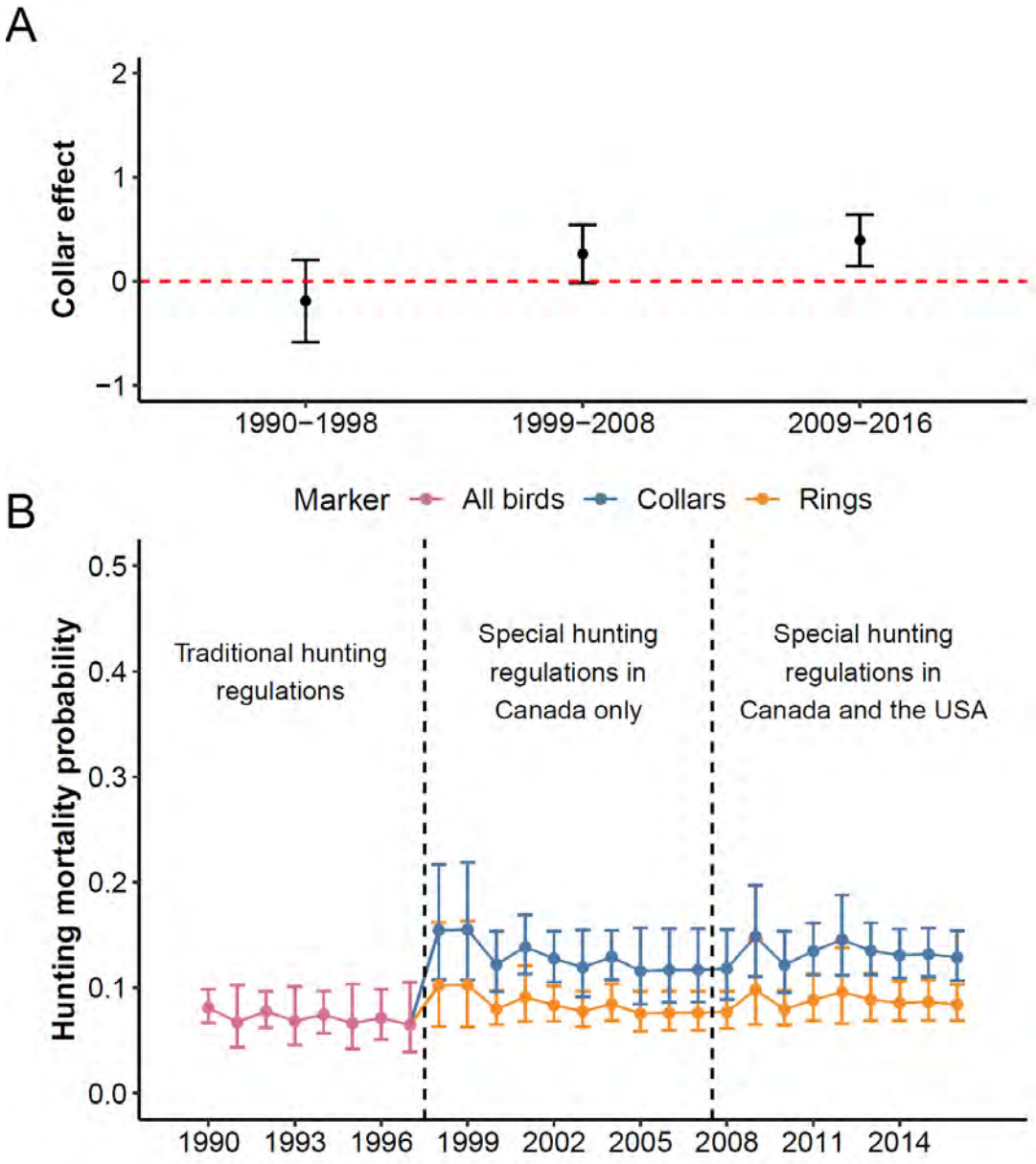

Figure 3.2 Effect of neck collars on hunting mortality probability of adult female greater snow geese marked between 1990 and 2016. A: Effect of collar on hunting mortality probability for three periods defined by different hunting regulations. Points represent the coefficient of the collar effect (β_{col}) estimated by model P5 (Table S3.4). B: Annual hunting mortality probabilities from the best-supported model (P10, Table S3.4). Dashed lines separate the three time periods with different hunting regulations. Error bars are 95% C.I.

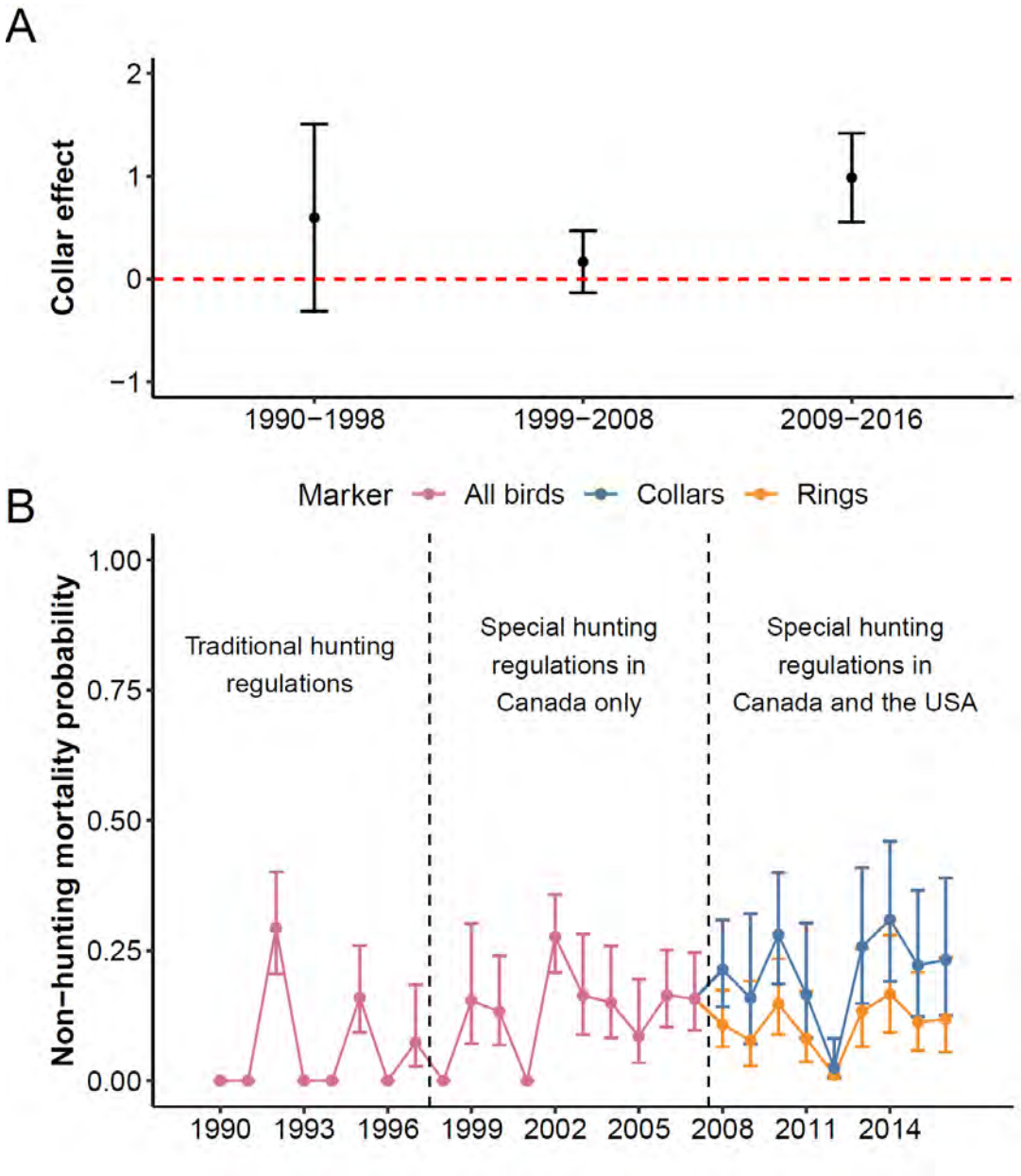

Figure 3.3 Effect of neck collars on annual non-hunting mortality probability of adult female greater snow geese marked between 1990 and 2016. A: Effect of collar on natural mortality probability for three periods defined by different hunting regulations. Points represent the coefficient of the collar effect (β_{col}) estimated by model P5 (Table S3.4). B: Annual non-hunting mortality probabilities from the best-supported model (P10, Table S3.4). Dashed lines separate the three time periods with different hunting regulations. Error bars are 95% C.I.

3.5.3 Interaction between stressors

We used model M17 (Table 3.1) to explore further the interaction between the effects of collars and hunting regulations on survival because it allowed comparing mean survival across time periods for both collared and non-collared birds. Changes in hunting regulations alone (i.e. measured in non-collared birds) led to an absolute

increase in mortality of 0.08 [0.05, 0.11] and 0.06 [0.02, 0.09] in periods 2 and 3, respectively, compared to period 1 (Fig. 3.4). When examining the same effects in collared birds, there was evidence that presence of a neck collar and changes in hunting regulations acted synergistically in increasing mortality. The combined effect of these stressors was marginally synergistic in period 2 considering the overlap in the 95% CIs of this effect and the additive null model. However, this combined effect was clearly synergistic in period 3 as the observed effect was almost three times stronger than that predicted by the additive model (Fig. 3.4).

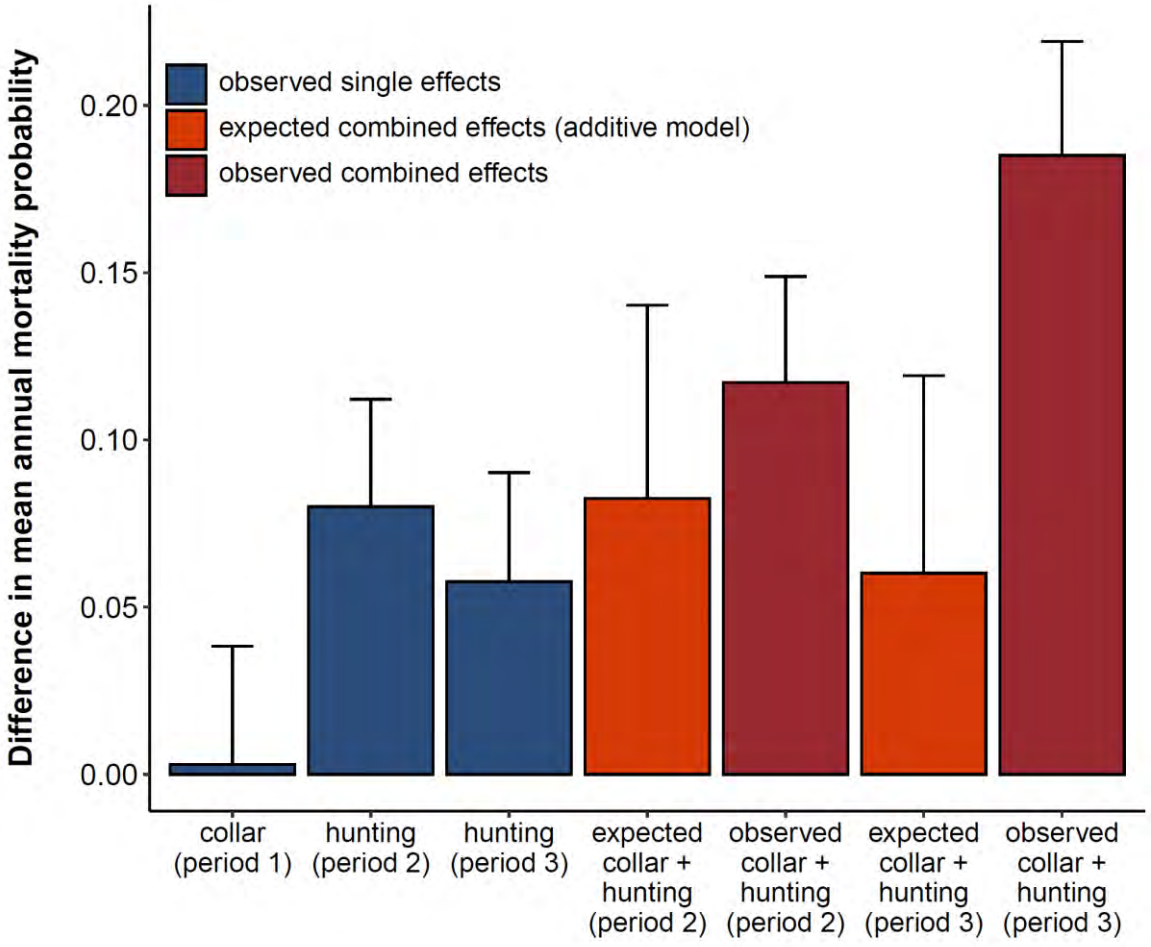

Figure 3.4 Difference in mean annual mortality probability between each 'treatment' group and the 'control' group based on estimates of model M17 (Table 3.1). The 'control' group refers to non-collared birds during period 1 (1990-1998), when hunting regulations were not yet liberalized. Error bars are the upper 95% CI.

3.6 Discussion

The quasi-experimental design of our 30-year study provided a rare opportunity to determine the presence and magnitude of synergistic effects between stressors in a natural setting. The presence of each stressor alone and in combination over long periods of time allowed us to decouple their effects from natural year-to-year variations on a vital rate. We provide strong evidence of a synergistic interaction between the effects of marking and hunting on goose survival. Indeed, we detected a negative effect of neck collars on survival only after hunting pressure considerably increased following the implementation of special hunting seasons. Furthermore, this negative effect was due to an increase in both hunting and non-hunting mortality in collared birds.

3.6.1 Hunting mortality

A possible mechanism to explain the increased hunting mortality of collared birds compared to non-collared ones after the implementation of a spring hunt in 1999 is through an adverse synergistic effect of both stressors on body condition. Both collars and hunting during spring staging were shown to affect body condition in this population (Féret et al., 2003; Legagneux et al., 2013; LeTourneux et al., 2021), and the combination of these impacts could increase the vulnerability of collared birds to hunting. This is supported by several lines of evidence. First, there was little evidence of an effect of collars on survival before spring hunting was allowed in 1999, supporting the results of past studies (Menu et al., 2000; Reed et al., 2005). Second, some studies have provided evidence that neck collars can negatively affect body condition (Legagneux et al., 2013), and reduce breeding propensity and clutch size (Reed et al., 2005), two nesting parameters strongly dependent on body condition in this species (Bêty et al., 2003). Given that hunting pressure also reduces goose body condition in spring (Féret et al., 2003; LeTourneux et al., 2021), we can imagine a situation where birds subjected to both stressors would be prone to take more risks to make up for their poor condition. While there is potentially a near-unlimited supply of food available to geese in agricultural fields, hunting disturbance can limit access to this resource. As such, hunting can reduce body condition of geese not only by inducing a chronic stress but also by limiting access to this food source, in addition to increasing energy expenditure and reducing foraging time. Results from LeTourneux et al. (2021) support this by providing evidence that geese use food-rich agricultural fields less when they are in good body condition, probably because these habitats represent a high risk due to hunting activity. This is also in line with recent work by Fowler et al. (2019) showing that lesser snow geese (*Anser caerulescens c.*) shot over decoys during spring migration are in poorer condition than those from the general population.

Another possible explanation is that hunters could preferentially target collared birds thereby increasing their hunting mortality. Indeed, collars are often considered trophies in the hunting community of North America, and this phenomenon has gained in popularity over time. However, a previous study on Ross' geese (*Anser rossii*)

found no difference in survival between birds marked with white collars that are difficult to detect on white geese, compared to strongly-contrasted collars (yellow and green; Caswell et al., 2012). This suggests that the overall effect of collar targeting on survival remains low despite gaining in popularity. The reduction in recovery probability detected in the last period of our study further supports that hunters have not become significantly better at killing collared snow geese. Therefore, although selection of collared birds by some hunters may contribute to the effects uncovered here, the available evidence does not support that this factor on its own could drive a reduction in survival of the magnitude observed in our dataset.

3.6.2 Multiple stressors and increased allostatic load

Long-term exposure to stressors can induce a chronic physiological stress response in animals, which may ultimately result in deleterious impacts on vital rates (Boonstra et al., 1998). To cope with stressors and maintain normal physiological balance (i.e. homeostasis), animals must make behavioral and physiological adjustments (allostasis; McEwen and Wingfield, 2003). Maintaining homeostasis under normal or unexpected circumstances incur energetic costs which make up the allostatic load. When the allostatic load is larger than the energy available in the environment, animals reach a state called allostatic overload (McEwen and Wingfield, 2003). In greater snow geese, both collars and disturbance from uninterrupted hunting (Béchet et al., 2004) during the non-breeding season constitute chronic stressors that contribute to the allostatic load. Collars may have increased allostatic load before 1999 when hunting activity was limited, but geese could have coped with this by reducing their reproductive investment. This would support the findings of Reed et al. (2005) that collared geese had a lower breeding propensity and clutch size than non-collared geese. Indeed, the environmental canalization hypothesis predicts that long-lived vertebrates like geese should evolve mechanisms to reduce the impacts of environmental variability on adult survival, their most important determinant of fitness (Gaillard and Yoccoz, 2003; Stearns and Kawecki, 1994). When hunting pressure increased after 1999 and 2009, the cumulative stress imposed by hunting and collars probably increased the allostatic load beyond the coping capacity of geese, leading to increased mortality.

3.6.3 Non-hunting mortality

The decrease in survival of collared birds was also partly mediated through increases in non-hunting mortality, which may involve several factors. First, formation of an ice layer on collars leading to mortality was reported in geese following extreme weather events (strong winds combined to temperatures below freezing; Greenwood and Bair, 1974; Zicus et al., 1983). Icing of collars following such events has also been reported in snow geese (G. Gauthier, pers. obs.) but those reports are rare. Moreover, this issue could be more common in the mid-continent where large swings in temperature are more common than on the Atlantic coast where greater snow

geese are found. Although these events probably contribute to increase natural mortality, it is unlikely to be the main factor driving this increase.

Second, birds injured during hunting but dying later may enter the “non-hunting mortality” component and such instances could have increased with hunting pressure and thus explain some of the non-hunting mortality. Unfortunately, since injured birds that eventually die are almost never found, the magnitude of this effect is impossible to assess. Nonetheless, a reduced condition of collared birds could also contribute to an increase in crippling loss if birds in poor condition take greater risks and get closer to hunters (e.g., Fowler et al., 2019). This effect might be exacerbated further if hunters target collared geese that are too far to be killed effectively.

Finally, allostatic overload due to cumulative stressors may ultimately have increased vulnerability of collared birds to disease, predation, or exhaustion during periods of high energy demand such as migration and spring staging. This could have contributed to the increase in non-hunting mortality observed during the last period of our study.

3.6.4 Limitations

Because we used time periods as a proxy for hunting pressure, some potential confounding environmental factors unrelated to hunting that have shown directional changes over the course of the study may have affected goose survival. For instance, the greater snow goose population has increased almost three-fold during the first period of this study, (Lefebvre et al., 2017), which may have led to density-dependent effects. However, the population did not exceed the estimated carrying capacity of its breeding habitat at that time (Massé et al., 2001) and has remained relatively stable during our periods 2 and 3 despite annual fluctuations (Lefebvre et al., 2017). Adult survival is also the demographic parameter usually least affected by density-dependent effects in long-lived species (Gaillard and Yoccoz, 2003). Moreover, any density-dependent effect on adult survival is unlikely to have differentially affected collared and non-collared birds, the question of primary interest in our study. Changes in the distribution of geese have also been reported in relation to changes in agricultural practices and climate warming (Calvert et al., 2005; Gauthier et al., 2005). However, most of these changes were reported to have started in the 1970s and 1980s, before this study and are thus unlikely to have affected our results. Some changes in the distribution and habitat use of this species were reported in the last 30 years (Béchet et al., 2004), but these were mostly attributed to changes in hunting regulations because of the increasing disturbance. All of this suggests that time periods were a suitable proxy for the effect of changes in hunting regulations in our study.

3.7 Conclusion

With the increasing pace of environmental change, there is a heightened potential for novel interactions between new and pre-existing stressors on wildlife species. Animal marking, especially with large conspicuous markers,

may impose a small but chronic physiological stress on animals. Although possible negative impacts of markers on wildlife are generally evaluated at the onset of research programs, such studies are often short-term and if no impacts are detected, the question is rarely revisited afterwards. Our study constitutes a rare demonstration in a natural setting that a combination of stressors can push animals beyond a threshold where vital rates are affected, even if the individually applied stressors may have initially had limited or undetectable impacts. In our case, neck-collars, which had no effect on survival of geese at the start of the study, later caused severe impacts to this key fitness parameter when the birds were exposed to increased hunting pressure. As such, we recommend that the use of plastic neck collars to monitor survival is discontinued in snow goose populations. Finally, we urge wildlife biologists to carefully consider the potential interactions between the effect of markers and changing environmental conditions during long-term marking programs, and to periodically revisit the potential impacts of the markers they are using. This is important not only for ethical considerations but also to ensure that valid scientific inferences can be made from studies based on marked animals.

3.8 Acknowledgements

We thank Alexandra Langwieder (Align Illustrations) for graciously providing pictograms for the graphical abstract. We thank G. Picard, M.C. Cadieux, C. Marcotte and Parks Canada for assistance in the field and M.C. Cadieux for managing our database. We further thank all the Inuit, students and field assistants that contributed to goose ringing in the past. We thank R. Alisauskas for bringing a potential effect of collars to our attention. We thank Eric Reed, Jillian Wettlauffer, and two other anonymous reviewers for comments that significantly improved this manuscript. We acknowledge logistic support from the Centre d'Études Nordiques and the Polar Continental Shelf Program (Natural Resources Canada), and funding from the Sentinel North program from the Canada First Research Excellence Fund, Arctic Goose Joint Venture and Canadian Wildilfe Service of Environment and Climate Change Canada, U.S. Fish & Wildlife Service, Atlantic Flyway Council, Northern Scientific Training Program of Polar Knowledge Canada, Natural Sciences and Engineering Research Council of Canada, ArcticNET Network of Centres of Excellence of Canada and Université Laval.

3.9 Supplementary material

Annexe S3.1 – Multievent model definition

Annexe S3.2 – Harvest rate estimation

Annexe S3.3 – Goodness-of-fit tests

Annexe S3.4 – Encounter probabilities

Annexe S3.5 – E-SURGE syntax for model M14 (Table 3.1)

Annexe S3.6 – Complete model selection tables

3.10 Bibliography

Alisauskas, R.T., Lindberg, M.S., 2002. Effects of neckbands on survival and fidelity of white-fronted and Canada geese captured as non-breeding adults. J. Appl. Stat. 29, 521–537. https://doi.org/10.1080/02664760120108575

Barron, D.G., Brawn, J.D., Weatherhead, P.J., 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods Ecol. Evol. 1, 180–187. https://doi.org/10.1111/j.2041-210X.2010.00013.x

Béchet, A., Giroux, J.-F., Gauthier, G., 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese: Effects of hunting on snow geese behaviour. J. Appl. Ecol. 41, 689–700. https://doi.org/10.1111/j.0021-8901.2004.00928.x

Bêty, J., Gauthier, G., Giroux, J., 2003. Body condition, migration, and timing of reproduction in snow geese: A test of the condition-dependent model of optimal clutch size. Am. Nat. 162, 110–121. https://doi.org/10.1086/375680

Boonstra, R., Hik, D., Singleton, G.R., Tinnikov, A., 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecol. Monogr. 68, 371–394. https://doi.org/10.2307/2657244

Burnham, K.P., 1993. A theory for combined analysis of ring recovery and recapture data, in: Lebreton, J.-D., North, P.M. (Eds.), Marked Individuals in the study of bird populations. Birkhäuser Verlag, Basel, Switzerland, pp. 199–213.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag, New York. https://doi.org/10.1007/b97636

Calvert, A.M., Gauthier, G., Reed, A., 2005. Spatiotemporal heterogeneity of greater snow goose harvest and implications for hunting regulations. J. Wildl. Manage. 69, 561–573. https://doi.org/10.2193/0022-541X(2005)069[0561:SHOGSG]2.0.CO;2

Carrier-Belleau, C., Drolet, D., McKindsey, C.W., Archambault, P., 2021. Environmental stressors, complex interactions and marine benthic communities' responses. Sci. Rep. 11, 4194. https://doi.org/10.1038/s41598-021-83533-1

Caswell, J.H., Alisauskas, R.T., Leafloor, J.O., 2012. Effect of neckband color on survival and recovery rates of Ross's geese. J. Wildl. Manage. 76, 1456–1461. https://doi.org/10.1002/jwmg.392

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., Pradel, R., 2009a. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. Ecography 32, 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Choquet, R., Rouan, L., Pradel, R., 2009b. Program E-Surge: A software application for fitting multievent models, in: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds.), Modeling demographic processes in marked populations. Springer US, Boston, MA, pp. 845–865. https://doi.org/10.1007/978-0-387-78151-8_39

Clausen, K.K., Madsen, J., 2014. Effects of neckbands on body condition of migratory geese. J. Ornithol. 155, 951–958. https://doi.org/10.1007/s10336-014-1080-6

Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. Proc. R. Soc. B. 283, 20152592. https://doi.org/10.1098/rspb.2015.2592

Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. Ecol. Lett. 11, 1278–1286. https://doi.org/10.1111/j.1461-0248.2008.01243.x

Féret, M., Gauthier, G., Bechet, A., Giroux, J.-F., Hobson, K.A., 2003. Effect of a spring hunt on nutrient storage by greater snow geese in southern Quebec. J. Wildl. Manage. 67, 796–807. https://doi.org/10.2307/3802687

Folt, C.L., Chen, C.Y., Moore, M.V., Burnaford, J., 1999. Synergism and antagonism among multiple stressors. Limnol. Oceanogr. 44, 864–877. https://doi.org/10.4319/lo.1999.44.3_part_2.0864

Fowler, D.N., Webb, E.B., Vrtiska, M.P., 2019. Condition bias of decoy-harvested light geese during the Conservation Order. J. Wildl. Manage. 84, 33–44. https://doi.org/10.1002/jwmg.21770

Fox, A.D., Walsh, A.J., Weegman, M.D., Bearhop, S., Mitchell, C., 2014. Spring ice formation on goose neck collars: effects on body condition and survival in Greenland white-fronted geese Anser albifrons flavirostris. Eur. J. Wildl. Res. 60, 831–834. https://doi.org/10.1007/s10344-014-0835-y

Gaillard, J.-M., Yoccoz, N.G., 2003. Temporal variation in survival of mammals: A case of environmental canalization? Ecology 84, 3294–3306. https://doi.org/10.1890/02-0409

Gauthier, G., Giroux, J.-F., Reed, A., Béchet, A., Bélanger, L., 2005. Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands? Glob. Chang. Biol. 11, 856–868. https://doi.org/10.1111/j.1365-2486.2005.00944.x

Gauthier, G., Lebreton, J.-D., 2008. Analysis of band-recovery data in a multistate capture-recapture framework. Can. J. Stat. 36, 59–73. https://doi.org/10.1002/cjs.5550360107

Greenwood, R.J., Bair, W.C., 1974. Ice on waterfowl markers. Wildl. Soc. Bull. 2, 130–134.

Johnsen, A., Lifjeld, J.T., Rohde, P.A., 1997. Coloured leg bands affect male mate-guarding behaviour in the bluethroat. Anim. Behav. 54, 121–130. https://doi.org/10.1006/anbe.1996.0437

Juillet, C., Choquet, R., Gauthier, G., Lefebvre, J., Pradel, R., 2012. Carry-over effects of spring hunt and climate on recruitment to the natal colony in a migratory species. J. Appl. Ecol. 49, 1237–1246. https://doi.org/10.1111/j.1365-2664.2012.02199.x

Juillet, C., Choquet, R., Gauthier, G., Pradel, R., 2011. A capture–recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss. J. Agric. Biol. Environ. Stat.16, 88–104. https://doi.org/10.1007/s13253-010-0035-5

Kleist, N.J., Guralnick, R.P., Cruz, A., Lowry, C.A., Francis, C.D., 2018. Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. Proc. Natl Acad. Sci. USA 115, E648–E657. https://doi.org/10.1073/pnas.1709200115

Lebreton, J., Nichols, J.D., Barker, R.J., Pradel, R., Spendelow, J.A., 2009. Chapter 3 Modeling individual animal histories with multistate capture–recapture models, in: Advances in ecological research. Elsevier, pp. 87–173. https://doi.org/10.1016/S0065-2504(09)00403-6

Lefebvre, J., Gauthier, G., Giroux, J.-F., Reed, A., Reed, E.T., Bélanger, L., 2017. The greater snow goose Anser caerulescens atlanticus: Managing an overabundant population. Ambio 46, 262–274. https://doi.org/10.1007/s13280-016-0887-1

Legagneux, P., Simard, A.-A., Gauthier, G., Bêty, J., 2013. Effect of neck collars on the body condition of migrating greater snow geese. J. Field Ornithol. 84, 201–209. https://doi.org/10.1111/jofo.12019

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Data from: Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species.

LeTourneux, F., Grandmont, T., Dulude-de Broin, F., Martin, M.-C., Lefebvre, J., Kato, A., Bêty, J., Gauthier, G., Legagneux, P., 2021. COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species. Biol. Conserv. 255, 108968. https://doi.org/10.1016/j.biocon.2021.108968

Mainguy, J., Bêty, J., Gauthier, G., Giroux, J.-F., 2002. Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? Condor 104, 156–161.

Massé, H., Rochefort, L., Gauthier, G., 2001. Carrying capacity of wetland habitats used by breeding greater snow geese. J. Wildl. Manage. 65, 271. https://doi.org/10.2307/3802906

McEwen, B.S., Wingfield, J.C., 2003. The concept of allostasis in biology and biomedicine. Horm. Behav. 43, 2–15. https://doi.org/10.1016/S0018-506X(02)00024-7

Menu, S., Hestbeck, J.B., Gauthier, G., Reed, A., 2000. Effects of neck bands on survival of greater snow geese. J. Wildl. Manage. 64, 544–552. https://doi.org/10.2307/3803252

Morez, V., Gauthier, G., Reed, A., 2000. Effect of body condition on vulnerability of greater snow geese to hunting and capture. J. Wildl. Manage. 64, 875–886. https://doi.org/10.2307/3802758

Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. Ecosystems 1, 535–545. https://doi.org/10.1007/s100219900049

Pennycuick, C.J., Fast, P.L.F., Ballerstädt, N., Rattenborg, N., 2012. The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration. J. Ornithol. 153, 633–644. https://doi.org/10.1007/s10336-011-0781-3

Pradel, R., 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics 61, 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Pradel, R., Wintrebert, C.M.A., Gimenez, O., 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. Biometrics 59, 43–53. https://doi.org/10.1111/1541-0420.00006

Reed, E.T., Gauthier, G., Pradel, R., 2005. Effects of neck bands on reproduction and survival of female greater snow geese. J. Wildl. Manage. 69, 91–100.

Romero, L.M., Wingfield, J.C., 2016. Tempests, poxes, predators, and people: stress in wild animals and how they cope, Oxford series in behavioral neuroendocrinology. Oxford University Press, Oxford ; New York.

Saraux, C., Le Bohec, C., Durant, J.M., Viblanc, V.A., Gauthier-Clerc, M., Beaune, D., Park, Y.-H., Yoccoz, N.G., Stenseth, N.C., Le Maho, Y., 2011. Reliability of flipper-banded penguins as indicators of climate change. Nature 469, 203–206. https://doi.org/10.1038/nature09630

Sih, A., Englund, G., Wooster, D., 1998. Emergent impacts of multiple predators on prey. Trends Ecol. Evol. 13, 350–355. https://doi.org/10.1016/S0169-5347(98)01437-2

Souchay, G., Gauthier, G., Pradel, R., 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. https://doi.org/10.1890/13-1277.1

Stearns, S.C., Kawecki, T.J., 1994. Fitness sensitivity and the canalization of life-history traits. Evolution 48, 1438–1450. https://doi.org/10.1111/j.1558-5646.1994.tb02186.x

Steffen, W., Persson, Å., Deutsch, L., Zalasiewicz, J., Williams, M., Richardson, K., Crumley, C., Crutzen, P., Folke, C., Gordon, L., Molina, M., Ramanathan, V., Rockström, J., Scheffer, M., Schellnhuber, H.J., Svedin, U., 2011. The Anthropocene: From global change to planetary stewardship. AMBIO 40, 739–761. https://doi.org/10.1007/s13280-011-0185-x

van Oudenhove, L., Gauthier, G., Lebreton, J.-D., 2014. Year-round effects of climate on demographic parameters of an arctic-nesting goose species. J. Anim. Ecol. 83, 1322–1333. https://doi.org/10.1111/1365-2656.12230

Yparraguirre, D.R., Sanders, T.A., Weaver, M.L., Skalos, D.A., 2020. Abundance of Tule geese Anser albifrons elgasi in the Pacific flyway 2003–2019. Wildfowl 70, 27.

Zicus, M.C., Schultz, D.F., Cooper, J.A., 1983. Canada goose mortality from neckband icing. Wildl. Soc. Bull. 11, 286–290.

Chapitre 4 – Evidence for seasonal compensation of hunting mortalities in a long-lived migratory bird

« I hate Mondays. »

Référence de la publication :

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P. 2024. Evidence for seasonal compensation of hunting mortalities in a long-lived migratory bird. J. Appl. Ecol. 61: 2169-2179. DOI: 10.1111/1365-2664.14731

4.1 Résumé

Pour gérer efficacement une population exploitée, il faut savoir si la mortalité à la chasse est additive ou compensatoire aux autres sources de mortalité. Chez les espèces longévives, la mortalité à la chasse est généralement additive, ce qui fait de la chasse sportive un outil de gestion de prédilection pour ces espèces. Les études sur ces processus se sont principalement intéressées à comprendre si la mortalité naturelle induite par les facteurs dépendant de la densité pouvait compenser la mortalité à la chasse. Cependant, lorsque la chasse a lieu durant des périodes distinctes, on pourrait également observer une compensation des mortalités dues à la chasse entre ces périodes s'il y a présence d'hétérogénéité individuelle dans la vulnérabilité à la chasse. Nous explorons cette nouvelle hypothèse chez la grande oie des neiges (*Anser caerulescens atlanticus*), une population devenue surabondante à la fin du XX^{e} siècle. Pour contrôler sa surabondance, les organismes de gestion de la faune ont mis en place des mesures sans précédent, comme l'ouverture de saisons de chasse spéciales au printemps au Canada en 1999 et en hiver aux États-Unis en 2009. Pour déterminer l'impact relatif de chaque mesure sur la population, nous avons estimé le taux de survie des adultes sur une base saisonnière grâce à 30 ans de données de capture-marquage-recapture analysées avec un modèle multi-évènement de mélange d'information. Nous avons aussi utilisé ce design quasi-expérimental pour évaluer la possibilité d'une compensation des mortalités à la chasse entre les saisons. Nos résultats indiquent que chaque mesure a causé une diminution du taux de survie des oies durant les saisons ou celles-ci ont été appliquées. Cependant, le taux de survie au printemps a augmenté après l'instauration des mesures spéciales à l'hiver aux États-Unis en 2009 malgré le maintien de la chasse printanière au Canada. Nous avons trouvé une relation négative entre les mortalités au printemps et à l'hiver, ce qui suggère que l'augmentation des mortalités de chasse à cette saison a été compensée par une réduction de la mortalité au printemps après 2009. À notre connaissance, nous rapportons ici le premier cas d'une compensation de la mortalité à la chasse à une saison par une réduction de cette mortalité lors d'une saison ultérieure. Nous suggérons que ce phénomène peut être expliqué par une hétérogénéité dans la vulnérabilité à la chasse parmi les individus, potentiellement liée à la présence de juvéniles avec leurs parents. Une meilleure compréhension des relations entre les évènements de mortalité inter-saisonniers devrait améliorer notre compréhension de la dynamique des populations et de la gestion des espèces exploitées ou surabondantes.

Mots clés: Mortalité compensatoire · Grande oie des neiges · Règlements de chasse · Modèles multi-évènement · Surabondance · Compensation saisonnière · Survie

4.2 Abstract

Understanding whether hunting mortality is additive to or compensated by other mortality sources is at the heart of managing harvested populations. Long-lived species are expected to exhibit hunting mortality additive to other sources of mortality, making them ideal candidates for population management through sport harvest. Previous studies on these processes have focussed on density-dependent natural mortality compensating for hunting mortality, but when harvest occurs in distinct periods of the year, heterogeneity in hunting vulnerability between individuals could also lead to compensatory mortality between these periods. We explore this new idea using the case of the greater snow goose (*Anser caerulescens atlantica*), a harvested species whose population became overabundant in the late 20th century. To control this population, wildlife agencies liberalized hunting regulations with unprecedented actions such as special hunting seasons implemented in spring 1999 in Canada and in winter 2009 in the USA. To determine the relative impact of each measure on survival, we estimated survival of adult geese on a seasonal basis using 30 years of capture-mark-reencounter data in a joint live-and-dead-encounter multievent model. We also used this quasi-experimental set-up to evaluate possible compensation in hunting mortality between seasons. We found that both special hunting seasons decreased goose survival in the seasons and periods in which they were implemented. However, survival increased during the spring hunting season after the establishment of the special winter hunting season in the USA in 2009. There was a negative relationship between annual spring and winter mortalities, suggesting that the increase in hunting mortality in winter was compensated by a reduction in spring mortality after 2009. To our knowledge, we report the first documented instance of hunting mortality in one season being compensated by a reduction in hunting mortality in a subsequent season. We suggest that heterogeneity in hunting vulnerability among individuals, possibly linked to the presence of juveniles accompanying their parents, may explain this phenomenon. A better knowledge of seasonal patterns and relationships between mortality components is needed to improve our understanding of population dynamics and management of harvested populations.

Keywords: Compensatory mortality · Geese · Hunting regulations · Multievent capture-recapture modeling · Overabundance · Seasonal compensation · Survival

4.3 Introduction

Adverse effects of humans on wildlife are numerous and include, among others, habitat destruction and overexploitation (Steffen et al., 2011). Paradoxically, some of the most dramatic impacts of human activity are mediated through indirect positive effects on some species. For instance, human activity can provide opportunities for native populations to grow well beyond their historical abundance, ultimately changing ecosystem balance (e.g., Côté et al., 2004; Jefferies & Rockwell, 2002). Additionally to their impacts on natural systems, overabundant native species are also the source of numerous human-wildlife conflicts (Bradbeer et al., 2017; Côté et al., 2004; Tombre et al., 2013; Wagner and Seal, 1992; Witmer, 2022).

Among existing tools to manage overabundant populations , sport harvest (hunting) is a cost-effective method when it can be implemented. Hunting may also have higher public acceptance compared to more direct control methods such as culling or hazing (Fix et al., 2010). Game species thus lend themselves well to such management actions because of long-standing hunting traditions. However, managers must understand how hunting impacts demographic rates for management through hunting to be successful.

The concepts of additive and compensatory mortality are central to population management through hunting (Anderson and Burnham, 1976). Compensatory mortality occurs when hunting mortality is compensated by a reduction of natural mortality later in the annual cycle (Boyce et al., 1999). This can happen if harvest lowers population density sufficiently to reduce density-dependent mortality, or if hunting selectively harvests weak individuals (e.g. Fowler et al., 2019; Guillemain et al., 2007) that would likely have died from other causes (i.e., individual heterogeneity, Lebreton, 2005). Harvest then has a reduced effect on annual survival because an increase in hunting mortality is compensated by a decrease in natural mortality (Lebreton, 2005). Additivity occurs when harvest mortality is added to natural mortality, leading to a reduced annual survival proportional to harvest mortality (Cooch et al., 2014). These two hypotheses are only points along a continuum of possibilities where natural mortality can partially compensate, overcompensate or be over-additive to hunting mortality (Grzegorczyk et al. 2024). This topic has received considerable attention, in part because of its central role in wild game management (Péron, 2013; Riecke et al., 2022). Hunting mortality must be additive to natural mortality to successfully reduce overabundant populations through harvest regulations.

Compensation mechanisms have traditionally been investigated in terms of natural mortality compensating for hunting mortality. Yet, in the presence of strong heterogeneity in hunting vulnerability among individuals, the same process could take place between hunting mortalities occurring in distinct seasons. For instance, if high harvest in one season eliminates individuals most vulnerable to hunting, this could reduce hunting mortality in subsequent seasons as fewer vulnerable individuals remain in the population. This seasonal compensation hypothesis is of particular interest for migratory species moving across several jurisdictions with different hunting

regulations (Holopainen et al., 2018). Indeed, many harvested populations need to be jointly managed either to provide equitable recreational harvest opportunities across jurisdictions (Anderson et al. 2018), manage subsistence vs. sport harvest practices (Muth et al. 1987) or reconcile recreational and commercial interests (Ricouard et al. 2023). In such cases, understanding the impacts of harvest timing on population dynamics may be critical for maximizing harvest opportunities among stakeholders.

Several goose populations have become overabundant worldwide as a result of human activity (Ankney, 1996; Fox and Madsen, 2017; Gauthier et al., 2005). Because hunting mortality is considered additive in geese (Alisauskas et al., 2006; Cooch et al., 2014; Gauthier et al., 2001), special hunting seasons have been implemented throughout their annual cycle to curb population growth (Koons et al., 2014; Lefebvre et al., 2017; Madsen et al., 2016; Sheaffer et al., 2005). Overabundant geese are thus well suited to examine possible seasonal compensation in hunting mortality as they migrate through different states. This could also have important consequences for the success of management actions implemented in different jurisdictions.

Greater snow geese (*Anser caerulescens atlantica*) are considered overabundant in North America, and numerous management actions were implemented over two decades to stop their population growth (Lefebvre et al., 2017). The main actions were the establishment of special hunting seasons (Lefebvre et al 2017). A first special hunting season (legally referred to as a Conservation Harvest) was implemented on the spring staging grounds in Québec, Canada in 1999. Then, 10 years later, another special hunting season was implemented in late winter in the USA (legally referred to as the Conservation Order). As a result, greater snow geese are now continuously exposed to hunting from arrival from their arctic breeding grounds in early September in Québec until their departure for the north in late May. These conservation efforts succeeded in stabilizing population size in recent years, in large part due to a decrease in annual survival after 1999 (Calvert and Gauthier, 2005; Lefebvre et al., 2017; LeTourneux et al., 2022). Unexpectedly however, LeTourneux et al. (2022) found no evidence of a further decrease in annual survival after 2009 when the special winter hunting season was established in the USA. We propose two alternative hypotheses for this result. First, the additional hunting pressure was insufficient to increase hunting mortality during winter. Alternately, the increase in winter hunting mortality was compensated by a reduced hunting mortality during spring. In presence of heterogeneity in hunting vulnerability, an increased winter mortality could reduce the pool of vulnerable individuals available for hunters during spring, leading to an increase in spring survival and offsetting any increase in winter hunting mortality.

In this study, we use 30 years of capture-marking-reencounter (CMR) data to determine the relative impact of two new hunting seasons (spring in Canada since 1999 and winter in the USA since 2009) on seasonal survival of greater snow geese. Because annual survival did not change after implementation of the special winter hunting season in the USA (LeTourneux et al., 2022), we also explore whether a potential increase in winter

mortality due to hunting after 2009 could be compensated by a decrease in mortality during the following spring (seasonal hunting compensation hypothesis).

4.4 Methods

4.4.1 Ringing data

Greater snow geese spend the winter on the east coast of the USA (November-March), migrate to the High Artic to breed during the summer (June-August) and stop in southern Québec, Canada, during spring (March-May) and fall (September-November) for staging. Geese were captured from 1990 to 2019 and marked at the end of the breeding season on Bylot Island, Nunavut (73N 80W), the largest known greater snow goose breeding colony, when they are moulting and flightless (details in (Menu et al., 2000). All captured birds were fitted with a metal leg-ring and 2/3 of adult females were also fitted with a plastic neck collar, which was accounted for in our analysis. Individuals were aged (young of the year vs adults, i.e. ≥ 1 year old) by plumage, sexed by cloacal eversion, and checked for presence of markers. Young are captured with adults in family groups but were excluded from this analysis. All capture methods and animal manipulations complied with the relevant ethics guidelines and were approved by the Canadian Bird Banding Office, the Mittimatalik Hunter and Trapper Organization, Parks Canada and the Animal Protection Committee of Université Laval.

Marked geese could be encountered in three ways. (1) Physical recaptures of birds wearing solely a leg-ring occurred during the ringing drives on the breeding grounds (summer occasions; see *Encounters* section in 4.4.2 below for definition of seasons). (2) Birds wearing a collar could be recaptured on the breeding ground but also resighted continuously during the year (breeding colony and on staging and wintering grounds) either by our field teams or birdwatchers. Physical recaptures of collared birds were pooled with summer resightings for our analysis (see details below). (3) Recoveries of rings from birds shot by hunters could occur during hunting seasons. Before the spring hunt was established in 1999, recoveries could only occur during fall staging in Québec and winter in the USA. Starting in spring 1999, recoveries could also occur during spring staging in Québec.

4.4.2 Data analysis

We used multi-event capture-mark-reencounter models (Pradel, 2005) to estimate adult survival on a seasonal basis. We used the parametrization developed by LeTourneux et al. (2022) to estimate survival (*S*), collar loss (*C*), live-encounter (*p*) and recovery (Seber's *r*) probabilities, but modified to estimate probabilities on a seasonal basis. This parametrization allowed us to account for heterogeneity in recovery probability with respect to collar loss (details in Juillet et al., 2011), as well as heterogeneity in live-encounter probability (see below). The detailed structure of our general model including transitions between states is presented in Appendix S4.1. We built

reduced models with parameter constraints representing biological hypotheses of interest and used Akaike's Information Criterion corrected for overdispersion (QAIC) to select the most parsimonious models (Burnham and Anderson, 2002). We used program E-SURGE for survival analyses (Choquet et al., 2009b) and U-Care for goodness-of-fit tests (Choquet et al., 2009a). Other analyses were conducted in the R statistical environment (R Core Team, 2020). Figures were generated with packages `ggplot2` and `tidyverse` (Wickham, 2016; Wickham et al., 2019).

Encounters

Over the course of their annual cycle, geese move across distinct geographical locations where hunting regulations differ (Fig. 4.1). To account for that, we divided the year into four encounter occasions (summer, fall, winter and spring) based on the geographic location and time of year. Live encounters on the breeding grounds during the summer (physical recaptures or resightings) were coded in the summer encounter occasions. Resightings occurring during fall and spring staging in southern Québec were coded in the fall and spring occasions, respectively, and those occurring in the USA during winter were coded in the winter occasion (see Fig. S4.1 for the temporal distribution of encounters at each season). Our model accounted for unequal time interval lengths between capture occasions (2.5 months between the summer-fall and fall-winter occasions, 3.5 months between the winter-spring and spring-summer occasions). Seasonal estimates reported in the results are raised to the length of the interval and thus represent the survival for the full length of each season.

Encounter probability of leg-ringed birds could be estimated only during summer when physical captures took place. For collared birds, observations occurred continuously during the year so their encounter probability could be estimated at each season. While continuous encounters violate the CMR model assumption of discrete encounter occasions (Lindberg, 2012), simulations revealed this did not significantly bias our survival estimates (Appendix S4.2).

The recovery probability (Seber's *r*) is defined as the probability, conditional on a bird dying between occasion *t* and *t+1*, that the cause of death is hunting and that the bird was retrieved and reported by the hunter (Gauthier and Lebreton, 2008). Dead recoveries also occurred continuously throughout the hunting seasons and were coded in the next encounter occasion (e.g., birds recovered in fall were coded in winter).

Model building

We used knowledge from the survival analysis of LeTourneux et al. (2022) on this population to determine our starting model (M0, Table 4.1; see Appendix S4.1 for model structure).. We included a sex effect on live encounter probability during summer because males have lower breeding site fidelity than females (Cooke et al., 1975). Goodness-of-fit tests revealed the presence of heterogeneity in seasonal encounter probabilities, as

previously found by LeTourneux et al. (2022) on an annual basis (details in Appendix S4.3). These effects were incorporated in our starting model as detailed in Appendix S4.1. We accounted for the remaining lack of fit by adjusting the AIC with a c-hat value ($\hat{c}$ = 2.0; Appendix S4.3).

We included a collar effect on survival probability that differed between seasons and time periods (see below for definition) as found by LeTourneux et al., (2022). However, because our dataset contains no information on survival of leg-ringed-only birds in spring before 1999 (no recoveries in spring before 1999), we did not include a collar effect on spring survival before 1999. This assumption is reasonable because previous studies found no evidence of a collar effect on survival in this population before hunting was liberalized in 1999 (LeTourneux et al., 2022; Menu et al., 2000; Reed et al., 2005).

We were interested in determining how seasonal survival rate changed in response to management actions implemented in Québec in 1999 and the USA in 2009. We therefore defined three time periods ('hunting periods' from now on): (1) 1990-1998 without special management actions, (2) 1999-2008 when spring hunting was introduced in Québec only and (3) 2009-2019 when the special hunting seasons were present in both Québec in spring and the USA in winter. We computed annual survival estimates by multiplying the seasonal survival of each season raised to the length of the interval for each season. Confidence intervals for these estimates were obtained by parametric bootstrap. Additional modelling considerations are addressed in Appendix S4.4.

Compensation between mortalities

We evaluated the hypothesis of a seasonal compensation between winter and spring mortality with a *post-hoc* logit-normal linear regression between spring and winter mortality estimates (i.e., 1 – survival). We accounted for uncertainty in mortality estimates using a parametric bootstrap approach. We generated 10,000 datasets of winter and spring survival by sampling values from logit-normal distributions defined by each survival estimate and its standard error obtained from the CMR analysis. We ran a linear regression between spring and winter mortality values derived from each simulated dataset and we calculated the mean slope and its 95% confidence interval from the distribution of the 10,000 slope estimates. To explore whether sampling correlation could yield a negative relationship between winter and spring mortality, we repeated the same procedure for pairs of seasons with hunting where no compensation was expected (i.e. fall-winter; fall-spring). All effects and estimates are reported with their 95% confidence intervals.

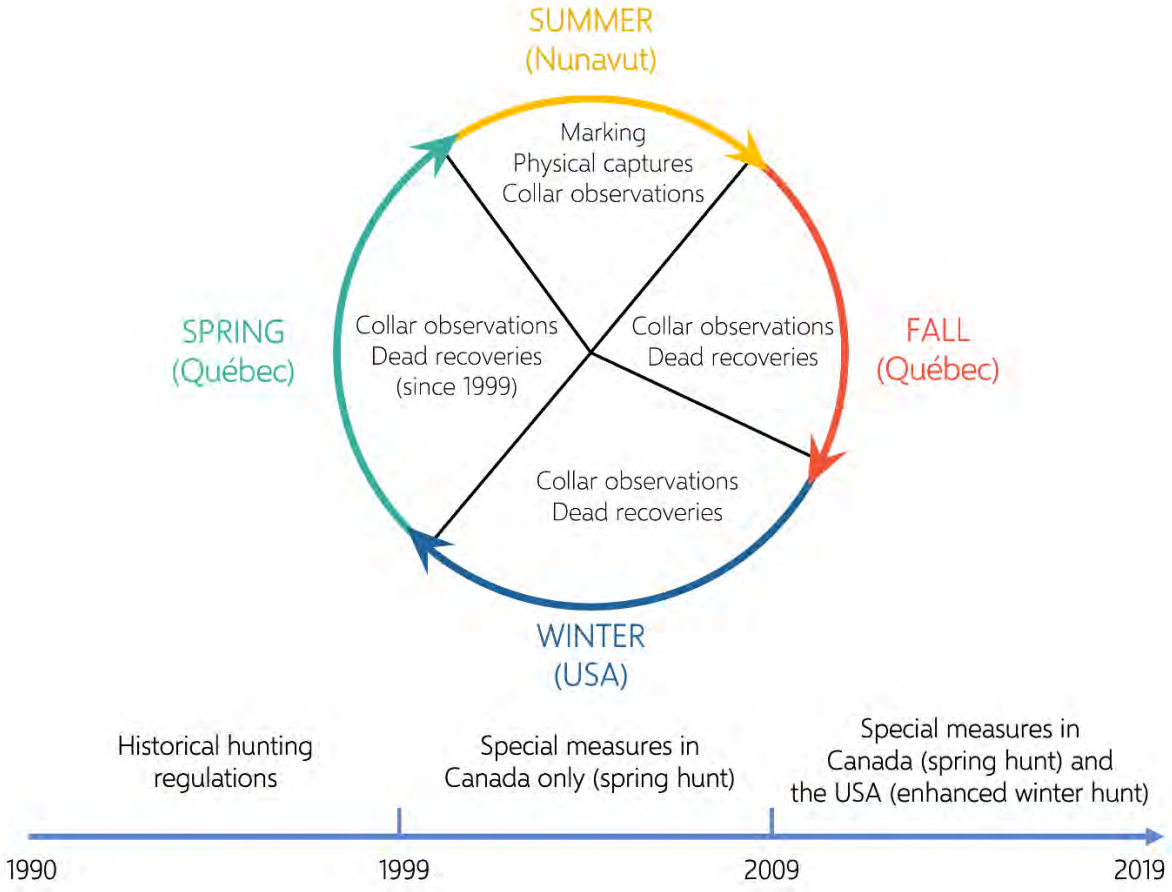

Figure 4.1 Graphical representation of the data sampling design. The circle depicts the information available for each season, and the length of each arrow represents the relative length of each season. The timeline indicates hunting periods with the hunting regulations associated with each.

4.5 Results

Between 1990 and 2019, we marked 30,043 adult geese (23, 198 males and 6,891 females) with leg rings only and 15,725 adult females with collars and leg rings. During that period, 14,533 birds were encountered alive at least once but up to 23 times for collared birds and up to 5 times for leg-ringed-only birds (11,969 only resighted, 2,276 only physically recaptured and 288 both). Additionally, 8,954 geese were shot and had their rings reported by hunters.

Table 4.1 Results of model selection for the analysis of seasonal survival, live encounter (physical capture of leg-ringed-only birds), and dead encounter (recovery) probabilities of adult greater snow geese marked between 1990 and 2018. For each model, deviance, number of estimated parameters (K) and difference in QAIC (ΔQAIC) between the current and the most parsimonious model (M10) are provided. Full time variation and heterogeneity in interaction with seasons was applied to live encounter probabilities of collared birds in all models. The complete model selection is provided in Table S4.3.

Model No	Survival	Capture	Recovery	K	**ΔQAIC**
M10	d . sp + su + $d_{1:2,3}$. wi + $d_{1,2:3}$. fa + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col . d	259	0.00
M11	d . sp + su + wi + $d_{1,2:3}$. fa + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col . d	258	0.98
M9	d . $seas_{fa,\ sp}$ + su + $d_{1:2,3}$. wi + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col . d	260	2.00
M13	d . $seas_{su,\ fa,\ sp}$ + wi + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col . d	261	5.87
M8	d . $seas_{su,\ fa,\ sp}$ + $d_{1:2,3}$. wi + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col . d	262	5.99
M6	t + col . $seas$. $d_{2,3}$	t_{su} + h + s	d . ($seas$ + col)	297	7.13
M7	d . $seas$ + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col . d	263	7.45
M14	d . $seas_{su,\ fa,\ sp}$ + $d_{1,2:3}$. wi + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col . d	262	7.85
M5	d . $seas$. col	t_{su} + h + s	t + col . d	266	10.73
M12	$d_{1:2,3}$. sp + su + $d_{1:2,3}$. wi + $d_{1,2:3}$. fa + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col . d	258	10.80
M4	d . $seas$ + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col	261	11.79
M0	t + col . $seas$. d	t_{su} + h + s	t + col	370	73.91
M2	t + col . $seas$. $d_{2,3}$	t_{su} + h + s	t + col	367	74.45
M3	t + col . $d_{2,3}$	t_{su} + h + s	t + col	361	136.20
M1	t + col . $seas$. d	t_{su} + h	t + col	369	296.37

Note: *t*, full time effect (seasons x years); *d*, year effect reduced to three periods (1: before special hunting regulations, 1990-1998; 2: special hunting regulations in Canada only, 1999-2008; 3: special hunting regulations in Canada and the USA, 2009-2019); *seas*, full seasonal effect (all seasons differ); *su* (summer), *fa* (fall), *wi* (winter) or *sp* (spring), seasonal effect present in the specified season; t_{su}, year effect for the summer season only; *s*, sex, *col*, collar effect; *h*, heterogeneity in encounter probability (groups with high and low encounter probability); '+', additive effect; '.', interaction. Notation for indices: ':' denotes a parameter constrained equal for two periods; ',' denotes a parameter varying between periods.

The preferred model (M10, Table 4.1) retained the following effects on encounter and survival probabilities. Live encounter probability of collared females showed full time variation and heterogeneity (as detected by the goodness-of-fit tests, Appendix S4.3), with birds from the highly observable group being encountered 2.4 to 7.8 times more than those of the weakly observable group depending on the season and year (Fig. S4.3). Probability of physical recapture of leg-ringed birds also varied over time, showed heterogeneity, and was 2.4 to 2.7 times higher in females than males (M0 vs. M1, Table 4.1; Fig. S4.3). Recovery probabilities varied over time (seasons and year) and between collar and leg-ringed-only birds in interaction with hunting period (M7 vs. M4, Table 4.1). Collared birds were always recovered more often than leg-ringed-only birds(Fig. S4.5). Finally, survival varied between seasons and between collared and leg-ringed geese (M2 vs. M3, Table 4.1), although the latter effect was only present during the 2nd and 3rd hunting periods (M7 vs. M5). The effect of collars on survival probability was strong during winter, but weaker in other seasons (Fig. S4.6)

4.5.1 Variations of survival across hunting periods

We found strong evidence that the spring hunt implemented in Québec in 1999 reduced spring survival of greater snow geese (β = -0.72 [-1.15, -0.29]) compared to the period before it was in place ($S_{spring\_1990-1998:}$ 0.95 [0.93, 0.97]; $S_{spring\_1999-2008}$: 0.91 [0.89, 0.92], Fig. 4.2). The liberalization of hunting regulations in fall also reduced survival (β = -0.57 [-0.87, -0.29]; $S_{fall\_1990-1998}$: 0.95 [0.93, 0.97]; $S_{fall\_1999-2019}$: 0.92 [0.91, 0.93], Fig. 4.2). However, we found no evidence for differences in winter before and after 1999 (M13 vs. M14; M7 point estimates: $S_{winter\_1990-1998}$: 0.94[0.92, 0.96]; $S_{winter\_1999-2008}$: 0.95[0.94, 0.97]).

We found evidence that the special hunting season in the USA negatively affected winter survival of geese compared to the period before it was implemented (β = -0.41 [-0.67, -0.14]). The absolute difference in survival was moderate ($S_{winter\_1990-2008}$: 0.95 [0.94, 0.96]; $S_{winter\_2009-2019}$: 0.93 [0.92, 0.94], Fig. 4.2) but represents a strong effect when reported on an annual basis (i.e., 0.85 vs. 0.78). However, spring survival increased after implementation of the special winter hunting season (β = 0.66 [0.16, 1.16]; $S_{spring\_1999-2008}$: 0.91 [0.89, 0.92]; $S_{spring\_2009-2019}$: 0.95 [0.93, 0.96]; Fig. 4.2). On the other hand, we found no evidence for differences in fall survival between these two periods (M10 vs. M9; M7 point estimates: $S_{fall\_1999-2008}$: 0.92[0.89, 0.94]; $S_{fall\_2009-2019}$: 0.92[0.90, 0.94]). Finally, summer survival was high (S_{summer}: 0.996 [0.990, 0.998], Fig. 4.2) and there was no evidence that it varied across hunting periods (M9 vs. M8).

4.5.2 Compensation in seasonal mortality and annual survival

We found evidence for an inverse relationship between winter and spring mortality between 1999 and 2018 (β = -0.58 [-1.19, 0.02]; Fig. 4.3). We found no evidence of similar relationships between other combinations of hunting seasons (winter vs fall: β = -0.03 [-0.27, 0.22]; spring vs fall: β = -0.05 [-0.42, 0.31]; Figs. S4.8 and S4.9). Annual survival estimates reconstructed from seasonal estimations (Fig. 4.4) show lower survival in period 2 ($S_{1999-2008:}$ 0.79 [0.77, 0.81]) compared to period 1 ($S_{1990-1998:}$ 0.86 [0.84, 0.88]) but virtually no change between periods 2 and 3 ($S_{2009-2018:}$ 0.81 [0.79, 0.83]). These annual survival estimates are very similar to those obtained by LeTourneux et al. (2022) directly on an annual basis (Fig. S4.7), indicating that our seasonal survival estimates are realistic. Finally, there was no relationship between annual survival estimates (1999-2019) and the annual harvest rate (Appendix S4.6: Section S4.6.2), further pointing to a compensatory relationship.

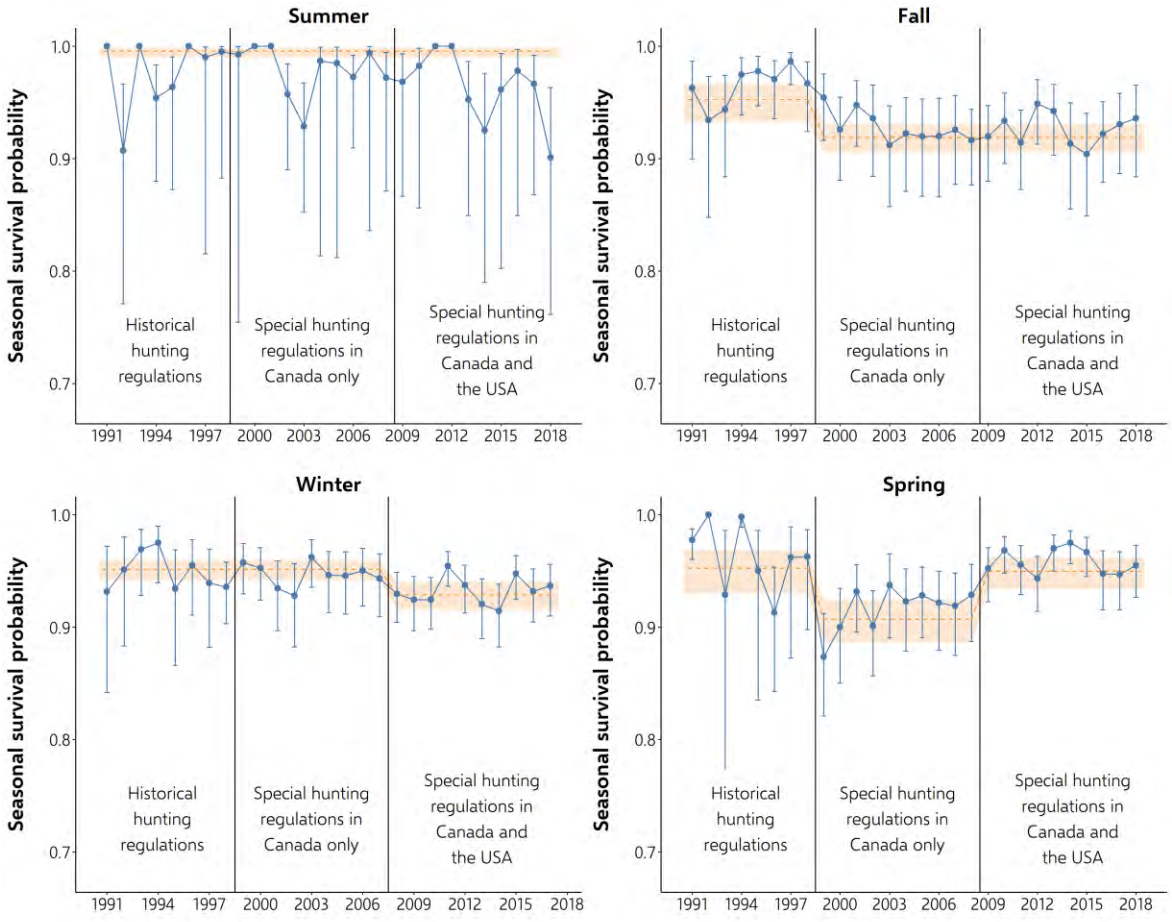

Figure 4.2 Seasonal survival estimates of leg-ringed adult greater snow geese between 1990 and 2019. The dotted line represents survival estimated from our best supported model (M10; Table 4.1) with its 95% confidence intervals (shading). Points represent yearly survival estimates from model M6 along with their 95% CI.

4.6 Discussion

The use of 30 years of capture-mark-reencounter data collected on a seasonal basis provided an unprecedented opportunity to examine potential compensation of mortalities between successive hunting seasons. While annual survival of greater snow geese has been stable since the implementation of the special spring conservation hunt in 1999 (LeTourneux et al., 2022), we find a different pattern at a seasonal level. Indeed, seasonal survival was reduced by both special hunting seasons when they were implemented, allowing us to reject the hypothesis that the special winter hunting season was inefficient in reducing survival after 2009. Instead, we find support for our seasonal hunting compensation hypothesis, where the increased winter mortality in 2009-2019 was offset by a reduction in spring mortality during the same period. Furthermore, we provide evidence that the adverse impacts of collars on survival of greater snow geese (LeTourneux et al., 2022) is highly seasonal, occurring mostly in winter.

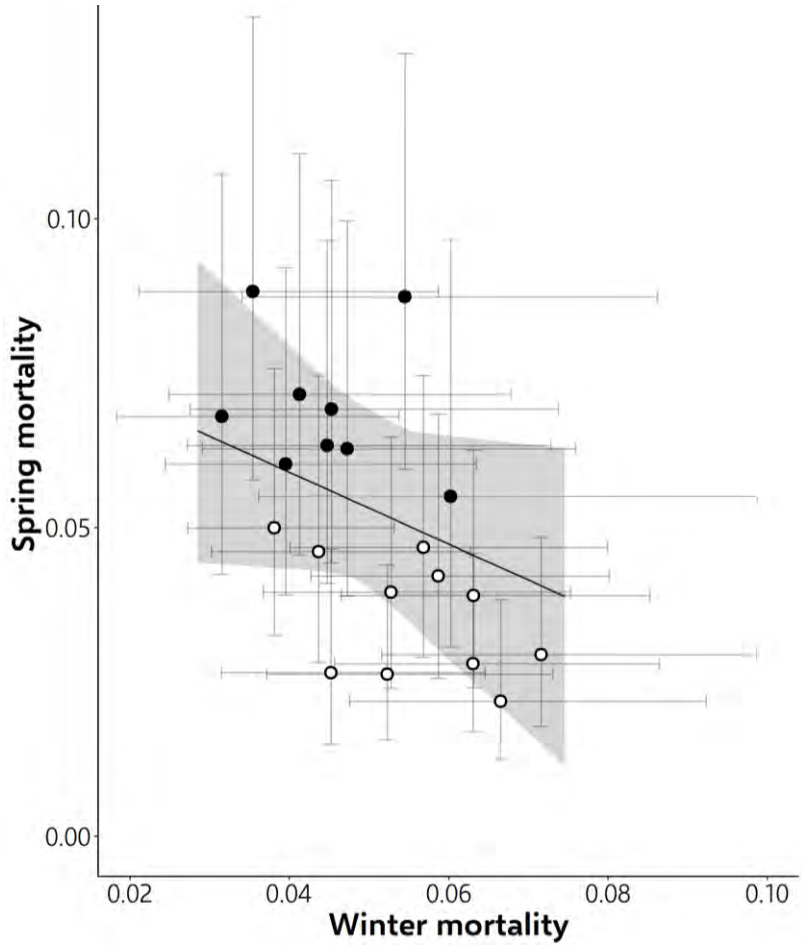

Figure 4.3 Relationship between spring and winter mortality estimates of adult greater snow geese between 1999 and 2018, after implementation of special hunting seasons in Canada only (spring only, 1999-2008, closed dots) and in Canada and USA (spring and winter, 2008-2019, open dots). Error bars are 95% C.I. of annual survival estimates computed as 1-survival from model M6 (Table 4.1). The black line represents the mean bootstrapped slope estimated from 10 000 simulations (see methods; β [95%CI] = -0.58 [-1.19, 0.02]). The gray shading represents the central 95% of the bootstrapped relationships.

4.6.1 Seasonal compensation of hunting mortalities

The presence of compensation in hunting mortality is surprising, especially in a long-lived species. Indeed, hunting mortality was found to be additive to other sources of mortality in adult greater snow geese (Gauthier et al., 2001) and other goose species (Fox, 2003; Koons et al., 2014; van der Jeugd and Kwak, 2017). Compensation in hunting mortality is commonly reported in species with relatively high natural mortality rates and explained by density-dependent mechanisms (Arnold et al., 2016; Cooch et al., 2014; Riecke et al., 2022; Sandercock et al., 2011). In those species, fall hunting mortality is typically compensated by reductions in natural mortality during winter due to reduced competition for resources (Boyce et al., 1999). This is unlikely in greater snow geese because they suffer from relatively low natural mortality (LeTourneux et al., 2022), and they have

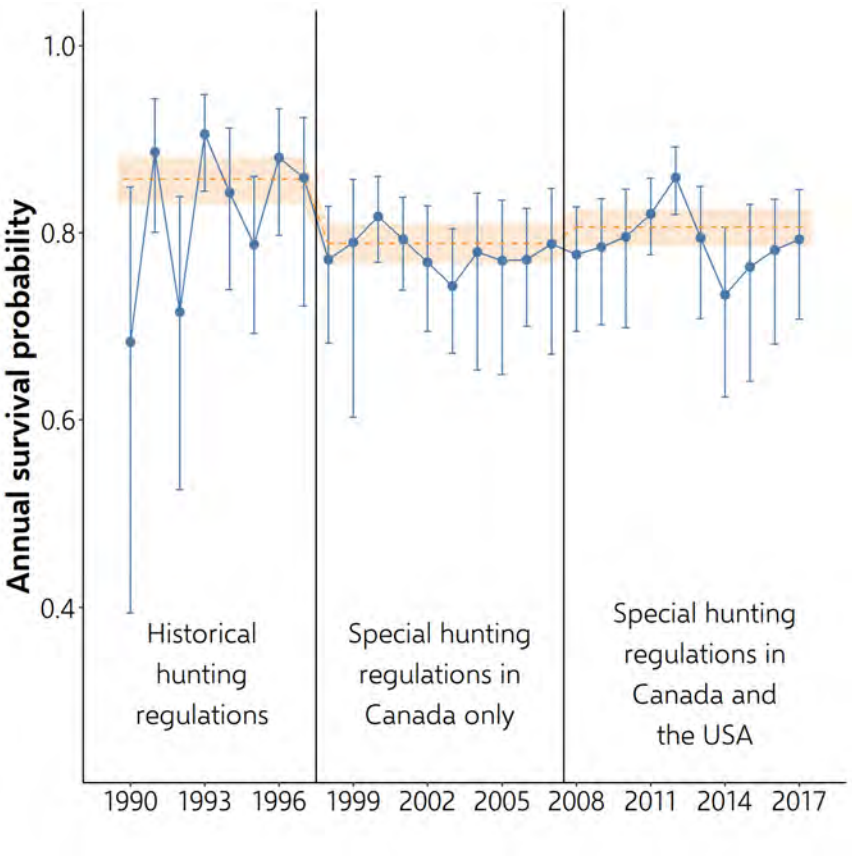

Figure 4.4 Annual survival estimates of leg-ringed adult greater snow geese between 1990 and 2019. Annual values were reconstructed from seasonal survival presented in Fig. 4.2 (see methods). The dotted line represents survival estimates calculated from our best supported model (M10; Table 4.1) with its 95% confidence intervals (shaded area). Points represent yearly survival estimates calculated from model M6 along with their 95% CI.

access to near-unlimited high-quality agricultural food sources in winter and spring (Fox and Abraham, 2017; Gauthier et al., 2005). Furthermore, if density-dependence was the driver of the compensatory relationship between winter and spring mortalities, we would expect to find a similar relationship before the implementation of new hunting regulations in 1999, which was not the case (Gauthier et al., 2001).

Several lines of evidence suggest that the seasonal compensation in mortality observed between winter and spring is driven by changes in hunting mortality. First, hunting is known to be the dominant source of mortality in adult snow geese (Francis et al., 1992a; Gauthier et al., 2001; LeTourneux et al., 2022). Second, the observed changes in seasonal survival perfectly match the changes in hunting regulations that took place in the different seasons. Third, a strength of our study is that we benefitted from a large scale, quasi-experimental situation with two major changes in hunting regulations during different seasons. Each of the three "experimental" periods were long (~10 years) and had relatively stable hunting regulations, which attenuates possible confounding effects caused by annual environmental variability. Furthermore, the seasonal hunting compensation occurred

during a period of stability in population size (Lefebvre et al., 2017), which also minimizes possible confounding density-dependent effects. To our knowledge, it is the first time that a seasonal compensation in hunting mortality is reported in a long-lived species.

A likely explanation for the seasonal compensation uncovered here is individual heterogeneity in hunting vulnerability (Lebreton, 2005) that generates a "pool" of individuals more vulnerable to hunting. Several mechanisms could lead to this heterogeneity. For instance, parents with young are more exposed to hunting mortality than those without young because juvenile geese are naïve and are more harvested by hunters (Calvert et al., 2005; Clausen et al., 2017; Koons et al., 2014). Hunters regularly report observations of one or two adults that follow juveniles lured by decoys (probably their parents) in an attempt to lead them away (LeTourneux and Gauthier, pers. obs.). This behavior has been anecdotally reported in the literature for snow geese (Giroux and Bedard, 1986), and was proposed as the cause of observed differences in survival between breeders and non-breeders (Francis et al., 1992b). This mechanism can also explain how the variation in vulnerability is maintained in the population as the 'pool' of vulnerable birds, i.e., parents with young, is renewed every year. Other factors such as individual variation in body condition could also lead to heterogeneity in hunting vulnerability as individuals in low body condition are less weary of decoys and more vulnerable to hunters (Fowler et al., 2019). Intra-generational selection due to heterogeneity in individual quality (sensu Cam et al. 2013) could be an alternative mechanism generating the observed seasonal survival pattern. The higher spring survival could then represent a within-year amelioration of the population. However, such a selection process may occur on a longer timescale than the duration of this study and predominantly affect young birds.

4.6.2 Seasonality in collar effect

Our results confirmed a reduced survival of collared females compared to leg-ringed-only birds after implementation of special hunting seasons in 1999 and 2009 as reported by LeTourneux et al. (2022). However, the increased mortality of collared females occurred almost exclusively during winter when geese are in the USA, suggesting a stronger contribution of collar targeting by hunters to the observed reduction in survival than proposed by LeTourneux et al. (2022). Goose collars are considered trophies in the hunting community, and this phenomenon has gained in popularity in the last 20 years with the advent of internet. Many US hunters specialize in finding and shooting neck-collared geese (N. Huck, M. Szymanski; pers. comm.), despite efforts to educate hunters in treating collared birds as normal individuals. The popularity of collecting goose collars among US hunters is thus a plausible explanation for our results (Fig. S4.6). Alternatively, if the impact of collars was solely due to factors such as chronic stress and adverse effects on body condition, survival of collared geese should be equally impacted in spring and fall. Our results also suggest that the phenomenon of targeting collared geese for trophies is less prevalent in Quebec where most greater snow geese are harvested in Canada.

4.6.3 Limitation of the study

Investigation of compensation between different mortality components is ideally carried out by modeling the relationship directly within the capture-mark-reencounter model. This allows disentangling sampling correlation from the true 'process correlation' between mortality estimates (i.e. compensation) while properly propagating errors (e.g., Koons et al., 2014; Servanty et al., 2010). This can be done using flexible tools available for Bayesian analysis (e.g., NIMBLE) but is much more difficult to implement using classical frequentist tools. Unfortunately, a Bayesian approach was not feasible here because the size of our dataset (> 30 000 birds with > 9 000 unique capture histories) and the complexity of our seasonal model (> 250 parameters) required prohibitive computing times for MCMC sampling. Although the presence of some unaccounted sampling correlation between winter and spring mortality estimates in our data may be a limitation, we believe that it did not seriously bias our calculation of compensation. First, if sampling correlation between winter and spring mortality estimates was large, we would expect to find similar relationships between mortalities in other seasons, which was not the case (Figs. S4.8 and S4.9). Second, the compensation uncovered here is perfectly in line with results of LeTourneux et al. (2022) who found no change in average annual survival of leg-ringed-only birds after the implementation of the special winter hunt in the USA in 2009 based on an annual analysis. Finally, we find no relationship between annual survival and harvest rate of greater snow geese (Fig. S4.10), as expected in presence of a compensatory relationship between mortality components.

4.6.4 Implications of seasonal compensation

The importance of understanding seasonal patterns when evaluating potential compensation between different mortality sources has often been emphasized (Boyce et al., 1999; Kokko and Lindström, 1998; Sandercock et al., 2011). To our knowledge, however, this has not been discussed in terms of compensation in hunting mortality alone between successive seasons. Our results highlight the importance of coordinating management efforts and of monitoring their impacts over the entire range of targeted populations. Otherwise, efforts to reduce populations in one part of their range may be thwarted by regulations in other jurisdictions, as has apparently been the case for greater snow geese over the last 10 years. Understanding the impacts of harvest timing on population dynamics and compensation mechanisms should help to better manage harvested populations. In co-managed harvest systems like the adaptive harvest management of North American waterfowl (Anderson et al. 2018) or fisheries managed to maintain maximum sustainable yields (Ricouard et al. 2023), determining seasonal mortality patterns may allow uncovering seasonal compensation mechanisms undetectable on an annual basis and improve decision-making regarding harvest.

The implications of seasonal compensation patterns in mortality transcends the management of harvested species. For instance, seasonal compensation phenomena can also occur in natural systems characterized by

strong predator-prey interactions. Indeed, an increase in predation mortality in one season may be compensated by a reduction of mortality in a later season, either through individual heterogeneity or density-dependence (Bender and Rosas-Rosas, 2016; Boyce et al., 1999), but remain unobservable on an annual basis. Taking into account these seasonal patterns is also essential to adequately model community dynamics (Hutchison et al., 2020; Sauve and Barraquand, 2020). In the context of global changes and drastic declines of numerous taxa, detecting changes in seasonal survival that may be unobservable on an annual basis due to compensation will be increasingly critical for species conservation.

4.7 Conclusion

Whether hunting mortality is additive to other sources of mortality and directly reduces annual survival is at the heart of the management of harvested populations. Historically, additivity and compensation between different mortality components of a population have been investigated in terms of natural mortality compensating for hunting mortality. Here, we present a new seasonal hunting compensation mechanism where the increase in hunting mortality in one season may decrease hunting mortality in a subsequent season, leading to an overall compensatory effect of an increase in harvest pressure. To our knowledge, this is the first time that compensatory hunting mortality is found in adult geese and possibly in a long-lived vertebrate species. We propose individual heterogeneity in hunting vulnerability as a biological mechanism through which this can occur. However, other potential mechanisms such as amelioration due to a selection process imposed by hunting deserves further study (Grzegorczyk et al. 2024). The rarity of long-term mortality datasets on a seasonal basis may have prevented researchers from uncovering similar effects in other species. Indeed, obtaining robust estimates of seasonal survival is notoriously difficult because it requires observations throughout the annual cycle of species (Allen et al., 2019; Leyrer et al., 2013; Robinson et al., 2010). However, with the rapid development of new bio-logging technologies that can be attached to ever smaller animals (Nathan et al., 2022), large continuous-time datasets will soon become available. This should provide opportunities to investigate novel mechanisms that can lead to seasonal compensation of mortalities and better assess its fundamental role in population dynamics.

4.8 Acknowledgements

We thank F. Dulude-de Broin for productive discussions on the analyses and interpretations. We thank G. Picard, M.C. Cadieux, C. Marcotte and Parks Canada for assistance in the field and M.C. Cadieux for managing our database. We further thank all the Inuit, students and field assistants who contributed to goose ringing. We acknowledge logistic support from the Centre d'Études Nordiques and the Polar Continental Shelf Program (Natural Resources Canada), and funding from the Sentinelle Nord program from the Canada First Research Excellence Fund, Arctic Goose Joint Venture and Canadian Wildilfe Service, U.S. Fish & Wildlife Service, Atlantic Flyway Council, Northern Scientific Training Program of Polar Knowledge Canada, Natural Sciences and

Engineering Research Council of Canada, ArcticNET Network of Centres of Excellence of Canada and Université Laval.

4.9 Supplementary material

Annexe S4.1 – Multievent model definition

Annexe S4.2 – Discrete analysis of continuous live encounter data

Annexe S4.3 – Goodness-of-fit tests

Annexe S4.4 – Additional modelling considerations

Annexe S4.5 – Survival of collared geese and encounter probabilities for all birds

Annexe S4.6 – Compensation relationships

Annexe S4.7 – Complete model selection table

4.10 Bibliography

Alisauskas, R.T., Drake, K.L., Slattery, S.M., Kellett, D.K., 2006. Neckbands, harvest, and survival of Ross's geese from Canada's central Arctic. J. Wildl. Manage. 70, 89–100. https://doi.org/10.2193/0022-541X(2006)70[89:NHASOR]2.0.CO;2

Allen, A.M., Ens, B.J., Van De Pol, M., Van Der Jeugd, H., Frauendorf, M., Oosterbeek, K., Jongejans, E., 2019. Seasonal survival and migratory connectivity of the Eurasian Oystercatcher revealed by citizen science. Auk 136, uky001. https://doi.org/10.1093/auk/uky001

Anderson, D.R., Burnham, K.P., 1976. Population ecology of the mallard VI: effects of exploitation on survival (No. 128), Population Ecology of the Mallard. U.S. Fish and Wildlife Service, Washington, D.C.

Ankney, C.D., 1996. An embarrassment of eiches: Too many geese. J. Wildl. Manage. 60, 217–223. https://doi.org/10.2307/3802219

Arnold, T.W., Afton, A.D., Anteau, M.J., Koons, D.N., Nicolai, C.A., 2016. Temporal variation in survival and recovery rates of lesser scaup. J. Wildl. Manage. 80, 850–861. https://doi.org/10.1002/jwmg.21074

Bender, L.C., Rosas-Rosas, O.C., 2016. Compensatory puma predation on adult female mule deer in New Mexico. J. Mammal. 97, 1399–1405. https://doi.org/10.1093/jmammal/gyw094

Boyce, M.S., Sinclair, A.R.E., White, G.C., 1999. Seasonal compensation of predation and harvesting. Oikos 87, 419–426. https://doi.org/10.2307/3546808

Bradbeer, D.R., Rosenquist, C., Christensen, T.K., Fox, A.D., 2017. Crowded skies: Conflicts between expanding goose populations and aviation safety. Ambio 46, 290–300. https://doi.org/10.1007/s13280-017-0901-2

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag, New York. https://doi.org/10.1007/b97636

Calvert, A.M., Gauthier, G., 2005. Effects of exceptional conservation measures on survival and seasonal hunting mortality in greater snow geese. J. Appl. Ecol. 42, 442–452. https://doi.org/10.1111/j.1365-2664.2005.01042.x

Calvert, A.M., Gauthier, G., Reed, A., 2005. Spatiotemporal heterogeneity of greater snow goose harvest and implications for hunting regulations. J. Wildl. Manage. 69, 561–573. https://doi.org/10.2193/0022-541X(2005)069[0561:SHOGSG]2.0.CO;2

Cam, E., Gimenez, O., Alpizar-Jara, R., Aubry, L.M., Authier, M., Cooch, E.G., Koons, D.N., Link, W.A., Monnat, J., Nichols, J.D., Rotella, J.J., Royle, J.A., & Pradel, R. (2013). Looking for a needle in a haystack: Inference about individual fitness components in a heterogeneous population. Oikos, 122(5), 739–753. https://doi.org/10.1111/j.1600-0706.2012.20532.x

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., Pradel, R., 2009a. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. Ecography 32, 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Choquet, R., Rouan, L., Pradel, R., 2009b. Program E-Surge: A software application for fitting multievent models, in: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds.), Modeling demographic processes in marked populations. Springer US, Boston, MA, pp. 845–865. https://doi.org/10.1007/978-0-387-78151-8_39

Clausen, K.K., Christensen, T.K., Gundersen, O.M., Madsen, J., 2017. Impact of hunting along the migration corridor of pink-footed geese Anser brachyrhynchus – implications for sustainable harvest management. J. Appl. Ecol. 54, 1563–1570. https://doi.org/10.1111/1365-2664.12850

Cooch, E.G., Guillemain, M., Boomer, G.S., Lebreton, J.-D., Nichols, J.D., 2014. The effects of harvest on waterfowl populations. Wildfowl Special Issue 4, 220–276.

Cooke, F., MacInnes, C.D., Prevett, J.P., 1975. Gene flow between breeding populations of lesser snow geese. Auk 92, 493–510. https://doi.org/10.2307/4084603

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Fix, P.J., Teel, T.L., Manfredo, M.J., Boston, S.S., 2010. Assessing public acceptance of wildlife management trade-offs: A case study of elk and vegetation management in Rocky Mountain National Park, Colorado. Hum. Dimens. of Wildl. 15, 405–417. https://doi.org/10.1080/10871209.2010.503235

Fowler, D.N., Webb, E.B., Vrtiska, M.P., 2019. Condition bias of decoy-harvested light geese during the Conservation Order. J. Wildl. Manage. 84, 33–44. https://doi.org/10.1002/jwmg.21770

Fox, A.D., 2003. The Greenland White-fronted goose Anser albifrons flavirostris. National Environmental Research Institute, Denmark.

Fox, A.D., Abraham, K.F., 2017. Why geese benefit from the transition from natural vegetation to agriculture. Ambio 46, 188–197. https://doi.org/10.1007/s13280-016-0879-1

Fox, A.D., Madsen, J., 2017. Threatened species to super-abundance: The unexpected international implications of successful goose conservation. Ambio 46, 179–187. https://doi.org/10.1007/s13280-016-0878-2

Francis, C.M., Richards, M.H., Cooke, F., Rockwell, R.F., 1992a. Long-term changes in survival rates of lesser snow geese. Ecology 73, 1346–1362. https://doi.org/10.2307/1940681

Francis, C.M., Richards, M.H., Cooke, F., Rockwell, R.F., 1992b. Changes in survival rates of lesser snow geese with age and breeding status. Auk 109, 731–747. https://doi.org/10.2307/4088149

Gauthier, G., Giroux, J.-F., Reed, A., Béchet, A., Bélanger, L., 2005. Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands? Glob. Chang. Biol. 11, 856–868. https://doi.org/10.1111/j.1365-2486.2005.00944.x

Gauthier, G., Lebreton, J.-D., 2008. Analysis of band-recovery data in a multistate capture-recapture framework. Can. J. Stat. 36, 59–73. https://doi.org/10.1002/cjs.5550360107

Gauthier, G., Pradel, R., Menu, S., Lebreton, J.-D., 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology 82, 3105–3119. https://doi.org/10.2307/2679838

Giroux, J.-F., Bedard, J., 1986. Sex-specific hunting mortality of greater snow geese along firing lines in Quebec. J. Wildl. Manage. 50, 416. https://doi.org/10.2307/3801097

Grzegorczyk, E., Caizergues, A., Eraud, C., Francesiaz, C., Le Rest, K., & Guillemain, M. (2024). Demographic and evolutionary consequences of hunting of wild birds. Biol. Rev. 13069, 1-16. https://doi.org/10.1111/brv.13069

Guillemain, M., Fritz, H., Johnson, A.R., Simon, G., 2007. What type of lean ducks do hunters kill? Weakest local ones rather than migrants. Wildlife Biol. 13, 102–107. https://doi.org/10.2981/0909-6396(2007)13[102:WTOLDD]2.0.CO;2

Holopainen, S., Arzel, C., Elmberg, J., Fox, A.D., Guillemain, M., Gunnarsson, G., Nummi, P., Sjöberg, K., Väänänen, V., Alhainen, M., Pöysä, H., 2018. Sustainable management of migratory European ducks: finding model species. Wildlife Biol. 2018, 1–11. https://doi.org/10.2981/wlb.00336

Hutchison, C., Guichard, F., Legagneux, P., Gauthier, G., Bêty, J., Berteaux, D., Fauteux, D., Gravel, D., 2020. Seasonal food webs with migrations: multi-season models reveal indirect species interactions in the Canadian Arctic tundra. Phil. Trans. R. Soc. A. 378, 20190354. https://doi.org/10.1098/rsta.2019.0354

Jefferies, R.L., Rockwell, R.F., 2002. Foraging geese, vegetation loss and soil degradation in an arctic salt marsh. Appl. Veg. Sci. 5, 7–16.

Juillet, C., Choquet, R., Gauthier, G., Pradel, R., 2011. A capture–recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss. J. Agric. Biol. Environ. Stat. 16, 88–104. https://doi.org/10.1007/s13253-010-0035-5

Kokko, H., Lindström, J., 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. Ecol. Modell. 110, 293–304. https://doi.org/10.1016/S0304-3800(98)00089-1

Koons, D.N., Rockwell, R.F., Aubry, L.M., 2014. Effects of exploitation on an overabundant species: the lesser snow goose predicament. J. Anim. Ecol. 83, 365–374. https://doi.org/10.1111/1365-2656.12133

Lebreton, J.-D., 2005. Dynamical and statistical models for exploited populations. Aust. N. Z. J. Stat. 47, 49–63. https://doi.org/10.1111/j.1467-842X.2005.00371.x

Lefebvre, J., Gauthier, G., Giroux, J.-F., Reed, A., Reed, E.T., Bélanger, L., 2017. The greater snow goose Anser caerulescens atlanticus: Managing an overabundant population. Ambio 46, 262–274. https://doi.org/10.1007/s13280-016-0887-1

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

Leyrer, J., Lok, T., Brugge, M., Spaans, B., Sandercock, B.K., Piersma, T., 2013. Mortality within the annual cycle: seasonal survival patterns in Afro-Siberian Red Knots Calidris canutus canutus. J. Ornithol. 154, 933–943. https://doi.org/10.1007/s10336-013-0959-y

Lindberg, M.S., 2012. A review of designs for capture–mark–recapture studies in discrete time. J. Ornithol. 152, 355–370. https://doi.org/10.1007/s10336-010-0533-9

Madsen, J., Clausen, K.K., Christensen, T.K., Johnson, F.A., 2016. Regulation of the hunting season as a tool for adaptive harvest management — first results for pink-footed geese *Anser brachyrhynchus*. Wildlife Biol. 22, 204–208. https://doi.org/10.2981/wlb.00234

Menu, S., Hestbeck, J.B., Gauthier, G., Reed, A., 2000. Effects of neck bands on survival of greater snow geese. J. Wildl. Manage. 64, 544–552. https://doi.org/10.2307/3803252

Muth, R.M., Ruppert, D.E., & Glass, R.J. (1987). Subsistence use of fisheries resources in Alaska: Implications for Great Lakes fisheries management. Trans. Am. Fish. Soc. 116(3), 510–518. https://doi.org/10.1577/1548-8659(1987)116<510:SUOFRI>2.0.CO;2

Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C.E., Bertram, M.G., Bijleveld, A.I., Brodin, T., Brooks, J.L., Campos-Candela, A., Cooke, S.J., Gjelland, K.Ø., Gupte, P.R., Harel, R., Hellström, G., Jeltsch, F., Killen, S.S., Klefoth, T., Langrock, R., Lennox, R.J., Lourie, E., Madden, J.R., Orchan, Y., Pauwels, I.S., Říha, M., Roeleke, M., Schlägel, U.E., Shohami, D., Signer, J., Toledo, S., Vilk, O., Westrelin, S., Whiteside, M.A., Jarić, I., 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. Science 375, eabg1780. https://doi.org/10.1126/science.abg1780

Nicolau, P.G., Ims, R.A., Sørbye, S.H., Yoccoz, N.G., 2022. Seasonality, density dependence, and spatial population synchrony. Proc. Natl. Acad. Sci. U.S.A. 119, e2210144119. https://doi.org/10.1073/pnas.2210144119

Péron, G., 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. J. Anim. Ecol. 82, 408–417. https://doi.org/10.1111/1365-2656.12014

R Core Team, 2020. R: A language and environment for statistical computing.

Reed, E.T., Calvert, A.M., 2007. Evaluation of the special conservation measures for greater snow geese: report of the greater snow goose working group, Arctic Goose Joint Venture special publication.

Reed, E.T., Gauthier, G., Pradel, R., 2005. Effects of neck bands on reproduction and survival of female greater snow geese. J. Wildl. Manage. 69, 91–100.

Ricouard, A., Lehuta, S., & Mahévas, S. (2023). Are maximum yields sustainable? Effect of intra-annual time-scales on MSY, stability and resilience. Ecol. Modell. 479, 1-20. https://doi.org/10.1016/j.ecolmodel.2023.110321

Riecke, T.V., Lohman, M.G., Sedinger, B.S., Arnold, T.W., Feldheim, C.L., Koons, D.N., Rohwer, F.C., Schaub, M., Williams, P.J., Sedinger, J.S., 2022. Density-dependence produces spurious relationships among demographic parameters in a harvested species. J. Anim. Ecol. 91, 2261–2272. https://doi.org/10.1111/1365-2656.13807

Robinson, W.D., Bowlin, M.S., Bisson, I., Shamoun-Baranes, J., Thorup, K., Diehl, R.H., Kunz, T.H., Mabey, S., Winkler, D.W., 2010. Integrating concepts and technologies to advance the study of bird migration. Front. Ecol. Environ. 8, 354–361. https://doi.org/10.1890/080179

Sandercock, B.K., Nilsen, E.B., Brøseth, H., Pedersen, H.C., 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan: Harvest and ptarmigan survival. J. Anim. Ecol. 80, 244–258. https://doi.org/10.1111/j.1365-2656.2010.01769.x

Sauve, A.M.C., Barraquand, F., 2020. From winter to summer and back: Lessons from the parameterization of a seasonal food web model for the Białowieża forest. J. Anim. Ecol. 89, 1628–1644. https://doi.org/10.1111/1365-2656.13227

Servanty, S., Choquet, R., Baubet, É., Brandt, S., Gaillard, J.-M., Schaub, M., Toïgo, C., Lebreton, J.-D., Buoro, M., Gimenez, O., 2010. Assessing whether mortality is additive using marked animals: a Bayesian state–space modeling approach. Ecology 91, 1916–1923. https://doi.org/10.1890/09-1931.1

Sheaffer, S.E., Kendall, W.L., Bowers, E.F., 2005. Impact of special early harvest seasons on subarctic-nesting and temperate-nesting Canada geese. J. Wildl. Manage. 69, 1494–1507. https://doi.org/10.2193/0022-541X(2005)69[1494:IOSEHS]2.0.CO;2

Steffen, W., Persson, Å., Deutsch, L., Zalasiewicz, J., Williams, M., Richardson, K., Crumley, C., Crutzen, P., Folke, C., Gordon, L., Molina, M., Ramanathan, V., Rockström, J., Scheffer, M., Schellnhuber, H.J., Svedin, U., 2011. The Anthropocene: From global change to planetary stewardship. Ambio 40, 739–761. https://doi.org/10.1007/s13280-011-0185-x

Tombre, I.M., Eythórsson, E., Madsen, J., 2013. Towards a solution to the goose-agriculture conflict in North Norway, 1988–2012: The interplay between policy, stakeholder influence and goose population dynamics. PLoS ONE 8, e71912. https://doi.org/10.1371/journal.pone.0071912

van der Jeugd, H.P., Kwak, A., 2017. Management of a Dutch resident barnacle goose Branta leucopsis population: How can results from counts, ringing and hunting bag statistics be reconciled? Ambio 46, 251–261. https://doi.org/10.1007/s13280-017-0900-3

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of earth's ecosystems. Science 277, 494–499. https://doi.org/10.1126/science.277.5325.494

Wagner, F.H., Seal, U.S., 1992. Values, problems, and methodologies in managing overabundant wildlife populations: An overview., in: Wildlife 2001: Populations. Presented at the Wildlife 2001: Populations, Elsevier Science Publishers Ltd, Oakland, CA, pp. 279–293.

White, E.R., Hastings, A., 2020. Seasonality in ecology: Progress and prospects in theory. Ecol. Complex. 44, 100867. https://doi.org/10.1016/j.ecocom.2020.100867

Wickham, H., 2016. ggplot2: Elegant graphics for data analysis, 2nd ed. 2016. ed, Use R! Springer International Publishing : Imprint: Springer, Cham. https://doi.org/10.1007/978-3-319-24277-4

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. J. Open Source Soft. 4, 1686. https://doi.org/10.21105/joss.01686

Witmer, G., 2022. Rodents in agriculture: A broad perspective. Agronomy 12, 6. https://doi.org/10.3390/agronomy12061458

Chapitre 5 – Environmental conditions outweigh the effect of hunting on juvenile survival in greater snow geese

Couple de grandes oies des neiges accompagnées de leurs jeunes à l'Île Bylot, Nunavut.

En préparation :

LeTourneux, F., Gauthier, G., Belke Brea, M., Pradel, R., Lefebvre, J., In prep. Environmental conditions outweigh the effect of hunting on juvenile survival in greater snow geese.

5.1 Résumé

Chez plusieurs espèces, il est crucial pour la croissance et la survie des juvéniles que les femelles synchronisent leur reproduction avec le pic de qualité et d'abondance des ressources. Cependant, le réchauffement du climat perturbe cette synchronie en devançant davantage la phénologie des ressources, ce qui peut induire un décalage temporel entre le moment de l'éclosion des jeunes et le pic de disponibilité des ressources. Pour la grande oie des neiges (*Anser caerulescens atlanticus*), une espèce nichant en Arctique, ces perturbations coïncident avec des changements de règlements de chasse établis pour contrôler la croissance de cette population surabondante. En combinant 30 ans de données de capture-marquage-recapture, de suivi de reproduction et de phénologie végétale sur les aires de reproduction, nous avons évalué les impacts relatifs d'un décalage trophique et des changements de règlements de chasse sur la survie des juvéniles. Nos résultats révèlent un fort effet du décalage entre l'éclosion des juvéniles et le pic de qualité nutritive des plantes sur leur survie. Étonnamment, cet effet semble compensé par la phénologie du printemps, avec une meilleure survie des juvéniles lors des printemps hâtifs. Ceci est probablement dû au fait que les années où le décalage trophique est important sont également caractérisées par une phénologie hâtive, ce qui fournit aux juvéniles une plus longue période de croissance. En contrepartie, nous n'avons détecté aucun effet des changements de règlements de chasse sur la survie des juvéniles, ce qui supporte l'hypothèse que les facteurs environnementaux durant le développement sont le déterminant principal des variations de la survie juvénile pour cette espèce. Ces résultats soulignent la complexité des impacts des changements climatiques sur les espèces nichant en Arctique. En effet, bien que les changements climatiques puissent perturber la synchronie entre l'éclosion des consommateurs et le pic de disponibilité des ressources, ils peuvent également fournir des bénéfices comme une plus longue période de croissance, ce qui est présentement un facteur limitant en Arctique. Conséquemment, l'impact global d'un climat changeant sur ces populations peut être particulièrement difficile à anticiper à cause de tels effets contradictoires.

Mots clés: Décalage trophique · Oie des neiges · Phénologie · Survie juvénile · Capture-recapture bayésien · Développement initial · Effet de la chasse

5.2 Abstract

Timing reproduction with the peak of food quality and abundance is critical for optimal growth and survival of juveniles in many species. However, climate warming disrupts this phenomenon by advancing the phenology of resources more rapidly than that of consumers, leading to a mismatch between timing of hatching of young and peak resource availability. In Arctic-nesting greater snow geese (*Anser caerulescens atlanticus*), this is occurring concurrently with changes in hunting regulations implemented to control the growth of this overabundant population. We combined data from 30 years of capture-recapture, nest monitoring, and plant phenology derived from satellite imagery to evaluate the relative impacts of a trophic mismatch and changes in hunting regulations on juvenile survival of greater snow geese. We found a strong negative effect of a mismatch between individual hatching dates and the annual peak of plant quality on survival of juvenile geese. Unexpectedly, this effect was offset by annual phenology, with better overall survival in years with early spring phenology. This probably occurs because years with an important trophic mismatch are also characterized by early phenology, which provides a longer growing season for goslings. We found no effect of changes in hunting regulations on juvenile survival, supporting the hypothesis that environmental factors during early development are the main driver of variations in first-year survival in this species. Our results highlight complex impacts of climate change on arctic-nesting species. Indeed, although climate change may disrupt the synchrony between hatching of consumers and peak resource availability, it may also provide benefits such as a longer growing season, which is presently a limiting factor in the Arctic. Therefore, the overall impact of a changing climate on these populations may be especially challenging to anticipate due to such opposing effects.

Keywords: Trophic mismatch · Snow geese · Phenology · Juvenile survival · Bayesian capture-recapture · Early development · Hunting impact

5.3 Introduction

Environmental conditions during early development affect subsequent quality and fitness of individuals in most wildlife species (Cam and Aubry, 2011; Lindström, 1999). Favorable conditions and access to abundant food resources generally allow juveniles to grow faster, ultimately providing them with better survival prospects, a larger size at maturity, and a higher reproductive output (Cam and Aubry, 2011; Hamel et al., 2009; Haywood and Perrins, 1992; Lindén et al., 1992; Madsen and Shine, 2008; Searcy et al., 2004). In birds, breeding phenology is also an important determinant of early development. Early hatched individuals generally do better because they have less competition for food in their early days of life, they often have access to food of better quality, and have a longer growth period (Brinkhof and Cavé, 1997; Sedinger et al., 1995, but see Aubry et al., 2013). Early-hatched individuals are thus better prepared for challenging events to come like migration, molting or the winter season (Verhulst and Nilsson, 2008).

Climate warming can affect phenology by advancing plant growth and animal reproduction schedules (Forchhammer et al., 1998; Post and Stenseth, 1999; Stenseth et al., 2002; Thackeray et al., 2016). Migratory birds exhibiting population declines are often those that do not adjust their migration phenology to match resource availability driven by local weather conditions at their breeding sites, i.e. the notorious trophic mismatch (Møller et al., 2008; Zhemchuzhnikov et al., 2021). This occurs because the life history of many migratory species prevents them from adjusting to phenological changes (Knudsen et al., 2011). Individuals may be penalized for arriving too early (cold weather, low food abundance; Newton, 2007) or too late (overshooting peak food availability; Both et al., 2009) on their breeding grounds, leading to strong stabilizing selection on timing of arrival. Trophic mismatches can be exacerbated if local cues triggering migration departure are not synchronized with conditions on distant breeding areas (Reséndiz-Infante and Gauthier, 2024; Tombre et al., 2008). It is thus not surprising that long-distance migratory birds are often those most severely affected by mismatches between their migration schedule and the phenology of food sources on breeding grounds (Both et al., 2010; Knudsen et al., 2011; Møller et al., 2008). Nonetheless, several recent studies have shown that the consequences of phenological changes and associated trophic mismatches on migratory birds can be complex and variable (Arlt and Pärt, 2017; Aubry et al., 2013; Nolet et al., 2020; Reed et al., 2013; Reneerkens et al., 2016; Visser and Gienapp, 2019).

In Arctic-nesting birds, timing of breeding is critical for a successful reproduction (e.g., Lameris et al., 2022; Sedinger and Raveling, 1986; Senner et al., 2017). The brief snow-free season only provides a short window of suitable conditions to rear a brood and allow juveniles to grow strong enough to complete the southward migration. To achieve this, herbivores like geese must synchronize the timing of hatching of goslings with the peak of plant nutritive quality (Clausen and Clausen, 2013; Lameris et al., 2018; Sedinger et al., 1995). In the Arctic, plants are most nutritious to young birds when they contain high concentrations of soluble nitrogen

(Piedboeuf and Gauthier, 1999; Sedinger and Raveling, 1986), which often peaks early in the season and declines steadily through the summer (Doiron et al., 2014; Lepage et al., 1998). Therefore, juveniles from parents that successfully time egg hatching before or at the peak in resource quality benefit from a high-quality diet in their early days of life, which should lead to a high growth rate and survival probability (Brook et al., 2015; Doiron et al., 2015; Menu et al., 2005). In recent decades, however, the rapid warming of arctic ecosystems has advanced tundra plant phenology (Oberbauer et al., 2013; Rantanen et al., 2022), which led to a mismatch between timing of hatching and peak of food quality for several goose species (Brook et al., 2015; Clausen and Clausen, 2013; Nolet et al., 2020). There is good evidence that such trophic mismatches negatively affect gosling growth (Brook et al., 2015; Doiron et al., 2015). Mismatches are usually stronger in years with early springs because plant phenology advances more than bird nesting phenology (Gauthier et al., 2013), but early years are also known to be advantageous for bird reproduction (see above), including in arctic-nesting geese (Lepage et al., 2000; Nolet et al., 2020). Consequently, the overall effect of phenological changes on goose populations remains ambiguous due to these opposing effects and could be situation-specific (Nolet et al., 2020).

Several arctic-nesting goose populations have become overabundant during the 20th century and have negatively affected tundra vegetation through overgrazing (Abraham et al., 2005; Jefferies et al., 2003). Bold management actions were thus implemented across North America to stop the growth of these populations by increasing sport hunting (Alisauskas et al., 2011; Lefebvre et al., 2017). In greater snow geese (*Anser caerulescens atlanticus*), the opening of a special hunting season in 1999 in Canada during spring and in 2009 in the USA during late winter reduced adult survival as intended (Calvert and Gauthier 2005, LeTourneux et al., 2024), but not for juveniles, at least in the first few years (Calvert and Gauthier, 2005). A possible explanation for the lack of effect of spring hunting on juvenile survival may be that environmental factors during early growth, and in particular a trophic mismatch, may be a more important determinant of their survival in the first year than hunting mortality. This would not be surprising considering that, in presence of high and variable natural mortality like in juvenile geese, hunting mortality is often compensatory to natural mortality, leading to weak or no effects of hunting on the overall annual survival rate (Boyce et al., 1999; Lebreton, 2005; Riecke et al., 2022). However, this hypothesis has yet to be evaluated over a sufficiently long period to account for interannual variations in environmental conditions.

The main objective of this study is to determine the relative contribution of the trophic mismatch between peak plant quality and hatching date of goslings and of changes in hunting regulations on first-year survival in greater snow geese. Our long-term study (30 years) benefitted from 3 periods with different hunting regulations (before vs. after implementation of spring/late winter hunt in Canada and USA) and large annual variations in environmental conditions during gosling growth in the Arctic within each period. Based on the available evidence, we expect that increased mismatch between hatch date and peak of plant quality will lead to a decrease in

survival due to reduced gosling growth and size (Dickey et al., 2008; Doiron et al., 2015), and that this will be the dominant factor affecting first year survival. Consequently, we expect little impact of changes in hunting regulations on first-year survival across time periods.

5.4 Methods

5.4.1 Study species, site, and data collection

The greater snow goose is a long-distance migratory species that winters on the eastern coast of the United States (November-March), migrates to the Canadian high Arctic to breed (June-August), and spends several weeks in the St. Lawrence River lowlands (Québec, Canada) for staging during the fall (September-November) and spring (March-May) migrations. Data collection took place between 1991 and 2019 on the south plain of Bylot Island, Nunavut (73N 80W), the largest known breeding greater snow goose colony (see Gauthier et al., 1995 for a description of the study area). Even though grazing by greater snow geese removes a significant amount of plant standing crop every year at this colony, grazing impact has been stable over the past 30 years with no evidence of habitat damage (Gauthier et al., 2004, 1995; Valéry et al., 2010). Moreover, the population has been relatively stable since the late 1990s when its abundance was still below the estimated carrying capacity of Arctic wetlands (Massé et al., 2001).

Every summer at the end of the nesting period (29 June to 21 July), observers on foot walked in the colony and systematically marked all newly hatched goslings encountered in their nests (within 24 hours of hatching) with uniquely numbered web-tags. A particular effort is made to mark goslings hatched early and late during the hatching period. Towards the end of the brood rearing period when juveniles are nearing completion of their growth and adults are still flightless due to moulting (5-20 August), goose families are captured and marked in mass banding drives (see Menu et al., 2001 for details). Birds are walked into corral traps and both adults and young are marked with a unique-coded leg band. A sample of adult females is also marked with neck collars. All birds are controlled for the presence of any previous marker. A sample of juveniles caught (300-1500/year) and all those recaptured with web-tags are measured to the nearest 0.1 millimeter (head, culmen, tarsus, 9th primary feather) and weighed to the nearest gram.

5.4.2 Calculation of the trophic mismatch

We determined the trophic mismatch for each individual gosling as the difference between its hatching date and the mean annual date of peak plant nutritive quality on Bylot Island. The date of peak plant quality was determined following the approach of Doiron et al. (2013), who demonstrated that peak plant quality at our study area was highly correlated to the date at which the NDVI (Normalized Difference Vegetation Index) reaches half of its maximum annual value ($NDVI_{50}$ date from now on).

Annual $NDVI_{50}$ date

The annual $NDVI_{50}$ date was determined using daily NDVI data (version 5) derived from the Surface Reflectance Climate Data Record at a resolution of approximately 6 km N x 1.5 km W at our study site (freely available from the US National Oceanic and Atmospheric Administration, NOAA; 1990-2013: AVHRR satellite, 2014-2019: VIIRS-land satellite; Vermote, 2018, 2022). We obtained a single daily NDVI value representative of the entire study area (318 km^2, the area over which goose banding took place on Bylot Island) using the median NDVI value of all pixels selected (Doiron et al., 2013). Variations in solar zenith angle, cloud cover, and other variables may affect daily NDVI values (Li et al., 2021). However, because NDVI values in spring can only increase (and not decrease) over time during the vegetation green up, we removed from the dataset all daily values that were inferior to the previous NDVI value until the annual maximum value is reached. We then linearly interpolated daily values between all retained values. This ensured preserving the finest temporal resolution possible compared to using the maximum of 10-day windows as is often done (Doiron et al., 2013; Ross et al., 2018). We then obtained an annual $NDVI_{50}$ date by selecting the date on which the NDVI value was closest to half of the annual maximum.

Calculation of individual hatching dates

Exact hatching date is only available for a small number of banded goslings (n = ~50 to 200 every year) as only a small fraction of goslings marked with web-tags at the nest are caught again during banding (~5%). Fortunately, the growth of primary flight feathers is relatively unsensitive to environmental conditions, making it possible to accurately estimate the age of goslings based on the length of the 9^{th} primary (r^2 of variation in age explained by 9^{th} primary length is ~ 70% in our dataset (n = 2 359); see Cooch et al., 1999 and Lepage et al., 1998 for similar applications). We thus estimated the age of all goslings measured during banding based on the relationship between the 9^{th} primary length and age in goslings of known age (i.e., those initially marked at hatching). We estimated the parameters of this relationship with a mixed effects model where age of goslings in days was the response variable and length of the 9^{th} primary was a fixed predictor. Years were fitted as random intercepts as it increased the predictive accuracy of the model. We then used the coefficients obtained to predict the age of unknown age goslings but measured at banding, allowing us to back-calculate their hatching date and obtain a measure of mismatch for these birds. We tested the performance of our model by predicting the age of a random sample of goslings of known age (20%, 669), using the rest of the individuals (80%, 2675) for parameter estimation. We repeated this step 200 times.

5.4.3 Statistical analyses

Capture-mark-recapture model

We analyzed capture histories and estimated annual survival of juveniles (synonymous of first-year birds) using a joint live-and-dead-encounter multievent capture-mark-recapture model (Burnham, 1993; Pradel, 2005). We used a parametrization analogous to LeTourneux et al. (2022) to estimate annual survival (*S*), live-encounter (*p*) and recovery (*r*) probabilities, but modified to 1) exclude collared birds and 2) model the probability of permanent emigration from the breeding colony, which is thought to be high for juveniles. Juveniles that survive to their first year can transition to one of three adult states (highly capturable, weakly capturable and permanently emigrated; see appendix S5.1 for details). From those states, they can be later encountered alive or dead, which informs on their first-year survival probability. We included birds marked as adults in the analysis to maximize the number of individuals in the adult states and obtain better parameter estimates.

We included in our model the probability that, conditional on survival, a juvenile emigrates permanently to another colony between years *t* and *t+1* (transition from state Alive Juvenile to Alive Adult Emigrated, see appendix S5.1). Adult birds can also emigrate, for instance when a male's mate dies, as he will follow his new mate to her breeding location (Lecomte et al., 2009). Consequently, we also included a permanent emigration probability for adult birds, which differed from that of juveniles. To limit the number of parameters to estimate, we assumed that all birds that emigrate do so permanently and have no probability of returning to breed on Bylot. We included an effect of sex on emigration probability to test whether females could have higher fidelity to their breeding colony than males (Lecomte et al., 2009). Live encounter probability for permanently emigrated birds was set to 0 as only birds breeding on Bylot Island can be recaptured.

Because there is heterogeneity in live encounter probabilities among our marked sample, we accounted for this by having two distinct states, highly capturable and weakly capturable individuals (see details in Appendices S3.1 and S3.3). We included a sex effect on heterogeneity in capturability as found for this population in a previous analysis (LeTourneux et al., 2022, 2024). The high interannual variability of arctic environments affects the probability to recapture an individual and we accounted for this by including a random year effect on this parameter. Juveniles automatically transition to adults upon surviving their first year of life and thus only the latter group can be recaptured.

The dead encounter probability is the recovery probability (Seber's *r*) and is defined as the probability that a bird that died between years *t* and *t+1* died from hunting, was recovered by the hunter, and had its band reported. All birds can be recovered, even those that have permanently emigrated from the breeding area, as the entire population is present on the staging and wintering grounds where hunting takes place. We included a random

year effect in interaction with age (adult vs. juvenile) on recovery probabilities as the probability that a juvenile dies from causes other than hunting is suspected to be higher than in adults.

Effects of mismatch and hunting on survival probabilities

To quantify the effect of a trophic mismatch on juvenile survival, we included the mismatch between each individual's hatching date and the annual peak of plant quality as a fixed effect on survival. To save memory and calculation time, we discretized the mismatch value into 11 bins of 3 to 5 days of mismatch. To compute a linear effect of the mismatch on survival, we used the mean mismatch value in each bin as the value of the covariate to be used into the linear predictor of our model (see Table 5.1). To account for any additional effect of annual spring phenology on juvenile survival (i.e., beyond the mismatch itself calculated at the individual level), we also included the annual $NDVI_{50}$ date as a fixed effect in the model. Although the individual mismatch and annual spring phenology variables are correlated, there is always a range of mismatch values for every phenology value as the former is included on an individual basis while the latter is on an annual basis (see discussion).

To evaluate whether changes in hunting regulations affected juvenile survival, we introduced as a fixed effect a 3-level categorical variable grouping years when different hunting regulations were in place: 1990-1998 (before changes in hunting regulations), 1999-2008 (special spring hunting season in Canada only), 2009-2018 (special hunting season in spring in Canada and late winter in the USA). This effect was put in interaction with age as the impact of regulation changes on survival probability is expected to differ between adults and juveniles (Calvert and Gauthier, 2005). Finally, we also included a random year effect on survival probability, which differed between adults and juveniles.

Modelling framework

Model parameters were estimated in a Bayesian framework using the `nimble` package and the specialized distributions for capture-recapture modelling from the `nimbleEcology` package in R (R Core Team, 2020). We used vague priors for all parameters and we ran 3 chains for 85 000 iterations with a burnin of 9000 iterations. We thinned 2/3^{rds} of samples to reduce memory use. Because there is uncertainty around the predicted age for goslings of unknown age, we ran the age-prediction model and the survival model in a single joint analysis, where the predicted ages and resulting mismatches were fed to the survival model at each iteration. The full model definition and matrices are described in Appendix S5.1. This allowed to fully capture the uncertainty around gosling age when computing the effect of the mismatch on survival probability. Detailed model code is publicly available on GitHub and data to reproduce the analyses will be made available upon submission of the manuscript.

Table 5.1 Reclassification of mismatch values into 11 bins to model the effect of trophic mismatch on survival of juvenile greater snow geese. The Value in model column shows the mismatch value used as the mismatch covariate in the model for individuals classified in each bin. This was done to estimate a continuous mismatch effect. Bins 3 to 9 represent observed mismatch values from birds of known age. Bins 1, 2, 10 and 11 were added to allow predicted ages to yield mismatch values beyond those observed.

Actual mismatch (days)	Bin	Value in model
≤ -6	1	-7.4
-5 to -2	2	-3.5
-1 to 1	3	0.0
2 to 5	4	3.5
6 to 9	5	7.5
10 to 13	6	11.5
14 to 18	7	16.0
19 to 23	8	21.0
24 to 28	9	26.0
29 to 33	10	31.0
≥ 34	11	34.0

5.5 Results

Between 1991 and 2018 we marked 55 621 goslings in 17 998 nests with web-tags (284 to 2978 per year), from which 2 359 were eventually recaptured during banding drives (17 to 261 per year). Over the same period, we marked and measured an additional 26 968 goslings of unknown age and 30 133 adults during the banding drives.

5.5.1 Age estimation

Our model for estimating gosling age based on 9th primary length performed well. There was no bias in the predicted age of goslings when estimating it on a sample of known age birds with our model (mean difference -0.007 d; maximum mean difference among 200 simulations: -0.32 d). The maximum individual difference between real and estimated ages was 11 days, but 95% of gosling ages were predicted within 3 days of their true age, showing that ages were also estimated with high precision. In comparison, hatching dates on Bylot typically span a 20-day period each year.

5.5.2 Encounter probabilities

The sex of adults affected the live encounter probabilities within each capturability group but not the proportion of individuals belonging to each group. Females were on average 1.5 times more likely to be encountered than males, and birds belonging to the highly capturable group were on average 4.5 times more likely to be encountered than those in the lowly capturable group (Figs. S5.1, S5.3A). Live encounter probabilities were quite variable between years (Fig S5.1). Finally, recovery probabilities differed between juveniles and adults,

with juvenile recovery probability being on average 2.7 times lower and 2 times more temporally variable than that of adults (Fig S5.2).

5.5.3 Emigration probabilities

The probability of emigrating from the breeding colony was also affected by sex and age (Fig. S5.3B). Adult females virtually never emigrated from the colony while the permanent emigration probability was around 0.13 [95% CI: 0.11-0.15] for adult males. This number fits remarkably well with the survival rate of adults (Fig. 5.1), providing support to the idea that males whose partners die follow their new partner to other breeding locations after pairing on the wintering grounds. Emigration probabilities of juveniles surviving the first year were particularly high for males (0.78 [0.70, 0.85]) and low for females (0.06 [0.0, 0.15]; Fig. S5.3B), also supporting the idea of high female-biased natal philopatry.

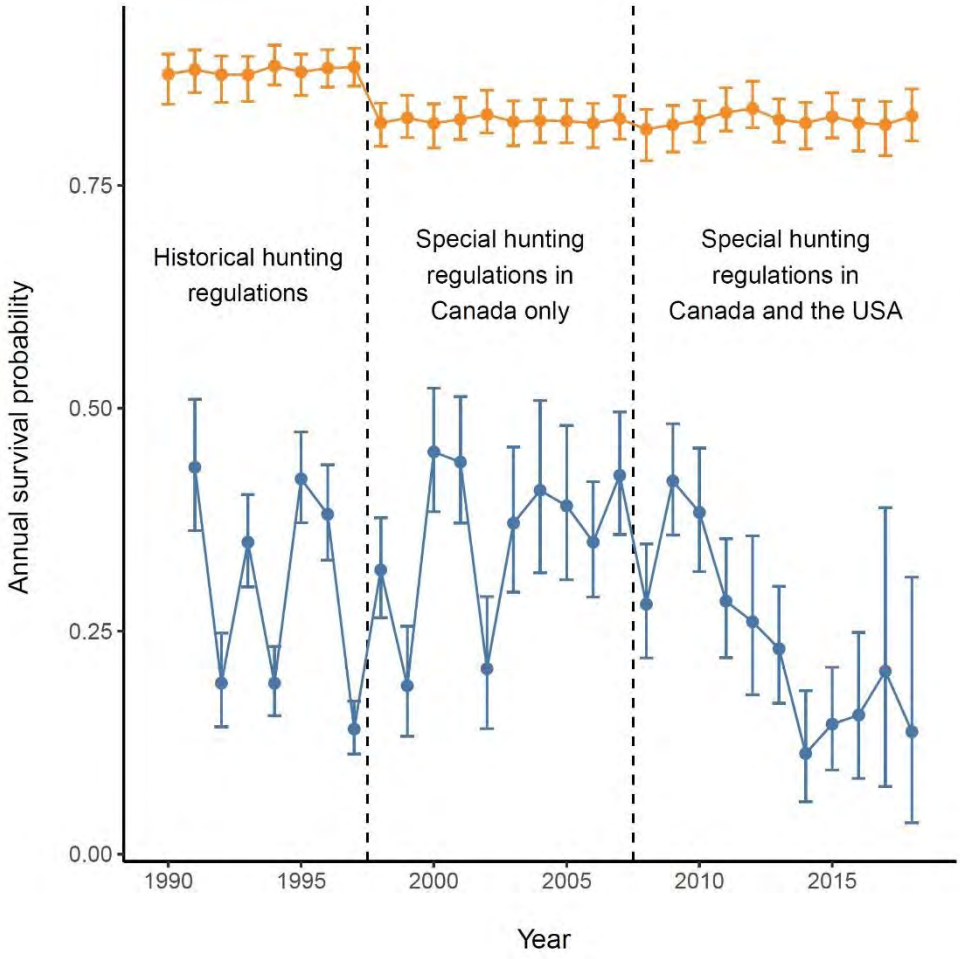

Figure 5.1 Annual survival probability estimated for adult (orange) and juvenile (blue) greater snow geese marked on Bylot Island between 1991 and 2018. Error bars are 95% credible intervals.

5.5.4 Survival rates and mismatch effect

Annual survival of adult geese was high and was reduced by changes in hunting regulations in 1999, but was not reduced further after 2009 as reported in earlier studies ($\beta_{1999\text{-}2008 \text{ vs } 1990\text{-}1998}$ = -0.44 [-0.62, -0.25], $\beta_{2009\text{-}2019 \text{ vs } 1990\text{-}1998}$ = -0.44 [-0.61, -0.26]; Fig. 5.1; LeTourneux et al., 2022, 2024). Annual variability, however, was relatively low compared to what was observed in those earlier studies (SE of annual values = 0.03 in this study vs. 0.08 in LeTourneux et al., 2022). In contrast, juvenile survival was much lower than adults and highly variable through time (SE of annual values = 0.11). However, juvenile survival was not affected by changes in hunting regulations as predicted ($\beta_{1999\text{-}2008 \text{ vs } 1990\text{-}1998}$ = 0.38 [-0.24, 0.97], $\beta_{2009\text{-}2019 \text{ vs } 1990\text{-}1998}$ = -0.24 [-0.84, 0.37]; Fig 5.1).

We found a strong inverse relationship between juvenile survival and the intensity of the mismatch between individual hatching date and the date of peak plant quality ($\beta_{mismatch}$ = -0.99 [-1.14, -0.84]; Fig. 5.2A). However, juvenile survival was also strongly affected by annual spring phenology as it decreased in years when spring phenology was late ($\beta_{phenology}$ = -0.82 [-1.13, -0.54]; Fig. 5.2B). In both cases, the estimated mean annual survival of juveniles did not align very well with the predicted relationships. However, when we predicted annual survival while holding the date of peak plant quality constant, mean annual survival estimates aligned much better with the annual mismatch relationship (Fig. 5.2C), whereas the reverse was true when holding the mismatch constant for the relationship with date of peak plant quality (Fig. 5.2D). The reason for these discrepancies is that these two effects somewhat compensate each other, at least at the population level, because the mismatch is generally smaller in years with late plant phenology, and larger in early years (Fig. 5.3).

5.6 Discussion

Our analysis of 30 years of capture-mark-recapture data supports the hypothesis that juvenile survival in greater snow geese is affected by environmental conditions during early development and did not respond to changes in hunting regulations. As expected, juvenile survival at the individual level was strongly negatively affected by the mismatch between hatching date and our index of peak plant quality. Unexpectedly however, this effect was substantially offset by the annual timing of spring phenology due to a strong negative effect of late phenology on juvenile survival.

5.6.1 Impact of environmental conditions during early development

The strong effect of the mismatch between hatching date and an index of spring phenology on juvenile survival that we observed corroborates other findings in similar systems (Brook et al., 2015; Lameris et al., 2018; Ross et al., 2018). In greater snow geese, previous studies have shown how gosling growth and size towards the end of brood rearing is negatively affected by this trophic mismatch (Dickey et al., 2008; Doiron et al., 2015). Because size at fledging is undoubtedly a strong determinant of the ability of goslings to leave the Arctic and survive the

3000-km migration to the fall staging grounds (Lepage et al., 2000, Cooch 2002), it is not surprising to find a strong negative effect of the mismatch on individual gosling survival.

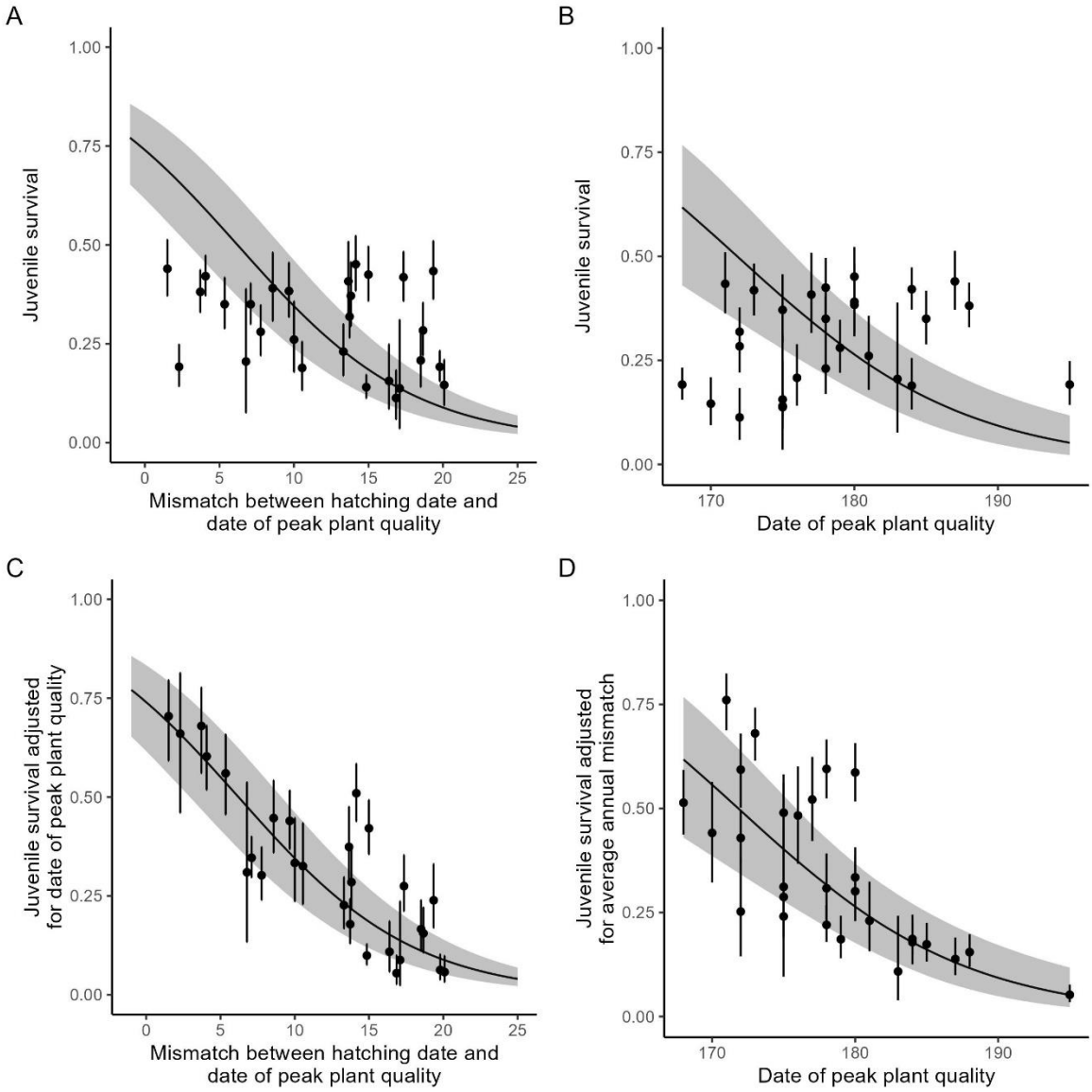

Figure 5.2 Relationship between annual survival of juvenile greater snow geese and the mismatch between hatching date and date of peak plant quality (A and C), or the annual date of peak plant quality (day of the year), an index of spring phenology (B and D). The black lines represent mean model predictions with their 95% credible interval (shaded area) over the range of observed mismatch or spring phenology values with all other covariates held constant. A positive mismatch indicates that goslings hatch after the peak in plant quality. Dots represent mean annual survival estimates along with their 95% credible intervals (error bars) plotted against the mean annual value of the environmental covariate in that year. In (A) and (B), mean annual survival predictions are obtained with all covariates included in the model whereas in (C) and (D), the predictions are obtained by holding the date of peak plant quality and the mismatch constant, respectively.

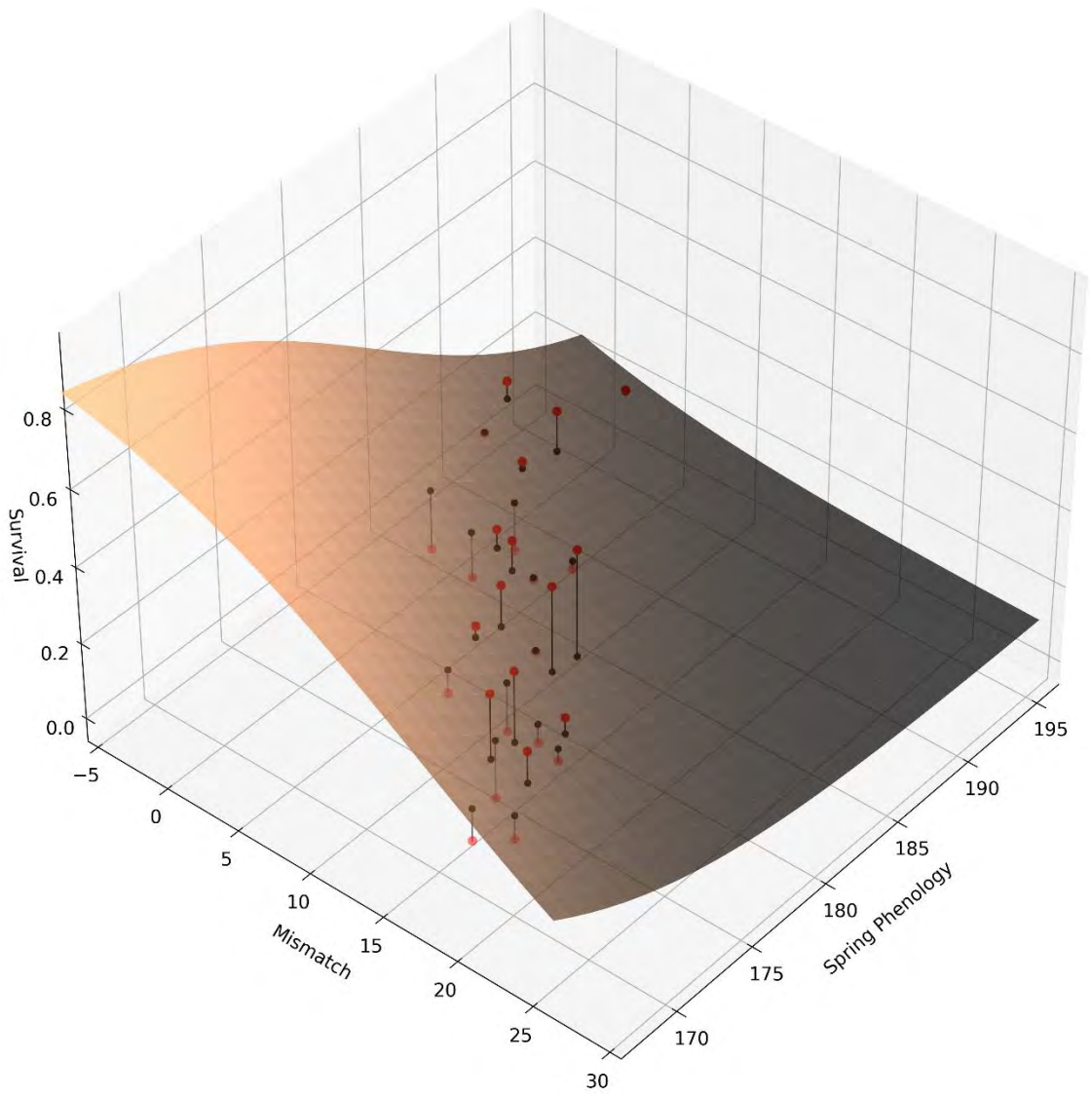

Figure 5.3 Relationship between annual survival of juvenile greater snow geese and mismatch between hatching date and date of peak plant quality, and spring phenology (date of peak plant quality; day of the year) simultaneously. The surface represents the model prediction for annual survival based on the mismatch and spring phenology covariates only. Red dots are annual survival estimates and black dots are predictions from the model for the corresponding values of annual mismatch and spring phenology (i.e. black dots are located on the 3D surface). Black lines link survival estimates (red) to model predictions (black).

Interestingly, the effect of the mismatch at an individual level was largely offset by a negative effect of late spring phenology, thereby explaining why mean annual survival was poorly related to mean annual mismatch. In a recent review, Nolet et al. (2020) showed that climate-induced phenological changes have opposing effects on different components of goose reproduction. Earlier springs are associated to higher female body condition, larger clutch size and higher nesting success, and thus have a positive effect on the pre-nesting and nesting phases of reproduction (Dickey et al., 2008; Madsen et al., 2007; Ross et al., 2017). On the other hand, because

goose nesting phenology is not as responsive to spring conditions as is plant phenology (Fig S5.4), earlier springs are associated with a stronger trophic mismatch, leading to reduced growth and ultimately survival of juvenile geese (Brook et al., 2015; Lameris et al., 2018; Ross et al., 2018). However, we found that spring phenology also has a direct but opposite effect at the gosling stage. This can be explained by several mechanisms. The most likely explanation is that in years with an early spring, hatching occurs earlier overall even if geese do not adjust completely to the advance in peak plant quality, which induces the mismatch (Fig S5.4). In those years, goslings have more time to grow before departure for migration and the additional days of growth can partially offset (by up to 70%, LeTourneux and Gauthier, unpublished data) the reduced growth rate induced by the lower quality of plants they encounter due to the mismatch. Another potential factor is that plants produce more overall biomass in early and warm years (Doiron et al., 2014; Gauthier et al., 2013), which could partly compensate for their lower quality. Although greater snow geese have not reached the carrying capacity of the Bylot Island ecosystem (Massé et al., 2001), the gregarious behavior of geese during brood rearing can lead to local depletion of food resources (e.g., Brook et al., 2015). This local depletion may be reduced in years with early spring phenology due to the increased plant biomass.

Our results highlight that examining the impact of a trophic mismatch can be more complex than anticipated and even misleading when examined alone. This is in line with conclusions from several reviews of the consequences of mismatched reproduction for migratory populations (Knudsen et al., 2011; Visser and Gienapp, 2019). The current analysis provides evidence that although mismatches can have important consequences on the fitness of individuals (Visser and Gienapp, 2019), other environmental factors linked to a warmer climate and earlier springs may provide benefits that offset this impact, with weak overall consequences on population growth (e.g., Reed et al., 2013; Dunn and Møller, 2014). Inadequate adjustment of long-distance migrants to spring phenology is often attributed to life history constraints or to the fact that a faster warming in the Arctic than in temperate zones (Rantanen et al., 2022) does not allow staging birds to properly predict environmental conditions on distant breeding grounds (Bauer et al., 2008; Lameris et al., 2018; Reséndiz-Infante and Gauthier, 2024). While this may be true, it is also possible that the fitness consequences of a mismatch offset by opposing environmental factors may not be strong enough to drive important phenological adjustments to migration, especially in geese that gain from arriving on the breeding grounds in good body condition (Bêty et al., 2003). Although phenological mismatches are likely to increase further with climate warming, our results suggest caution when trying to use our current understanding of these processes to predict future impacts. In the present case, the mismatch could be largely compensated for by other environmental factors and thus we are unsure of the extent to which juvenile survival would decrease in the face of an increased mismatch in the future.

5.6.2 Population dynamics and the canalization hypothesis

The high and relatively stable adult survival of greater snow geese over the past 30 years supports the idea that adult survival is a highly canalized trait in geese (Souchay, 2013). The only factor that significantly reduced adult survival was the opening of a spring hunt in Canada in 1999 (LeTourneux et al., 2022, 2024). Canalization theory predicts that mechanisms have evolved to reduce the variability of species traits that have the highest potential to affect population growth rates (Gaillard and Yoccoz, 2003; Wagner et al., 1997). In long-lived species like geese, those mechanisms should reduce the vulnerability of adults to varying environmental conditions, thereby reducing annual variability in adult survival (e.g. Gaillard et al., 2000; Gaillard and Yoccoz, 2003; Pfister, 1998). In contrast to the low variability in adult survival documented here (see also Gauthier et al., 2001; LeTourneux et al., 2022, 2024), annual reproductive effort and in particular breeding propensity is known to be highly variable in this species (Bêty et al., 2003; van Oudenhove et al., 2014; Grandmont et al., 2023). The modulation of reproductive effort in response to environmental factors (Legagneux et al., 2012; Reed et al., 2004) may be a mechanism that contributes to reduce the vulnerability of adults to natural mortality factors.

In contrast to adults, juvenile survival was highly variable and strongly affected by environmental conditions. This can explain why we detected no change in juvenile survival coinciding with changes in hunting regulations contrary to adults. Lack of response of juvenile survival to increased hunting pressure has also been reported in other goose populations (Traylor et al., 2012). Although compensation of hunting mortality by a reduction in natural mortality could be a mechanism explaining this result, we believe that alternative mechanisms are more likely considering that a high proportion of juvenile mortality occurs during the fall migration from the Arctic, before any significant hunting has occurred (Menu et al., 2005). Recovery probability of juveniles was consistently lower than that of adults, which also indicates that a lower proportion of mortality is due to hunting in juveniles compared to adults. Indeed, the probability that a bird died from hunting is the only process included in the recovery probability that could differ between juveniles and adults as there is no reason to believe that the probability that a shot bird is found by the hunter or that bands are reported should differ between age classes. Still, an interaction between environmental conditions during the summer and hunting mortality in the subsequent seasons remains possible. Juveniles that survive the fall migration despite being exposed to a strong trophic mismatch may be in poor condition and thus more vulnerable to hunting than those that benefited from more favorable conditions during early development (Fowler et al., 2019). Under this hypothesis, variation in juvenile mortality, both due to hunting and natural factors, would be mostly driven by environmental conditions rather than by hunting pressure, which would explain why we detected no effect of changes in hunting regulations on juvenile survival.

5.6.3 Study limitations

A potential limitation of our dataset is that there is a limited number of combinations of annual phenology and mismatch values. Because years with early spring phenology generate important mismatches and vice-versa, there is no year with, for instance, a late spring phenology and large mismatch values. This means that observed combinations of mean annual mismatch and spring phenology occupy a limited range of the parameter space, as they are mostly located along the back-to-front diagonal of Figure 5.3, which results in limited variation in observed annual survival rate in relation to our two environmental covariates. This situation makes it difficult to differentiate between the opposing effects of the mismatch and phenology, and particularly to determine if one effect is more important than the other. Fortunately, because the mismatch variable is calculated at an individual level, there is a large range of individual mismatch values for every date of peak plant quality and likewise, a mismatch value can occur in a relatively wide range of dates of peak plant quality (Fig S5.5). Consequently, this still allows the model to partition between the effect of these two variables.

A second limitation of our analysis is that some model parameters are unstable, as evidenced by the trace plots of the analysis of both the real and simulated datasets (Appendices S5.4 and S5.5). For instance, MCMC chains are not mixing well for the probability that an individual female belongs to either the highly or weakly capturable groups of individuals, or the effect of sex on recapture probability (Fig. S5.10 L, T, V and X). Fortunately, the parameters of interest (average annual survival estimates, mismatch effect and emigration probabilities) seem unaffected by this instability as evidenced by the comparison between simulated and estimated survival values and mismatch effect on juvenile survival. This behavior can be expected in complex models where some parameters are estimated with no a-priori information, like whether an individual belongs to a highly capturable or weakly capturable group. Nonetheless, the similarity of the results obtained with the simulated dataset for the mismatch effect and annual survival values (see Appendix S5.4) indicates that our conclusions are not biased by this instability.

5.7 Conclusion

With the projected increasing pace of climate change (IPCC, 2023), trophic mismatches in consumer-resource interactions are expected to become more prevalent and could result in growing adverse effects for populations. However, our results along with several recent studies suggest caution when drawing conclusions and projecting future impacts of a trophic mismatch on its own (Nolet et al., 2020; Visser and Gienapp, 2019). Indeed, even though juvenile survival of greater snow geese was strongly affected by a mismatch between individual hatching date and annual peak of plant quality, this effect was offset by the timing of spring phenology, with earlier phenology acting positively on juvenile survival despite generating a stronger mismatch. We attribute this unexpected result to a longer growth period for juveniles in years with earlier spring phenology, although this

remains to be directly tested. In contrast, our results showed no impact of changes in hunting regulations on juvenile survival despite a clear effect of these measures on adult survival (LeTourneux et al., 2024). Consequently, environmental conditions during brood rearing and not anthropogenic factors like hunting are the main drivers of juvenile survival in this species. Finally, our results highlight the complexity of climate change effects on populations of Arctic-nesting birds. Synchrony between hatching of consumers and peak resource quality is crucial when the window of environmental conditions favorable to reproduction is short, but potentially less so if constraints imposed by the harsh Arctic environment are relaxed.

5.8 Acknowledgements

We thank G. Picard, M.C. Cadieux, C. Marcotte and Parks Canada for assistance in the field and M.C. Cadieux for managing our database. We further thank all the Inuit, students and field assistants who contributed to goose ringing and nest monitoring in the past. We acknowledge logistic support from the Centre d'Études Nordiques and the Polar Continental Shelf Program (Natural Resources Canada), and funding from the Sentinelle Nord program from the Canada First Research Excellence Fund, Arctic Goose Joint Venture and Canadian Wildilfe Service of Environment and Climate Change Canada, U.S. Fish & Wildlife Service, Atlantic Flyway Council, Northern Scientific Training Program of Polar Knowledge Canada, Natural Sciences and Engineering Research Council of Canada, ArcticNET Network of Centres of Excellence of Canada and Université Laval. This research was conducted according to the relevant national and institutional regulations on animal welfare and was approved by the Comité de Protection des Animaux de l'Université Laval, the Canadian Bird Banding Office, the Mittimatalik Hunter and Trapper Organization and Parks Canada.

5.9 Supplementary material

Annexe S5.1 – Multievent model definition

Annexe S5.2 – Encounter and emigration probabilities

Annexe S5.3 – Relationships between phenology and hatching

Annexe S5.4 – Model validation: analysis of simulated data

Annexe S5.5 – Trace plots and density plots from the analysis of the real dataset

5.10 Bibliography

Abraham, K.F., Jefferies, R.L., Alisauskas, R.T., 2005. The dynamics of landscape change and snow geese in mid-continent North America. Glob. Chang. Biol. 11, 841–855. https://doi.org/10.1111/j.1365-2486.2005.00943.x

Alisauskas, R.T., Rockwell, R.F., Dufour, K.W., Cooch, E.G., Zimmerman, G., Drake, K.L., Leafloor, J.O., Moser, T.J., Reed, E.T., 2011. Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. Wildl. Monogr. 179, 1–42. https://doi.org/10.1002/wmon.5

Arlt, D., Pärt, T., 2017. Marked reduction in demographic rates and reduced fitness advantage for early breeding is not linked to reduced thermal matching of breeding time. Ecol. Evol. 7, 10782–10796. https://doi.org/10.1002/ece3.3603

Aubry, L.M., Rockwell, R.F., Cooch, E.G., Brook, R.W., Mulder, C.P.H., Koons, D.N., 2013. Climate change, phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. Glob. Chang. Biol. 19, 149–160. https://doi.org/10.1111/gcb.12013

Bauer, S., Gienapp, P., Madsen, J., 2008. The relevance of environmental conditions for departure decisions changes en route in migrating geese. Ecology 89, 1953–1960. https://doi.org/10.1890/07-1101.1

Bêty, J., Gauthier, G., Giroux, J., 2003. Body condition, migration, and timing of reproduction in snow geese: A test of the condition-dependent model of optimal clutch size. Am. Nat. 162, 110–121. https://doi.org/10.1086/375680

Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B., Visser, M.E., 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? J. Anim. Ecol. 78, 73–83. https://doi.org/10.1111/j.1365-2656.2008.01458.x

Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J., Foppen, R.P.B., 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc. R. Soc. B. 277, 1259–1266. https://doi.org/10.1098/rspb.2009.1525

Boyce, M.S., Sinclair, A.R.E., White, G.C., 1999. Seasonal compensation of predation and harvesting. Oikos 87, 419–426. https://doi.org/10.2307/3546808

Brinkhof, M.W.G., Cavé, A.J., 1997. Food supply and seasonal variation in breeding success: an experiment in the European coot. Proc. R. Soc. Lond. B 264, 291–296. https://doi.org/10.1098/rspb.1997.0041

Brook, R.W., Leafloor, J.O., Abraham, K.F., Douglas, D.C., 2015. Density dependence and phenological mismatch: consequences for growth and survival of sub-arctic nesting Canada Geese. Avian Conserv. Ecol. 10, art1. https://doi.org/10.5751/ACE-00708-100101

Burnham, K.P., 1993. A theory for combined analysis of ring recovery and recapture data, in: Lebreton, J.-D., North, P.M. (Eds.), Marked individuals in the study of bird populations. Birkhäuser Verlag, Basel, Switzerland, pp. 199–213.

Calvert, A.M., Gauthier, G., 2005. Effects of exceptional conservation measures on survival and seasonal hunting mortality in greater snow geese. J. Appl. Ecol. 42, 442–452. https://doi.org/10.1111/j.1365-2664.2005.01042.x

Cam, E., Aubry, L., 2011. Early development, recruitment and life history trajectory in long-lived birds. J. Ornithol. 152, 187–201. https://doi.org/10.1007/s10336-011-0707-0

Clausen, K.K., Clausen, P., 2013. Earlier Arctic springs cause phenological mismatch in long-distance migrants. Oecologia 173, 1101–1112. https://doi.org/10.1007/s00442-013-2681-0

Cohen, J.M., Lajeunesse, M.J., Rohr, J.R., 2018. A global synthesis of animal phenological responses to climate change. Nat. Clim. Chang. 8, 224–228. https://doi.org/10.1038/s41558-018-0067-3

Cooch, E.G., Dzubin, A., Rockwell, R.F., 1999. Using body size to estimate gosling age. J. Field Ornithol. 70, 214–229.

Dickey, M.-H., Gauthier, G., Cadieux, M.-C., 2008. Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species: Glob. Chang. Biol. 14, 1973–1985. https://doi.org/10.1111/j.1365-2486.2008.01622.x

Doiron, M., Gauthier, G., Lévesque, E., 2015. Trophic mismatch and its effects on the growth of young in an Arctic herbivore. Glob. Chang. Biol. 21, 4364–4376. https://doi.org/10.1111/gcb.13057

Doiron, M., Gauthier, G., Lévesque, E., 2014. Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. J. Ecol. 102, 508–517. https://doi.org/10.1111/1365-2745.12213

Doiron, M., Legagneux, P., Gauthier, G., Lévesque, E., 2013. Broad-scale satellite Normalized Difference Vegetation Index data predict plant biomass and peak date of nitrogen concentration in Arctic tundra vegetation. Appl. Veg. Sci. 16, 343–351. https://doi.org/10.1111/j.1654-109X.2012.01219.x

Dunn, P.O., Møller, A.P., 2014. Changes in breeding phenology and population size of birds. J. Anim. Ecol. 83, 729–739. https://doi.org/10.1111/1365-2656.12162

Flynn, D.F.B., Wolkovich, E.M., 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. New Phytol. 219, 1353–1362. https://doi.org/10.1111/nph.15232

Forchhammer, M.C., Post, E., Stenseth, N.Chr., 1998. Breeding phenology and climate. Nature 391, 29–30. https://doi.org/10.1038/34070

Fowler, D.N., Webb, E.B., Vrtiska, M.P., 2019. Condition bias of decoy-harvested light geese during the Conservation Order. J. Wildl. Manage. 84, 33–44. https://doi.org/10.1002/jwmg.21770

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toïgo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annu. Rev. Ecol. Syst. 31, 367–393. https://doi.org/10.1146/annurev.ecolsys.31.1.367

Gaillard, J.-M., Yoccoz, N.G., 2003. Temporal variation in survival of mammals: A case of environmental canalization? Ecology 84, 3294–3306. https://doi.org/10.1890/02-0409

Gauthier, G., Bêty, J., Cadieux, M.-C., Legagneux, P., Doiron, M., Chevallier, C., Lai, S., Tarroux, A., Berteaux, D., 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. Phil. Trans. R. Soc. B 368, 1–12. https://doi.org/10.1098/rstb.2012.0482

Gauthier, G., Bêty, J., Giroux, J., Rochefort, L., 2004. Trophic interactions in a high arctic snow goose colony. Integr. Comp. Biol. 44, 119–129. https://doi.org/10.1093/icb/44.2.119

Gauthier, G., Hughes, R.J., Reed, A., Beaulieu, J., Rochefort, L., 1995. Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). J. Ecol. 83, 653–664. https://doi.org/10.2307/2261633

Gauthier, G., Lebreton, J.-D., 2008. Analysis of band-recovery data in a multistate capture-recapture framework. Can. J. Stat. 36, 59–73. https://doi.org/10.1002/cjs.5550360107

Gauthier, G., Pradel, R., Menu, S., Lebreton, J.-D., 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology 82, 3105–3119. https://doi.org/10.2307/2679838

Grandmont, T., Fast, P., Grentzmann, I., Gauthier, G., Bêty, J., Legagneux, P., 2023. Should I breed or should I go? Manipulating individual state during migration influences breeding decisions in a long-lived bird species. Funct. Ecol. 37, 602–613. https://doi.org/10.1111/1365-2435.14256

Hamel, S., Gaillard, J.-M., Festa-Bianchet, M., Côté, S.D., 2009. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90, 1981–1995. https://doi.org/10.1890/08-0596.1

Haywood, S., Perrins, C.M., 1992. Is clutch size in birds affected by environmental conditions during growth? Proc. R. Soc. Lond. B 249, 195–197. https://doi.org/10.1098/rspb.1992.0103

IPCC, 2023. Climate Change 2022 – Impacts, adaptation and vulnerability: Working group II contribution to the sixth assessment report of the intergovernmental panel on climate change, 1st ed. Cambridge University Press. https://doi.org/10.1017/9781009325844

Jefferies, R.L., Rockwell, R.F., Abraham, K.F., 2003. The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands — a continuing saga. Environ. Rev. 11, 193–232. https://doi.org/10.1139/A04-002

Kéry, M., Schaub, M., 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective, 1st ed. ed. Academic Press, Boston.

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W.J., Bach, L.A., Coppack, T., Ergon, T., Gienapp, P., Gill, J.A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P.P., Møller, A.P., Nilsson, A.L.K., Péron, G., Ranta, E., Rubolini, D., Sparks, T.H., Spina, F., Studds, C.E., Saether, S.A., Tryjanowski, P., Stenseth, N.Chr., 2011. Challenging claims in the study of migratory birds and climate change. Biol. Rev. 86, 928–946. https://doi.org/10.1111/j.1469-185X.2011.00179.x

Lameris, T.K., Tomkovich, P.S., Johnson, J.A., Morrison, R.I.G., Tulp, I., Lisovski, S., DeCicco, L., Dementyev, M., Gill, R.E., Ten Horn, J., Piersma, T., Pohlen, Z., Schekkerman, H., Soloviev, M., Syroechkovsky, E.E., Zhemchuzhnikov, M.K., Van Gils, J.A., 2022. Mismatch-induced growth reductions in a clade of Arctic-breeding shorebirds are rarely mitigated by increasing temperatures. Glob. Chang. Biol. 28, 829–847. https://doi.org/10.1111/gcb.16025

Lameris, T.K., Van Der Jeugd, H.P., Eichhorn, G., Dokter, A.M., Bouten, W., Boom, M.P., Litvin, K.E., Ens, B.J., Nolet, B.A., 2018. Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. Curr. Biol. 28, 2467-2473.e4. https://doi.org/10.1016/j.cub.2018.05.077

Lebreton, J.-D., 2005. Dynamical and statistical models for exploited populations. Aust. N. Z. J. Stat. 47, 49–63. https://doi.org/10.1111/j.1467-842X.2005.00371.x

Lecomte, N., Gauthier, G., Giroux, J.-F., Milot, E., Bernatchez, L., 2009. Tug of war between continental gene flow and rearing site philopatry in a migratory bird: the sex-biased dispersal paradigm reconsidered. Mol. Ecol. 18, 593–602. https://doi.org/10.1111/j.1365-294X.2008.04067.x

Lefebvre, J., Gauthier, G., Giroux, J.-F., Reed, A., Reed, E.T., Bélanger, L., 2017. The greater snow goose Anser caerulescens atlanticus: Managing an overabundant population. Ambio 46, 262–274. https://doi.org/10.1007/s13280-016-0887-1

Legagneux, P., Fast, P.L.F., Gauthier, G., Bêty, J., 2012. Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proc. R. Soc. Lond. B 279, 876–883. https://doi.org/10.1098/rspb.2011.1351

Lepage, D., Gauthier, G., Menu, S., 2000. Reproductive consequences of egg-laying decisions in snow geese. J. Anim. Ecol. 69, 414–427.

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

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2024. Evidence for seasonal compensation of hunting mortalities in a long-lived migratory bird. J. Appl. Ecol. 61: 2169-2179. https://doi.org/10.1111/1365-2664.14731

Li, Y., Jiao, Z., Zhao, K., Dong, Y., Zhou, Y., Zeng, Y., Xu, H., Zhang, X., Hu, T., Cui, L., 2021. Influence of varying solar zenith angles on land surface phenology derived from vegetation indices: A case study in the Harvard forest. Remote Sens. 13, 4126. https://doi.org/10.3390/rs13204126

Lindén, M., Gustafsson, L., Part, T., 1992. Selection on fledging mass in the collared flycatcher and the great tit. Ecology 73, 336–343. https://doi.org/10.2307/1938745

Lindström, J., 1999. Early development and fitness in birds and mammals. Trends Ecol. Evol. 14, 343–348. https://doi.org/10.1016/S0169-5347(99)01639-0

Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., Nyegaard, H., Cottaar, F., 2007. Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese Anser brachyrhynchus. Polar Biol. 30, 1363–1372. https://doi.org/10.1007/s00300-007-0296-9

Madsen, T., Shine, R., 2008. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. J. Anim. Ecol. 69, 952–958. https://doi.org/10.1111/j.1365-2656.2000.00477.x

Massé, H., Rochefort, L., Gauthier, G., 2001. Carrying capacity of wetland habitats used by breeding greater snow geese. J. Wildl. Manage. 65, 271. https://doi.org/10.2307/3802906

Menu, S., Gauthier, G., Reed, A., 2005. Survival of young greater snow geese (Chen caerulescens atlantica) during fall migration. Auk 122, 479–496.

Menu, S., Gauthier, G., Reed, A., 2001. Survival of juvenile greater snow geese immediately after banding. J. Field Ornithol. 72, 282–290.

Møller, A.P., Rubolini, D., Lehikoinen, E., 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proc. Natl. Acad. Sci. U.S.A. 105, 16195–16200. https://doi.org/10.1073/pnas.0803825105

Newton, I., 2007. Weather-related mass-mortality events in migrants: Weather-related mass-mortality events in migrants. Ibis 149, 453–467. https://doi.org/10.1111/j.1474-919X.2007.00704.x

Nolet, B.A., Schreven, K.H.T., Boom, M.P., Lameris, T.K., 2020. Contrasting effects of the onset of spring on reproductive success of Arctic-nesting geese. Auk 137, ukz063. https://doi.org/10.1093/auk/ukz063

Oberbauer, S.F., Elmendorf, S.C., Troxler, T.G., Hollister, R.D., Rocha, A.V., Bret-Harte, M.S., Dawes, M.A., Fosaa, A.M., Henry, G.H.R., Høye, T.T., Jarrad, F.C., Jónsdóttir, I.S., Klanderud, K., Klein, J.A., Molau, U., Rixen, C., Schmidt, N.M., Shaver, G.R., Slider, R.T., Totland, Ø., Wahren, C.-H., Welker, J.M., 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. Phil. Trans. R. Soc. B 368, 20120481. https://doi.org/10.1098/rstb.2012.0481

Pfister, C.A., 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proc. Natl. Acad. Sci. U.S.A. 95, 213–218. https://doi.org/10.1073/pnas.95.1.213

Piedboeuf, N., Gauthier, G., 1999. Nutritive quality of forage plants for greater snow goose goslings: when is it advantageous to feed on grazed plants? Can. J. Zool. 77.

Post, E., Stenseth, N.Chr., 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80, 1322–1339. https://doi.org/10.1890/0012-9658(1999)080[1322:CVPPAN]2.0.CO;2

Pradel, R., 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics 61, 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

R Core Team, 2020. R: A language and environment for statistical computing.

Rantanen, M., Karpechko, A.Yu., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., Laaksonen, A., 2022. The Arctic has warmed nearly four times faster than the globe since 1979. Commun. Earth Environ. 3, 168. https://doi.org/10.1038/s43247-022-00498-3

Reed, E.T., Gauthier, G., Giroux, F., 2004. Effects of spring conditions on breeding propensity of greater snow goose females. Anim. Behav. 27, 25–46.

Reed, T.E., Grøtan, V., Jenouvrier, S., Sæther, B.-E., Visser, M.E., 2013. Population growth in a wild bird is buffered against phenological mismatch. Science 340, 488–491. https://doi.org/10.1126/science.1232870

Reneerkens, J., Schmidt, N.M., Gilg, O., Hansen, J., Hansen, L.H., Moreau, J., Piersma, T., 2016. Effects of food abundance and early clutch predation on reproductive timing in a high Arctic shorebird exposed to advancements in arthropod abundance. Ecol Evol 6, 7375–7386. https://doi.org/10.1002/ece3.2361

Reséndiz-Infante, C., Gauthier, G., 2024. Can arctic migrants adjust their phenology based on temperature encountered during the spring migration? The case of the greater snow goose. Front. Bird Sci. 3:1307628. doi: 10.3389/fbirs.2024.1307628

Riecke, T.V., Lohman, M.G., Sedinger, B.S., Arnold, T.W., Feldheim, C.L., Koons, D.N., Rohwer, F.C., Schaub, M., Williams, P.J., Sedinger, J.S., 2022. Density-dependence produces spurious relationships among demographic parameters in a harvested species. J. Anim. Ecol. 91, 2261–2272. https://doi.org/10.1111/1365-2656.13807

Ross, M.V., Alisauskas, R.T., Douglas, D.C., Kellett, D.K., 2017. Decadal declines in avian herbivore reproduction: density-dependent nutrition and phenological mismatch in the Arctic. Ecology 98, 1869–1883. https://doi.org/10.1002/ecy.1856

Ross, M.V., Alisauskas, R.T., Douglas, D.C., Kellett, D.K., Drake, K.L., 2018. Density-dependent and phenological mismatch effects on growth and survival in lesser snow and Ross's goslings. J. Avian. Biol. 49, jav.01748. https://doi.org/10.1111/jav.01748

Searcy, W.A., Peters, S., Nowicki, S., 2004. Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*. J. Avian Biol. 35, 269–279. https://doi.org/10.1111/j.0908-8857.2004.03247.x

Sedinger, J.S., Flint, P.L., Lindberg, M.S., 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (Branta bernicla). Ecology 76, 2404–2414. https://doi.org/10.2307/2265816

Sedinger, J.S., Raveling, D.G., 1986. Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. J. Anim. Ecol. 55, 1083. https://doi.org/10.2307/4435

Senner, N.R., Stager, M., Sandercock, B.K., 2017. Ecological mismatches are moderated by local conditions for two populations of a long-distance migratory bird. Oikos 126, 61–72. https://doi.org/10.1111/oik.03325

Souchay, G., 2013. Aspects non-canalisés de la dynamique de population de la grande oie des neiges Probabilités de reproduction et de survie juvénile. Université Laval, Québec.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., Lima, M., 2002. Ecological effects of climate fluctuations. Science 297, 1292–1296. https://doi.org/10.1126/science.1071281

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Høye, T.T., Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I., Winfield, I.J., Wanless, S., 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535, 241–245. https://doi.org/10.1038/nature18608

Tombre, I.M., Høgda, K.A., Madsen, J., Griffin, L.R., Kuijken, E., Shimmings, P., Rees, E., Verscheure, C., 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*. J. Avian Biol. 39, 691–703. https://doi.org/10.1111/j.1600-048X.2008.04440.x

Traylor, J.J., Alisauskas, R.T., Slattery, S.M., Drake, K.L., 2012. Comparative survival and recovery of Ross's and lesser snow geese from Canada's central arctic. J. Wildl. Manage. 76, 1135–1144. https://doi.org/10.1002/jwmg.375

Valéry, L., Cadieux, M.-C., Gauthier, G., 2010. Spatial heterogeneity of primary production as both cause and consequence of foraging patterns of an expanding greater snow goose colony. Écoscience 17, 9–19. https://doi.org/10.2980/17-1-3279

Verhulst, S., Nilsson, J.-Å., 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Phil. Trans. R. Soc. B 363, 399–410. https://doi.org/10.1098/rstb.2007.2146

Vermote, E., 2022. NOAA climate data record (CDR) of VIIRS Normalized Difference Vegetation Index (NDVI), Version 1. https://doi.org/10.25921/GAKH-ST76

Vermote, E., 2018. NOAA climate data record (CDR) of AVHRR Normalized Difference Vegetation Index (NDVI), Version 5. https://doi.org/10.7289/V5ZG6QH9

Visser, M.E., Gienapp, P., 2019. Evolutionary and demographic consequences of phenological mismatches. Nat. Ecol. Evol. 3, 879–885. https://doi.org/10.1038/s41559-019-0880-8

Wagner, G.P., Booth, G., Bagheri-Chaichian, H., 1997. A population genetic theory of canalization. Evolution 51, 329–347. https://doi.org/10.1111/j.1558-5646.1997.tb02420.x

Zhemchuzhnikov, M.K., Versluijs, T.S.L., Lameris, T.K., Reneerkens, J., Both, C., Van Gils, J.A., 2021. Exploring the drivers of variation in trophic mismatches: A systematic review of long-term avian studies. Ecol. Evol. 11, 3710–3725. https://doi.org/10.1002/ece3.7346

Conclusion

Il est essentiel de parvenir à gérer convenablement les populations d'oie des neiges car cette espèce est importante socialement et écologiquement (Bélanger et al., 2007; Gauthier et al., 2004). On veut préserver son rôle dans les écosystèmes qu'elle occupe mais également éviter les graves impacts qui peuvent découler de sa surabondance (e.g., Srivastava and Jefferies, 1996; Jefferies et al., 2003; Flemming et al., 2019). Presque chassée jusqu'à l'extinction au début du XXe siècle et maintenant surabondante surtout grâce à son utilisation des riches terres agricoles, cette espèce est manifestement sensible aux perturbations humaines (Gauthier et al., 2005; Lefebvre et al., 2017; White and Lewis, 1937). Cela souligne toutefois qu'il devrait être possible d'entreprendre des actions pour gérer cette espèce, notamment en modulant les réglementations de chasse. La chasse semble l'outil de prédilection pour gérer des populations comme celle de la grande oie des neiges à cause du faible coût lié aux interventions (libéralisations ou restrictions des règlements de chasse) et du succès que cet outil a vraisemblablement eu pour contrôler cette population durant 25 ans. Cependant, on avait jusqu'ici une compréhension assez limitée des mécanismes proximaux par lesquels la chasse agit sur la dynamique de cette population, ce que mes travaux ont en partie permis d'élucider. Dans son ensemble, ma thèse révèle que l'impact des mesures de gestion par la chasse sur la dynamique de la population de la grande oie des neiges est dû à la combinaison d'un effet direct mais variable selon les saisons sur le taux de survie des adultes et d'un effet indirect sur les déterminants de la reproduction par le biais de la condition physique prénuptiale.

Effets directs et indirects de la chasse sur les paramètres démographiques

Effet direct : impact sur la survie

Sans surprise, mes travaux confirment l'hypothèse que la chasse a un effet direct sur le taux de survie des oies adultes (Chapitres 3 et 4). En effet, l'instauration des saisons de chasse spéciales au printemps en 1999 et à l'hiver en 2009 ont causé une diminution absolue de la survie saisonnière des oies de 4% au printemps et 2% à l'hiver, respectivement, une baisse non-négligeable pour une espèce longévive (Chapitre 4). Cela appuie les conclusions de Calvert et Gauthier (2005) dans les premières années après la mise en place des mesures au printemps, et l'idée que la mortalité à la chasse est largement additive à la mortalité naturelle chez les oies adultes (Gauthier et al., 2001). Néanmoins, ces résultats sont à l'opposé de ceux des études sur l'impact de mesures similaires sur la population continentale de la petite oie des neiges (e.g., Koons et al., 2019). Cela peut s'expliquer principalement par deux différences importantes entre ces populations. Premièrement, la taille de la population de la petite oie des neiges était beaucoup plus importante au moment de la libéralisation des règlements de chasse (~ 12 000 000, Alisauskas et al., 2022, vs. ~1 000 000 pour la grande oie des neiges, Lefebvre et al., 2017). Le taux de récolte à la chasse pour cette population n'a donc jamais été assez important

pour avoir un impact sur son taux de croissance (taux de récolte <3% depuis 20 ans, Koons et al., 2019, vs. 10~15% pour la grande oie des neiges, Chapitre 3). Deuxièmement, la répartition géographique de la petite oie des neiges en dehors de l'Arctique est beaucoup plus étendue que celle de la grande oie des neiges qui est principalement confinée à une bande d'une centaine de kilomètres sur la côte Atlantique durant l'hiver et aux basses terres du St-Laurent durant les migrations automnale et printanière (Sliwinski et al., 2023). Durant toute la période non-reproductrice, les oies sont confinées à un territoire relativement restreint où la densité des populations humaines et la pression de chasse sont élevées. La grande oie des neiges a donc peu d'options pour échapper à la forte pression de chasse, contrairement à sa consœur plus à l'ouest. Le succès des mesures de gestion pour la grande oie des neiges comparé à la petite est donc probablement dû au moment de la mise en place des mesures par rapport à la taille de la population et d'une absence relative de sites alternatifs où les oies peuvent échapper aux chasseurs. Tel que les travaux de Calvert et Gauthier (2005) ont laissé présager, je n'ai trouvé aucun impact des libéralisations des réglementations de chasse sur la survie des oiseaux juvéniles. Cela n'est pas surprenant compte tenu que la survie juvénile est relativement faible et très variable entre les années (Chapitre 5). Mes résultats appuient plutôt l'idée que les conditions environnementales durant l'élevage des jeunes sont le déterminant principal de la survie juvénile.

Effet indirect : impacts sur la condition pré nuptiale

Mes résultats montrent que l'impact de la chasse au printemps va au-delà d'une simple réduction du taux de survie. En effet, l'intensité de la chasse a un impact direct sur la condition physique des oies avant la migration vers les aires de reproduction (Chapitres 1 et 2). La chasse printanière peut donc affecter l'investissement reproducteur, car celui-ci est en partie déterminé par la condition des oies à leur départ pour l'Arctique (Bêty et al., 2003; Gauthier et al., 2003; Mainguy et al., 2002). Les décomptes d'oiseaux juvéniles sur la halte migratoire à l'automne appuient cette hypothèse. En effet, la proportion de juvéniles dans la volée d'automne dépasse rarement la barre des 30% depuis l'instauration de la chasse printanière, alors que c'était régulièrement le cas avant cela (Fig. 3 de Lefebvre et al., 2017). Une analyse préliminaire suggère bien un lien entre la condition physique, qui dépend en partie de l'intensité de la chasse au printemps, et la proportion de jeunes présents dans la volée d'automne (LeTourneux et Gauthier, données non-publiées), ce qui mérite d'être creusé davantage.

Mes résultats montrent également que l'effet du dérangement par la chasse au printemps sur la condition prénuptiale des oies est toujours présent, même après 20 ans d'exposition à cette mesure. Les oies étaient en excellente condition très tôt à la fin du printemps en 2020, alors que la pression de chasse était grandement réduite suite au confinement lié à la pandémie de COVID-19, contrairement aux années qui ont précédé et suivi (Chapitres 1 et 2). Cela appuie les résultats de Féret et al. (2003) et de Béchet et al. (2004), lors des premières années de ces mesures et indique que les oies n'ont pas vraiment réussi à s'adapter à cette contrainte depuis.

De tels effets du dérangement durant l'engraissement prénuptial ont aussi été observés chez d'autres espèces (e.g., Madsen, 1995). Cet effet est probablement en partie médié par une augmentation du temps de vol car la présence de chasseurs dans les champs et le dérangement occasionné par les évènements de chasse force les oies à parcourir de plus grandes distances pour trouver des sites d'alimentation. L'énergie dépensée pour ces plus longs vols s'additionne donc à une réduction du temps disponible pour l'alimentation (Bélanger and Bédard, 1990).

On peut donc conclure que l'impact des mesures de gestion par la chasse sur la dynamique de population de la grande oie des neiges est dû avant tout à une combinaison d'effets sur les déterminants de la reproduction (condition physique printanière) et sur la survie des adultes.

Apprentissage et habituation à la chasse

Bien que les oies n'aient pas réussi à pallier totalement aux effets négatifs de la chasse au printemps sur leur condition physique, on dispose tout de même d'indices suggérant un apprentissage et une certaine habituation des oies à la chasse. D'abord, les communautés de chasseurs sont unanimes : l'oie des neiges est beaucoup plus difficile à chasser aujourd'hui qu'il y a 20 ans (Johnson et al., 2012, LeTourneux and Gauthier, communications personnelles). Même si les techniques de chasse pour attirer ces oiseaux dans les champs se sont continuellement raffinées depuis les 20 dernières années, les oies continuent de déjouer les chasseurs, suggérant un apprentissage continu des nouvelles techniques. Mes travaux appuient cette hypothèse. Par exemple, les résultats de mes chapitres 1 et 2 sur l'utilisation des champs agricoles par les oies suggèrent qu'elles utilisent cet habitat à haut risque (la chasse est permise uniquement dans cet habitat au printemps) pour s'engraisser, mais qu'elles l'évitent lorsqu'elles sont en bonne condition physique. On peut donc penser qu'elles reconnaissent le potentiel accru de mortalité associé à cet habitat mais qu'elles continuent malgré tout de l'utiliser pour maximiser leur engraissement en prévision de la migration jusqu'en Arctique et de la reproduction à venir. Les travaux de Fowler (2019) montrent que les oies récoltées au printemps à l'aide d'appelants dans les champs sont généralement en moins bonne condition physique que la population générale, ce qui appuie également cette hypothèse.

La compensation dans la mortalité à la chasse entre l'hiver et le printemps suggère la présence à la fois d'individus très vulnérables à la chasse et d'autres qui le sont moins (Chapitre 4). Il est probable qu'une faible vulnérabilité soit au moins en partie liée à la capacité de certains individus à reconnaître les signes de la présence de chasseurs et à éviter ces endroits. Béchet et al. (2003) ont montré que dès l'instauration de la chasse de printemps, la probabilité que les oies se déplacent vers des régions où elles ont subi peu ou pas de pression de chasse était plus élevée que l'inverse, indiquant qu'elles ont la capacité d'adapter rapidement leur comportement face à une nouvelle contrainte. Les travaux de Lemoine (2003) fournissent des indications

similaires, en montrant que le succès de certaines techniques de chasse a rapidement diminué suivant l'instauration de la chasse de printemps, un effet qu'ils attribuent à un apprentissage des oies qui seraient devenues plus farouches à l'approche de chasseurs dans les champs. On peut donc imaginer qu'une sélection se soit opérée sur une période de 20 ans, favorisant les individus qui apprennent rapidement à reconnaître les indices de la présence de chasseurs. La présence de jeunes plus naïfs et moins expérimentés (Calvert et al., 2005) accompagnant un couple pourrait également fournir un mécanisme qui contribue au maintien d'une vulnérabilité différentielle des individus à la chasse à travers le temps au sein de la population (Chapitre 4).

La survie adulte est le paramètre avec le plus fort potentiel d'affecter le taux de croissance chez les oies (Gauthier and Brault, 1998; Gauthier and Lebreton, 2004). Conséquemment, ce paramètre devrait théoriquement être fortement canalisé (Gaillard and Yoccoz, 2003; Souchay, 2013). La capacité des oies à apprendre les signes associés à un risque accru pour leur survie (champs, présence d'appelants, etc.) et à adapter leur comportement en conséquence pourrait donc constituer un mécanisme permettant la canalisation de la survie des adultes, réduisant ainsi l'impact de la chasse sur le taux de survie des adultes.

La chasse: un outil de gestion puissant et flexible, mais avec ses limites

On peut dire que l'instauration des mesures de gestion par la chasse a été un succès incontestable pour la grande oie des neiges: la population s'est instantanément stabilisée suivant l'implantation des mesures (Lefebvre et al., 2017), et cela a été surtout causé par une diminution du taux de survie adulte, tel qu'espéré initialement (Gauthier and Brault, 1998; Giroux et al., 1998). En comparaison avec la petite oie des neiges, on ne recense pas d'impacts négatifs sévères de la grande oie des neiges sur la végétation de ses aires de reproduction ou de sa halte migratoire (Gauthier et al., 2006; Valéry et al., 2010), ce qui était l'objectif initial de l'instauration des mesures spéciales pour cette population (Giroux et al., 1998). De plus, la taille de la population s'est maintenue au même niveau depuis 20 ans, bien que légèrement au-delà de l'objectif de population de 500 000 – 750 000 individus (Fig. 0.1). Mes travaux suggèrent également que les effets des règlements de chasse spéciaux sur les paramètres démographiques sont facilement réversibles, c'est-à-dire qu'ils ne perdurent pas dans le temps advenant un retrait des mesures. Par exemple, lors de deux printemps avec une pression de chasse réduite (2019, 2020), on a observé une amélioration immédiate de la condition physique des oies, avec un effet encore plus marqué lors de l'année avec la plus faible pression de chasse (2020, Chapitres 1 et 2). Évidemment, l'impact direct de la chasse sur la mortalité des oies ne devrait pas perdurer non plus dans le temps lorsque la chasse cesse, à condition que celle-ci ne soit pas compensée par une réduction de la mortalité naturelle. Aucune de ces mesures ne semble donc induire d'effets persistants à long terme malgré qu'elles soient demeurées assez efficaces durant plus de 20 ans. Ces résultats encourageants combinés aux ressources

relativement limitées qui sont requises pour l'implantation de telles mesures font donc de la chasse sportive un puissant outil de gestion.

Cela dit, malgré l'atteinte des objectifs initiaux dans le cas de la grande oie des neiges et des avantages de la chasse comme outil de gestion, ce n'est pas une panacée qui peut être appliqué à toutes les situations. Visiblement, le succès de cet outil dépend des conditions dans lesquelles il est mis en place, l'échec des mêmes mesures pour la petite oie des neiges en étant un exemple flagrant (Koons et al., 2019). Même dans le cas de la grande oie des neiges, on dispose maintenant d'éléments suggérant qu'on a probablement atteint les limites de cet outil. Par exemple, on observe des indices d'un apprentissage et d'une habituation des oies à la chasse (voir plus haut), et la compensation observée dans la mortalité à la chasse entre l'hiver et le printemps suggère qu'il y aurait probablement peu d'impact d'une libéralisation supplémentaire des règlements de chasse, tel qu'on l'a observé avec l'ajout des mesures aux États-Unis en 2009. De plus, le succès de la chasse sportive dépend entièrement de la participation des chasseurs, dont plusieurs semblent perdre de plus en plus d'intérêt au fur et à mesure que les oiseaux s'adaptent aux nouvelles techniques de chasse (Calvert et al., 2007; Johnson et al., 2012).

En dernier lieu, mes travaux démontrent qu'au moins un autre facteur que la chasse a probablement contribué à maintenir un faible taux de croissance pour cette population, du moins dans les années récentes. En effet, les résultats de mon cinquième chapitre révèlent un impact des conditions estivales en Arctique sur le taux de survie des oiseaux juvéniles de première année. Même si l'effet négatif du décalage trophique semble être compensé dans une certaine mesure par d'autres facteurs environnementaux, l'effet n'est pas complètement compensé, et le fort décalage des années récentes (~2014~2018), lui, coïncide avec une survie juvénile annuelle moyenne particulièrement faible (Fig. 5.1). Ces années de fort décalage semblent être de plus en plus fréquentes (Fig. S5.4), ce qui pourrait mener à une diminution du taux de croissance de la population si le recrutement des juvéniles demeure faible durant plusieurs années consécutives.

Importance de la saisonnalité

Dans la plupart des populations animales, les évènements qui se produisent à différents moments du cycle annuel peuvent affecter différemment la dynamique d'une population. Il faut donc bien comprendre comment ces évènements affectent les paramètres d'intérêt pour pouvoir gérer ces populations, que ce soit pour conserver une espèce ou pour contrôler sa croissance. Certains évènements peuvent même affecter différents paramètres selon la saison où ils se produisent, comme c'est le cas pour la chasse chez la grande oie des neiges. Cette activité affecte à la fois la survie et la reproduction, mais l'ampleur des effets sur chacun des traits démographiques diffère selon la saison où elle est pratiquée. Au printemps, la chasse peut affecter l'investissement reproducteur par le biais d'une réduction de la condition physique prénuptiale des femelles

(Bêty et al., 2003; Mainguy et al., 2002). La chasse affecte également la survie à toutes les saisons, mais cet effet est fort à l'automne, modéré à l'hiver, et faible au printemps, du moins dans les 10 dernières années. On montre également que l'effet de la chasse sur la survie printanière s'est estompé après l'implantation des mesures à l'hiver aux États-Unis. Actuellement, la chasse au printemps affecte donc probablement la dynamique de la population davantage par le biais d'un effet sur la fécondité que sur la survie. Même si la fécondité a une moins grande élasticité que la survie adulte, si les variations dans la fécondité sont très fortes, il est possible que ce soit présentement le paramètre avec la contribution la plus importante aux variations annuelles dans la taille de la population (e.g., Gauthier and Brault, 1998; Gaillard et al., 2000).

Ces résultats démontrent l'importance de considérer les phénomènes saisonniers lorsqu'on tente de comprendre la dynamique d'une population. Dans une optique de gestion et de conservation, il est important de bien cerner les paramètres démographiques affectés par les mesures de gestion mises en place car les paramètres touchés peuvent varier en fonction du moment de l'application des mesures dans le cycle annuel d'une espèce.

Limitations

Durant ma thèse j'ai bénéficié d'imposants jeux de données qui s'étendent sur plusieurs décennies et comportent de l'information sur plusieurs dizaines de milliers d'individus. Cela m'a permis d'estimer de nombreux paramètres avec une grande précision et de répondre à certaines questions demeurées jusqu'ici peu explorées, comme l'impact de la chasse sur la survie des oies à l'échelle saisonnière. Toutefois, c'est un avantage à double tranchant : lorsqu'on dispose d'autant d'information, on essaie de tirer davantage de réponses de nos jeux de données, et on atteint alors certaines limites que je dois exposer ici.

Les modèles de CMR où l'on utilise plusieurs types de données peuvent rapidement devenir complexes et nécessiter l'estimation d'un grand nombre de paramètres. Par exemple, l'utilisation d'observations d'individus vivants marqués avec des bagues ou des colliers combinées avec les reprises de bagues à la chasse nécessite l'estimation d'une probabilité de détection distincte pour chaque type d'information. Si ces probabilités de détection varient dans le temps et dépendent de facteurs comme le sexe ou l'âge des individus, on perd rapidement le contrôle sur le nombre de paramètres d'un modèle, particulièrement dans le cas d'études qui s'étendent sur une longue période et estiment les paramètres sur une base saisonnière. Il est donc primordial de bien réfléchir à l'avance aux contraintes qu'on peut utiliser pour réduire le nombre de paramètres à estimer tout en conservant un modèle utile et réaliste, tel que le recommandent Burnham et Anderson (2002). De par le nombre élevé de paramètres analogues (e.g. diverses probabilités de détection) requis pour l'estimation des paramètres d'intérêt (e.g. survie, probabilités de transition entre états, etc.), les modèles de CMR peuvent être relativement instables. Pour cette raison, il faut faire attention de ne pas surinterpréter les variations associées

à chaque estimation annuelle. Les estimations moyennes sur de longues périodes sont cependant beaucoup plus robustes. Par exemple, dans le cas de la compensation révélée par les analyses du Chapitre 4, on est conforté dans notre interprétation de la relation de compensation entre les estimations saisonnières interannuelles de l'hiver et du printemps par l'estimation de la survie moyenne sur chaque période qui montre également un effet compensatoire reflétant exactement ce qu'on observe au niveau interannuel.

Un autre aspect limitant de l'ampleur de mon jeu de données est le temps de calcul requis pour estimer les paramètres de modèles relativement complexes (Chapitres 3, 4 et 5). Pour mon 4e chapitre par exemple, des contraintes de temps et de mémoire nous ont empêché d'explorer des modèles avec une plus grande complexité pour estimer de manière plus précise la compensation entre les mortalités à l'hiver et au printemps. L'utilisation d'outils bayésiens aurait permis de tenir compte directement de la corrélation d'échantillonnage entre les survies estimées à l'hiver et au printemps, et d'écarter tout biais potentiel dans la relation de compensation entre ces mortalités (e.g., Koons et al., 2014). Malheureusement, le temps de calcul requis pour l'utilisation de tels outils (e.g., MCMC) était prohibitif pour ce modèle. Néanmoins, même si on doit interpréter avec prudence le coefficient de la relation entre ces mortalités, nous avons tout de même pris des mesures pour tenir compte de l'incertitude associée aux estimations de mortalité lors de l'estimation du degré de compensation, ce qui nous permet d'avancer avec assez de certitude la présence d'une relation compensatoire entre les mortalités à ces deux saisons.

Dans le troisième chapitre sur l'effet des colliers sur la survie, une importante limite est que le partitionnement de la mortalité à la chasse et de la mortalité naturelle est basé uniquement sur le taux de récolte des individus. Cela peut induire certains biais par exemple dû au fait que cette valeur ne tienne pas compte des oiseaux blessés par des chasseurs et morts par la suite mais qui ne sont jamais récupérés (le fameux 'crippling loss'). Si on assume que la proportion d'oiseaux blessés est relativement stable entre les années, cela nous permet tout de même de statuer avec confiance sur les variations relatives de chaque type de mortalité entre les périodes. Cependant, même si cette prémisse semble raisonnable, il faut faire attention à l'interprétation de ces résultats. Comme on l'indique dans le quatrième chapitre, on trouve que l'effet du collier sur la survie est fortement concentré à l'hiver et non à toutes les saisons où on retrouve de la chasse. Dans ce chapitre, nous avons donc accordé plus d'importance à l'hypothèse que les chasseurs visent préférentiellement les oiseaux à colliers et contribuent ainsi significativement à l'impact du collier sur la survie de ces oiseaux. Je dois donc admettre que plusieurs mécanismes contribuent probablement à l'impact des colliers sur la survie des oiseaux et que les données disponibles ne nous permettent pas de départager avec certitude la contribution relative de chacun d'entre eux à l'effet global. Par contre, l'objectif initial de ce chapitre était de quantifier un impact potentiel des colliers sur la survie des femelles, ce que nous avons réussi à faire, nous permettant ensuite d'inclure cet effet dans les analyses sur l'impact de la chasse sur une base saisonnière.

Finalement, une limite générale de ma thèse est que la plupart de mes analyses sur l'impact de la chasse sur les oies adultes ignorent des effets potentiellement confondants de facteurs annuels comme la phénologie ou les conditions météo ainsi que des facteurs dépendant de la densité. Par exemple, dans mes deux premiers chapitres, si l'effort de chasse à chaque printemps était lié aux conditions météo, on pourrait attribuer des changements dans la condition des femelles à la chasse alors que cela pourrait être dû en réalité à une variation des conditions environnementales ayant affecté la récolte des oies. Cette limite est également vraie pour les Chapitres 3 et 4, bien que les biais potentiels soient assez faibles à mon avis. En effet, comme la survie adulte est un paramètre fortement canalisé (Souchay, 2013), les adultes devraient être relativement insensibles aux changements dans les conditions climatiques d'une année à l'autre (Gaillard and Yoccoz, 2003; Pfister, 1998). Les femelles devraient donc plutôt réduire leur investissement reproducteur, voire sauter un évènement de reproduction pour conserver l'énergie disponible et maximiser leur probabilité de survie (Bêty et al., 2003; Grandmont et al., 2023; Souchay et al., 2014). Dans cette optique, l'impact des conditions environnementales sur la survie adulte devraient être relativement faible. De plus, les changements temporels dans la survie annuelle et saisonnière des oies coïncident remarquablement bien avec les changements des règlements de chasse, ce qui renforce l'idée que ces changements soient dus à la chasse (Chapitre 4). Finalement, comme la taille de population s'est maintenue au même niveau depuis plusieurs années sans tendance à long-terme (Fig. 0.1) et que la végétation sur les aires de reproduction, d'hivernage et de la halte migratoire ne montrent pas de signes de dommages (Calvert et al., 2007; Gauthier et al., 2004; Massé et al., 2001; Valéry et al., 2010), on peut également exclure que des effets liés aux facteurs dépendant de la densité aient pu biaiser nos résultats.

Perspectives

Dans toute grande entreprise scientifique, de nouvelles questions émergent au fur et à mesure qu'on répond à nos objectifs initiaux, et ma thèse ne fait pas exception à cette règle. Comme on dispose de plus de 20 années de données depuis l'instauration des mesures de gestion, mes travaux ont permis de faire une synthèse assez complète des impacts à long-terme de la chasse sur les paramètres démographiques de la grande oie des neiges.

On sait maintenant que la combinaison des impacts de la chasse sur la reproduction et sur la mortalité a probablement contribué au succès continu de la gestion de la population de grandes oies des neiges par la chasse. Bien que ma thèse ait permis d'identifier les mécanismes proximaux par lesquels la chasse agit sur la dynamique de population, nous ne savons toujours pas l'ampleur de la contribution de chacun. Conséquemment, une autre étape importante pour compléter les travaux de ma thèse serait de modéliser la contribution relative des effets de la chasse (directs et indirects) et des conditions environnementales (e.g. décalage trophique) aux variations interannuelles dans la taille de la population et à son taux de croissance

depuis 30 ans. De plus, il serait intéressant de déterminer si cela a changé avec le temps, considérant la compensation qui s'opère entre les mortalités à la chasse à l'hiver et au printemps depuis 10 ans. Gauthier et Reed (2007) ont déjà évalué cela, mais leur estimation de l'effet de la chasse sur la reproduction était assez rudimentaire : ils ont comparé la différence entre la proportion de juvéniles à l'automne avant et après l'implantation de la chasse de printemps et attribué cette différence à un effet de la chasse sur la reproduction. Cependant, mes travaux sur l'impact du décalage trophique en été sur la survie des juvéniles soulignent que plusieurs autres paramètres peuvent affecter la productivité des oies, comme les conditions environnementales durant la croissance des jeunes. Il serait donc pertinent de revisiter cette question avec une nouvelle analyse.

Il serait aussi intéressant de pousser cette analyse encore plus loin. En combinant les résultats de cette thèse à d'autres travaux récents, on dispose maintenant de données exhaustives sur la valeur des paramètres qui régissent la dynamique de cette population, ainsi qu'une bonne compréhension des variables qui les affectent (Reséndiz-Infante, 2020; Souchay, 2013; van Oudenhove et al., 2014). Nous sommes donc en bonne position pour déterminer la contribution relative des différents paramètres démographiques au taux de croissance de la population. Récemment, des méthodes ont été développées expressément pour aborder ces questions lorsqu'on a de bonnes estimations des variations temporelles des paramètres régissant la dynamique d'une population, comme c'est maintenant le cas pour la grande oie des neiges ('transient Life Table Response Experiments', Koons et al., 2016). L'application de cette méthode à notre population permettrait de comprendre les paramètres qui ont eu la plus forte contribution à la dynamique de la population d'une année à l'autre depuis 30 ans.

La propension à se reproduire une année donnée, un important déterminant de la productivité annuelle des oies, demeure néanmoins un paramètre difficile à estimer tant chez les oies que pour la plupart des espèces aviaires (Etterson et al., 2011). Il y a eu des tentatives d'estimer ce paramètre par le passé pour plusieurs espèces d'oies (Reed et al., 2004; Sedinger et al., 2001; Souchay et al., 2014). Cependant, comme plusieurs de ces études se basent sur des individus portant des colliers, qui affectent justement la propension à nicher (Reed et al., 2005), ces estimations sont difficilement généralisables aux individus non-marqués et à la population générale. La miniaturisation des technologies GPS offre cependant des avenues prometteuses pour permettre de déterminer si un individu tente de se reproduire sans induire de biais. Lorsque des appareils suffisamment petits pour être posés sur une bague seront disponibles, l'obtention de cette dernière pièce permettra d'avoir un portrait complet de la démographie de cette espèce.

Dans mes travaux, je montre que les conditions environnementales estivales peuvent avoir un effet important sur la survie des juvéniles la première année (Chapitre 5). Les mécanismes exacts qui entraînent la mortalité et les moments de l'année où celle-ci a lieu demeurent toutefois inconnus. Menu et al. (2005) suggèrent que cela

se produit en grande partie durant la migration d'automne, du moment de l'envol de l'Arctique à l'arrivée sur la halte migratoire du sud du Québec. Une partie de cette mortalité est probablement due à l'abandon par leurs parents des jeunes trop faibles pour quitter l'aire de reproduction avant la saison hivernale. Une autre partie se produit certainement en route vers le Québec lorsque les jeunes trop faibles sont eux aussi laissés derrière. Cependant, il n'est pas exclu qu'une partie de la mortalité due à la chasse pourrait être liée à la condition des jeunes. On dispose d'indices que les oiseaux en moins bonne condition sont plus vulnérables à la chasse (Chapitre 3; Fowler et al., 2019), et cela devrait également s'appliquer aux juvéniles. Conséquemment, il serait possible que les années où davantage de juvéniles sont récoltés soient également celles où les jeunes sont en moins bonne condition physique à cause de conditions environnementales peu favorable durant leur développement. Il serait donc pertinent d'estimer la survie des juvéniles sur une base saisonnière pour bien isoler les mécanismes proximaux par lesquels les conditions environnementales estivales affectent cette population. Finalement, les conditions hivernales pourraient également avoir un impact sur la survie des juvéniles, puisque ceux-ci sont plus fragiles que les adultes. Cela pourrait être une variable qui explique les variations interannuelles dans la survie juvénile, ce que je n'ai pas réussi à identifier durant ma thèse.

Finalement, mon parcours souligne l'importance de remettre en question ses propres travaux ainsi que la littérature publiée. Les études précédentes n'ayant pas trouvé d'effet des colliers sur la survie de la grande oie des neiges, nous n'avons revisité l'impact des colliers que tardivement et de façon fortuite. En fait, dans mes premières analyses, cet effet se manifestait plutôt par une différence de survie entre les sexes mais ce n'est que plus tard que nous avons réalisé que cet effet était engendré par la présence de colliers chez les femelles seulement. Une remise en question plus rapide de la littérature publiée au préalable m'aurait permis d'avancer plus rapidement au début de ma thèse.

Recommandations

Considérant la stabilité relative de la population depuis 20 ans et sa taille actuelle, je recommanderais que les mesures actuelles de contrôle continuent d'être appliquées, car on a plusieurs indications qu'elles ont largement contribué à l'atteinte des objectifs de gestion initiaux. Cependant, au moment d'écrire ces lignes, la dernière estimation de la taille de la population de la grande oie des neiges (printemps 2023) recense 585 000 oiseaux, le nombre le plus faible depuis presque 30 ans (J. Lefebvre, communication personnelle). Il est donc primordial de maintenir un suivi serré de cette population et de ses paramètres démographiques. Ce faible nombre pourrait être la conséquence de la faible reproduction des années récentes (données non-publiées), ou encore de la survie médiocre des juvéniles depuis quelques années (Chapitre 5). Dans tous les cas, il sera nécessaire de reconsidérer l'étendue des mesures en place

actuellement si la population continue de diminuer dans les prochaines années. Finalement, dans l'éventualité d'une reprise de la croissance de la population de grandes oies des neiges ou d'autres populations surabondantes comme la petite oie des neiges, il sera intéressant de considérer des mesures qui pourraient affecter prioritairement d'autres paramètres démographiques comme le recrutement ou la reproduction. En effet, à la lumière des résultats de ma thèse, il est peu probable qu'une libéralisation supplémentaire des règlements de chasse affecte davantage la dynamique de cette population via un effet direct sur la survie.

Bibliographie

Abraham, K.F., Jefferies, R.L., Alisauskas, R.T., 2005. The dynamics of landscape change and snow geese in mid-continent North America. Glob. Chang. Biol. 11, 841–855. https://doi.org/10.1111/j.1365-2486.2005.00943.x

Alisauskas, R.T., Calvert, A.M., Leafloor, J.O., Rockwell, R.F., Drake, K.L., Kellett, D.K., Brook, R.W., Abraham, K.F., 2022. Subpopulation contributions to a breeding metapopulation of migratory arctic herbivores: survival, fecundity and asymmetric dispersal. Ecography 2022. https://doi.org/10.1111/ecog.05653

Alisauskas, R.T., Drake, K.L., Caswell, J.H., Kellett, D.K., 2012. Movement and persistence by Ross's geese (Chen rossii) in Canada's arctic. J. Ornithol. 152, 573–584. https://doi.org/10.1007/s10336-010-0635-4

Alisauskas, R.T., Drake, K.L., Slattery, S.M., Kellett, D.K., 2006. Neckbands, harvest, and survival of Ross's geese from Canada's central Arctic. J. Wildl. Manage. 70, 89–100. https://doi.org/10.2193/0022-541X(2006)70[89:NHASOR]2.0.CO;2

Alisauskas, R.T., Lindberg, M.S., 2002. Effects of neckbands on survival and fidelity of white-fronted and Canada geese captured as non-breeding adults. J. Appl. Stat. 29, 521–537. https://doi.org/10.1080/02664760120108575

Alisauskas, R.T., Rockwell, R.F., Dufour, K.W., Cooch, E.G., Zimmerman, G., Drake, K.L., Leafloor, J.O., Moser, T.J., Reed, E.T., 2011. Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. Wildl. Monogr. 179, 1–42. https://doi.org/10.1002/wmon.5

Allen, A.M., Ens, B.J., Van De Pol, M., Van Der Jeugd, H., Frauendorf, M., Oosterbeek, K., Jongejans, E., 2019. Seasonal survival and migratory connectivity of the Eurasian Oystercatcher revealed by citizen science. Auk 136, uky001. https://doi.org/10.1093/auk/uky001

Allombert, S., Stockton, S., Martin, J.-L., 2005. A natural experiment on the impact of overabundant deer on forest invertebrates. Conserv. Biol. 19, 1917–1929. https://doi.org/10.1111/j.1523-1739.2005.00280.x

Anderson, D.R., Burnham, K.P., 1976. Population ecology of the mallard VI: effects of exploitation on survival (No. 128), Population Ecology of the Mallard. U.S. Fish and Wildlife Service, Washington, D.C.

Ankney, C.D., 1996. An embarrassment of riches: Too many geese. J. Wildl. Manage. 60, 217–223. https://doi.org/10.2307/3802219

Anonymous, 1917. Convention between the United States and Great Britain for the protection of migratory birds. Am. j. int. law 11, 62–66. https://doi.org/10.2307/2212197

Appelhans, T., Russell, K., Busetto, L., O'Brien, J., Gutschlhofer, J., 2020. mapedit: Interactive editing of spatial data in R.

Arlt, D., Pärt, T., 2017. Marked reduction in demographic rates and reduced fitness advantage for early breeding is not linked to reduced thermal matching of breeding time. Ecol. Evol. 7, 10782–10796. https://doi.org/10.1002/ece3.3603

Arnold, T.W., Afton, A.D., Anteau, M.J., Koons, D.N., Nicolai, C.A., 2016. Temporal variation in survival and recovery rates of lesser scaup: Lesser Scaup Survival. J. Wildl. Manage. 80, 850–861. https://doi.org/10.1002/jwmg.21074

Aubry, L.M., Rockwell, R.F., Cooch, E.G., Brook, R.W., Mulder, C.P.H., Koons, D.N., 2013. Climate change, phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. Glob. Chang. Biol. 19, 149–160. https://doi.org/10.1111/gcb.12013

Barron, D.G., Brawn, J.D., Weatherhead, P.J., 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods Ecol. Evol. 1, 180–187. https://doi.org/10.1111/j.2041-210X.2010.00013.x

Bates, A.E., Primack, R.B., Biggar, B.S., Bird, T.J., Clinton, M.E., Command, R.J., Richards, C., Shellard, M., Geraldi, N.R., Vergara, V., et al., 2021. Global COVID-19 lockdown highlights humans as both threats and custodians of the environment. Biol. Conserv. 263, 109175. https://doi.org/10.1016/j.biocon.2021.109175

Bates, A.E., Primack, R.B., Moraga, P., Duarte, C.M., 2020. COVID-19 pandemic and associated lockdown as a "Global Human Confinement Experiment" to investigate biodiversity conservation. Biol. Conserv. 248, 108665. https://doi.org/10.1016/j.biocon.2020.108665

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Soft. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Batt, B.D.J., 1998. The greater snow goose: report of the arctic goose habitat working group. U.S. Fish and Wildlife Service, and Canadian Wildlife Service, Washington, D.C., and Ottawa, Ontario.

Bauer, S., Gienapp, P., Madsen, J., 2008. The relevance of environmental conditions for departure decisions changes en route in migrating geese. Ecology 89, 1953–1960. https://doi.org/10.1890/07-1101.1

Bazely, D.R., Jefferies, R.L., 1986. Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. J. Ecol. 74, 693. https://doi.org/10.2307/2260392

Beardsell, A., Berteaux, D., Dulude-de Broin, F., Gauthier, G., Clermont, J., Gravel, D., Bêty, J., 2023. Predator-mediated interactions through changes in predator home range size can lead to local prey exclusion. Proc. R. Soc. Lond. B. 290, 11p. https://doi.org/10.1098/rspb.2023.1154

Béchet, A., Giroux, J.-F., Gauthier, G., 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese: Effects of hunting on snow geese behaviour. J. Appl. Ecol. 41, 689–700. https://doi.org/10.1111/j.0021-8901.2004.00928.x

Béchet, A., Giroux, J.-F., Gauthier, G., Nichols, J.D., Hines, J.E., 2003. Spring hunting changes the regional movements of migrating greater snow geese. J. Appl. Ecol. 40, 553–564. https://doi.org/10.1046/j.1365-2664.2003.00812.x

Bédard, J., Gauthier, G., 1989. Comparative energy budgets of greater snow geese Chen caerulescens atlantica staging in two habitats in spring. Ardea 77, 3–20.

Bélanger, L., Bédard, J., 1990. Energetic cost of man-induced disturbance to staging snow geese. J. Wildl. Manage. 54, 36. https://doi.org/10.2307/3808897

Bélanger, L., Gauthier, G., Giroux, J.-F., Lefebvre, J., Reed, A., Reed, E.T., 2007. Conclusion, in: Reed, E.T., Calvert, A.M. (Eds.), Evaluation of the special conservation measures for greater snow geese: Report of the greater snow goose working group. Arctic Goose Joint Venture Special Publication, Canadian Wildlife Service, Sainte-Foy, Québec., pp. 75–78.

Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a driver of recent extinctions. Biol. Lett. 12, 20150623. https://doi.org/10.1098/rsbl.2015.0623

Bender, L.C., Rosas-Rosas, O.C., 2016. Compensatory puma predation on adult female mule deer in New Mexico. J. Mammal. 97, 1399–1405. https://doi.org/10.1093/jmammal/gyw094

Bêty, J., Gauthier, G., Giroux, J., 2003. Body condition, migration, and timing of reproduction in snow geese: A test of the condition-dependent model of optimal clutch size. Am. Nat. 162, 110–121. https://doi.org/10.1086/375680

Boonstra, R., Hik, D., Singleton, G.R., Tinnikov, A., 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecol. Monogr. 68, 371–394. https://doi.org/10.2307/2657244

Both, C., Van Asch, M., Bijlsma, R.G., Van Den Burg, A.B., Visser, M.E., 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? J. Anim. Ecol. 78, 73–83. https://doi.org/10.1111/j.1365-2656.2008.01458.x

Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J., Foppen, R.P.B., 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. Proc. R. Soc. B. 277, 1259–1266. https://doi.org/10.1098/rspb.2009.1525

Boyce, M.S., Sinclair, A.R.E., White, G.C., 1999. Seasonal compensation of predation and harvesting. Oikos 87, 419–426. https://doi.org/10.2307/3546808

Bradbeer, D.R., Rosenquist, C., Christensen, T.K., Fox, A.D., 2017. Crowded skies: Conflicts between expanding goose populations and aviation safety. Ambio 46, 290–300. https://doi.org/10.1007/s13280-017-0901-2

Brinkhof, M.W.G., Cavé, A.J., 1997. Food supply and seasonal variation in breeding success: an experiment in the European coot. Proc. R. Soc. Lond. B 264, 291–296. https://doi.org/10.1098/rspb.1997.0041

Brook, R.W., Leafloor, J.O., Abraham, K.F., Douglas, D.C., 2015. Density dependence and phenological mismatch: consequences for growth and survival of sub-arctic nesting Canada Geese. Avian Conserv. Ecol. 10, art1. https://doi.org/10.5751/ACE-00708-100101

Brownie, C., Anderson, D.R., Burnham, K.P., Robson, D.S., 1985. Statistical inference from band recovery data: a handbook (No. 156), Resource Publication. U.S. Fish and Wildlife.

Burnham, K.P., 1993. A theory for combined analysis of ring recovery and recapture data, in: Lebreton, J.-D., North, P.M. (Eds.), Marked Individuals in the study of bird populations. Birkhäuser Verlag, Basel, Switzerland, pp. 199–213.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. Springer-Verlag, New York. https://doi.org/10.1007/b97636

Cadieux, M.-C., 2023. Ecological studies and environmental monitoring at Bylot Island, Sirmilk national park [WWW Document]. URL https://www.cen.uqar.ca/fr/animalgoose.php (accessed 8.18.23).

Calvert, A.M., Gauthier, G., 2005. Effects of exceptional conservation measures on survival and seasonal hunting mortality in greater snow geese. J. Appl. Ecol. 42, 442–452. https://doi.org/10.1111/j.1365-2664.2005.01042.x

Calvert, A.M., Gauthier, G., Reed, A., 2005. Spatiotemporal heterogeneity of greater snow goose harvest and implications for hunting regulations. J. Wildl. Manage. 69, 561–573. https://doi.org/10.2193/0022-541X(2005)069[0561:SHOGSG]2.0.CO;2

Calvert, A.M., Gauthier, G., Reed, E.T., Bélanger, L., Giroux, J., Gobeil, J.-F., Huang Min, Lefebvre, J., Reed, A., 2007. Present status of the population and evaluation of the effects of the special conservation measures., in: Reed, E.T., Calvert, A.M. (Eds.), Reed, E.T., Calvert, A.M. (Eds.), Evaluation of the special conservation measures for greater snow geese: Report of the greater snow goose working group. Arctic Goose Joint Venture special publication, U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, DC and Ottawa, Canada, pp. 5–64.

Cam, E., Aubry, L., 2011. Early development, recruitment and life history trajectory in long-lived birds. J. Ornithol. 152, 187–201. https://doi.org/10.1007/s10336-011-0707-0

Cam, E., Gimenez, O., Alpizar-Jara, R., Aubry, L.M., Authier, M., Cooch, E.G., Koons, D.N., Link, W.A., Monnat, J., Nichols, J.D., Rotella, J.J., Royle, J.A., & Pradel, R. (2013). Looking for a needle in a haystack: Inference about individual fitness components in a heterogeneous population. Oikos, 122(5), 739–753. https://doi.org/10.1111/j.1600-0706.2012.20532.x

Carrier-Belleau, C., Drolet, D., McKindsey, C.W., Archambault, P., 2021. Environmental stressors, complex interactions and marine benthic communities' responses. Sci. Rep. 11, 4194. https://doi.org/10.1038/s41598-021-83533-1

Casas, F., Mougeot, F., Viñuela, J., Bretagnolle, V., 2009. Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. Anim. Conserv. 12, 346–354. https://doi.org/10.1111/j.1469-1795.2009.00259.x

Castro, M., Araújo, A., Monteiro, P., 2005. Fate of discards from deep water crustacean trawl fishery off the south coast of Portugal. N. Z. J. Mar. Freshwater Res. 39, 437–446. https://doi.org/10.1080/00288330.2005.9517323

Caswell, J.H., Alisauskas, R.T., Leafloor, J.O., 2012. Effect of neckband color on survival and recovery rates of Ross's geese. J. Wildl. Manage. 76, 1456–1461. https://doi.org/10.1002/jwmg.392

Caughley, G., 1994. Directions in conservation biology. J. Anim. Ecol. 63, 215. https://doi.org/10.2307/5542

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., Pradel, R., 2009a. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. Ecography 32, 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Choquet, R., Rouan, L., Pradel, R., 2009b. Program E-Surge: A software application for fitting multievent models, in: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds.), Modeling demographic processes in marked populations. Springer US, Boston, MA, pp. 845–865. https://doi.org/10.1007/978-0-387-78151-8_39

Clausen, K.K., Christensen, T.K., Gundersen, O.M., Madsen, J., 2017. Impact of hunting along the migration corridor of pink-footed geese Anser brachyrhynchus – implications for sustainable harvest management. J. Appl. Ecol. 54, 1563–1570. https://doi.org/10.1111/1365-2664.12850

Clausen, K.K., Clausen, P., 2013. Earlier Arctic springs cause phenological mismatch in long-distance migrants. Oecologia 173, 1101–1112. https://doi.org/10.1007/s00442-013-2681-0

Clausen, K.K., Madsen, J., 2014. Effects of neckbands on body condition of migratory geese. J. Ornithol. 155, 951–958. https://doi.org/10.1007/s10336-014-1080-6

Cohen, J.M., Lajeunesse, M.J., Rohr, J.R., 2018. A global synthesis of animal phenological responses to climate change. Nat. Clim. Chang. 8, 224–228. https://doi.org/10.1038/s41558-018-0067-3

Conn, P.B., Kendall, W.L., Samuel, M.D., 2004. A general model for the analysis of mark-resight, mark-recapture, and band-recovery data under tag loss. Biometrics 60, 900–909.

Cooch, E.G. 2002. Fledging size and survival in snow geese: timing is everything (or is it?). J. Appl. Stat., 29, 143-162. https://doi.org/10.1080/02664760120108494

Cooch, E.G., Dzubin, A., Rockwell, R.F., 1999. Using body size to estimate gosling age. J. Field Ornithol. 70, 214–229.

Cooch, E.G., Guillemain, M., Boomer, G.S., Lebreton, J.-D., Nichols, J.D., 2014. The effects of harvest on waterfowl populations. Wildfowl Special Issue 4, 220–276.

Cooke, F., MacInnes, C.D., Prevett, J.P., 1975. Gene flow between breeding populations of lesser snow geese. Auk 92, 493–510. https://doi.org/10.2307/4084603

Corlett, R.T., Primack, R.B., Devictor, V., Maas, B., Goswami, V.R., Bates, A.E., Koh, L.P., Regan, T.J., Loyola, R., Pakeman, R.J., Cumming, G.S., Pidgeon, A., Johns, D., Roth, R., 2020. Impacts of the coronavirus pandemic on biodiversity conservation. Biol. Conserv. 246, 108571. https://doi.org/10.1016/j.biocon.2020.108571

Cormack, R.M., 1964. Estimates of survival from the sighting of marked animals. Biometrika 51, 429. https://doi.org/10.2307/2334149

Corsini, M., Jagiello, Z., Walesiak, M., Redlisiak, M., Stadnicki, I., Mierzejewska, E., Szulkin, M., 2022. Breeding in the pandemic: short-term lockdown restrictions in a European capital city did not alter the life-history traits of two urban adapters. Urban Ecosyst. https://doi.org/10.1007/s11252-022-01309-5

Côté, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. Proc. R. Soc. B. 283, 20152592. https://doi.org/10.1098/rspb.2015.2592

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Coulson, G., 2007. Exploding kangaroos: assessing the problem and setting targets, in: Lunney, D., Eby, P., Hutchings, P., Burgin, S. (Eds.), Pest or guest: The zoology of overabundance. Royal Zoological Society of New South Wales, P.O. Box 20, Mosman NSW 2088, Australia, pp. 174–181. https://doi.org/10.7882/9780980327212

Cromsigt, J.P.G.M., Kuijper, D.P.J., Adam, M., Beschta, R.L., Churski, M., Eycott, A., Kerley, G.I.H., Mysterud, A., Schmidt, K., West, K., 2013. Hunting for fear: innovating management of human–wildlife conflicts. J. Appl. Ecol. 50, 544–549. https://doi.org/10.1111/1365-2664.12076

Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. Ecol. Lett. 11, 1278–1286. https://doi.org/10.1111/j.1461-0248.2008.01243.x

Derryberry, E.P., Phillips, J.N., Derryberry, G.E., Blum, M.J., Luther, D., 2020. Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. Science 370, 575–579. https://doi.org/10.1126/science.abd5777

Descamps, S., Aars, J., Fuglei, E., Kovacs, K.M., Lydersen, C., Pavlova, O., Pedersen, Å.Ø., Ravolainen, V., Strøm, H., 2017. Climate change impacts on wildlife in a High Arctic archipelago - Svalbard, Norway. Glob. Chang. Biol. 23, 490–502. https://doi.org/10.1111/gcb.13381

Deschamps, L., Maire, V., Chen, L., Fortier, D., Gauthier, G., Morneault, A., Hardy-Lachance, E., Dalcher-Gosselin, I., Tanguay, F., Gignac, C., McKenzie, J.M., Rochefort, L., Lévesque, E., 2023. Increased nutrient availability speeds up permafrost development, while goose grazing slows it down in a Canadian High Arctic wetland. J. Ecol. 111, 449–463. https://doi.org/10.1111/1365-2745.14037

Diagne, C., Leroy, B., Vaissière, A.-C., Gozlan, R.E., Roiz, D., Jarić, I., Salles, J.-M., Bradshaw, C.J.A., Courchamp, F., 2021. High and rising economic costs of biological invasions worldwide. Nature 592, 571–576. https://doi.org/10.1038/s41586-021-03405-6

Dickey, M.-H., Gauthier, G., Cadieux, M.-C., 2008. Climatic effects on the breeding phenology and reproductive success of an arctic-nesting goose species: Glob. Chang. Biol. 14, 1973–1985. https://doi.org/10.1111/j.1365-2486.2008.01622.x

Doiron, M., Gauthier, G., Lévesque, E., 2015. Trophic mismatch and its effects on the growth of young in an Arctic herbivore. Glob. Chang. Biol. 21, 4364–4376. https://doi.org/10.1111/gcb.13057

Doiron, M., Gauthier, G., Lévesque, E., 2014. Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. J. Ecol. 102, 508–517. https://doi.org/10.1111/1365-2745.12213

Doiron, M., Legagneux, P., Gauthier, G., Lévesque, E., 2013. Broad-scale satellite Normalized Difference Vegetation Index data predict plant biomass and peak date of nitrogen concentration in Arctic tundra vegetation. Appl. Veg. Sci. 16, 343–351. https://doi.org/10.1111/j.1654-109X.2012.01219.x

Dokter, A.M., Fokkema, W., Ebbinge, B.S., Olff, H., Jeugd, H.P., Nolet, B.A., 2018. Agricultural pastures challenge the attractiveness of natural saltmarsh for a migratory goose. J. Appl. Ecol. 55, 2707–2718. https://doi.org/10.1111/1365-2664.13168

Duchesne, É., Lamarre, J., Gauthier, G., Berteaux, D., Gravel, D., Bêty, J., 2021. Variable strength of predator-mediated effects on species occurrence in an arctic terrestrial vertebrate community. Ecography 44, 1236–1248. https://doi.org/10.1111/ecog.05760

Dueñas, A., Jiménez-Uzcátegui, G., Bosker, T., 2021. The effects of climate change on wildlife biodiversity of the galapagos islands. Clim. Chang. Ecol. 2, 100026. https://doi.org/10.1016/j.ecochg.2021.100026

Dunn, P.O., Møller, A.P., 2014. Changes in breeding phenology and population size of birds. J. Anim. Ecol. 83, 729–739. https://doi.org/10.1111/1365-2656.12162

Erikstad, K.E., Fauchald, P., Tveraa, T., Steen, H., 1998. On the cost of reproduction in long-lived birds: The influence of environmental variability. Ecology 79, 1781–1788. https://doi.org/10.1890/0012-9658(1998)079[1781:OTCORI]2.0.CO;2

Errington, P.L., 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. Ecol. Monogr. 15, 1–34. https://doi.org/10.2307/1943293

Etterson, M.A., Ellis-Felege, S.N., Evers, D., Gauthier, G., Grzybowski, J.A., Mattsson, B.J., Nagy, L.R., Olsen, B.J., Pease, C.M., Van Der Burg, M.P., Potvien, A., 2011. Modeling fecundity in birds: Conceptual overview, current models, and considerations for future developments. Ecol. Model. 222, 2178–2190. https://doi.org/10.1016/j.ecolmodel.2010.10.013

Féret, M., Bêty, J., Gauthier, G., Giroux, J.-F., Picard, G., 2005. Are abdominal profiles useful to assess body condition of spring staging greater snow geese? Condor 107, 694–702.

Féret, M., Gauthier, G., Bechet, A., Giroux, J.-F., Hobson, K.A., 2003. Effect of a spring hunt on nutrient storage by greater snow geese in southern Quebec. J. Wildl. Manage. 67, 796–807. https://doi.org/10.2307/3802687

Ferraz, G., 2020. The privilege of longevity. Nat. Clim. Chang. 10, 890–891. https://doi.org/10.1038/s41558-020-0890-1

Filion, B., Luszcz, D., Allard, G., 1998. Chapter 3: Impact of geese on farmlands., in: The greater snow goose: Report of the arctic goose habitat working group. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C. and Ottawa, Ontario, pp. 58–64.

Fix, P.J., Teel, T.L., Manfredo, M.J., Boston, S.S., 2010. Assessing public acceptance of wildlife management trade-offs: A case study of elk and vegetation management in Rocky Mountain National Park, Colorado. Hum. Dimens. Wildl. 15, 405–417. https://doi.org/10.1080/10871209.2010.503235

Flemming, S.A., Calvert, A., Nol, E., Smith, P.A., 2016. Do hyperabundant Arctic-nesting geese pose a problem for sympatric species? Environ. Rev. 24, 393–402. https://doi.org/10.1139/er-2016-0007

Flemming, S.A., Smith, P.A., Rausch, J., Nol, E., 2019. Broad-scale changes in tundra-nesting bird abundance in response to hyperabundant geese. Ecosphere 10. https://doi.org/10.1002/ecs2.2785

Flynn, D.F.B., Wolkovich, E.M., 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. New Phytol. 219, 1353–1362. https://doi.org/10.1111/nph.15232

Folt, C.L., Chen, C.Y., Moore, M.V., Burnaford, J., 1999. Synergism and antagonism among multiple stressors. Limnol. Oceanogr. 44, 864–877. https://doi.org/10.4319/lo.1999.44.3_part_2.0864

Forchhammer, M.C., Post, E., Stenseth, N.Chr., 1998. Breeding phenology and climate. Nature 391, 29–30. https://doi.org/10.1038/34070

Fowler, D.N., Webb, E.B., Vrtiska, M.P., 2019. Condition bias of decoy-harvested light geese during the Conservation Order. J. Wildl. Manage. 84, 33–44. https://doi.org/10.1002/jwmg.21770

Fox, A.D., 2003. The Greenland White-fronted goose Anser albifrons flavirostris. National Environmental Research Institute, Denmark.

Fox, A.D., Abraham, K.F., 2017. Why geese benefit from the transition from natural vegetation to agriculture. Ambio 46, 188–197. https://doi.org/10.1007/s13280-016-0879-1

Fox, A.D., Madsen, J., 2017. Threatened species to super-abundance: The unexpected international implications of successful goose conservation. Ambio 46, 179–187. https://doi.org/10.1007/s13280-016-0878-2

Fox, A.D., Walsh, A.J., Weegman, M.D., Bearhop, S., Mitchell, C., 2014. Spring ice formation on goose neck collars: effects on body condition and survival in Greenland white-fronted geese Anser albifrons flavirostris. Eur. J. Wildl. Res. 60, 831–834. https://doi.org/10.1007/s10344-014-0835-y

Francis, C.M., Richards, M.H., Cooke, F., Rockwell, R.F., 1992a. Long-term changes in survival rates of lesser snow geese. Ecology 73, 1346–1362. https://doi.org/10.2307/1940681

Francis, C.M., Richards, M.H., Cooke, F., Rockwell, R.F., 1992b. Changes in survival rates of lesser snow geese with age and breeding status. Auk 109, 731–747. https://doi.org/10.2307/4088149

Frederick, C., Girard, C., Wong, G., Lemire, M., Langwieder, A., Martin, M.-C., Legagneux, P., 2021. Communicating with Northerners on the absence of SARS-CoV-2 in migratory snow geese. Écoscience. 28, 217-223. https://doi.org/10.1080/11956860.2021.1885803

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toïgo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annu. Rev. Ecol. Syst. 31, 367–393. https://doi.org/10.1146/annurev.ecolsys.31.1.367

Gaillard, J.-M., Yoccoz, N.G., 2003. Temporal variation in survival of mammals: A case of environmental canalization? Ecology 84, 3294–3306. https://doi.org/10.1890/02-0409

Gauthier, G., Bedard, J., Huot, J., Bedard, Y., 1984. Spring accumulation of fat by greater snow geese in two staging habitats. Condor 86, 192–199. https://doi.org/10.2307/1367040

Gauthier, G., Bedard, Y., Bedard, J., 1988. Habitat use and activity budgets of greater snow geese in spring. J. Wildl. Manage. 52, 191–201. https://doi.org/10.2307/3801222

Gauthier, G., Bêty, J., Cadieux, M.-C., Legagneux, P., Doiron, M., Chevallier, C., Lai, S., Tarroux, A., Berteaux, D., 2013. Long-term monitoring at multiple trophic levels suggests heterogeneity in responses to climate change in the Canadian Arctic tundra. Phil. Trans. R. Soc. B 368, 1–12. https://doi.org/10.1098/rstb.2012.0482

Gauthier, G., Bêty, J., Giroux, J., Rochefort, L., 2004. Trophic interactions in a high arctic snow goose colony. Integr. Comp. Biol. 44, 119–129. https://doi.org/10.1093/icb/44.2.119

Gauthier, G., Bêty, J., Hobson, K.A., 2003. Are greater snow geese capital breeders? New evidence from a stable-isotope model. Ecology 84, 3250–3264. https://doi.org/10.1890/02-0613

Gauthier, G., Brault, S., 1998. Population model of the greater snow goose: projected impacts of reduction in survival on population growth rate, in: Batt, B.D.J. (Ed.), The greater snow goose: Report of the arctic goose habitat working group. Canadian Wildlife Service and U.S. Fish and Wildlife Service, Ottawa, Ontario and Washington, D.C., pp. 65–80.

Gauthier, G., Giroux, J.-F., Bédard, J., 1992. Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. Can. J. Zool. 70, 2077–2087. https://doi.org/10.1139/z92-280

Gauthier, G., Giroux, J.-F., Reed, A., Béchet, A., Bélanger, L., 2005. Interactions between land use, habitat use, and population increase in greater snow geese: what are the consequences for natural wetlands? Glob. Chang. Biol. 11, 856–868. https://doi.org/10.1111/j.1365-2486.2005.00944.x

Gauthier, G., Giroux, J.-F., Rochefort, L., 2006. The impact of goose grazing on arctic and temperate wetlands. Curr. Zool. 52, 108–111.

Gauthier, G., Hughes, R.J., Reed, A., Beaulieu, J., Rochefort, L., 1995. Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). J. Ecol. 83, 653–664. https://doi.org/10.2307/2261633

Gauthier, G., Lebreton, D., 2004. Population models for greater snow geese: A comparison of different approaches to assess potential impacts of harvest. Anim. Biodivers. Conserv. 27.

Gauthier, G., Lebreton, J.-D., 2008. Analysis of band-recovery data in a multistate capture-recapture framework. Can. J. Stat. 36, 59–73. https://doi.org/10.1002/cjs.5550360107

Gauthier, G., Pradel, R., Menu, S., Lebreton, J.-D., 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology 82, 3105–3119. https://doi.org/10.2307/2679838

Gauthier, G., Reed, E.T., 2007. Section II: Projected growth rate of the greater snow goose population under alternative harvest scenarios, in: Reed, E.T., Calvert, A.M. (Eds.), Evaluation of the special conservation measures for greater snow geese: Report of the greater snow goose working group. Arctic Goose Joint Venture special publication, Canadian Wildlife Service, Sainte-Foy, Québec., pp. 65–74.

Gibson, G., Wagner, G., 2000. Canalization in evolutionary genetics: a stabilizing theory? Bioessays 22, 372–380. https://doi.org/10.1002/(SICI)1521-1878(200004)22:4<372::AID-BIES7>3.0.CO;2-J

Gilby, B.L., Henderson, C.J., Olds, A.D., Ballantyne, J.A., Bingham, E.L., Elliott, B.B., Jones, T.R., Kimber, O., Mosman, J.D., Schlacher, T.A., 2021. Potentially negative ecological consequences of animal redistribution on beaches during COVID-19 lockdown. Biol. Conserv. 253, 108926. https://doi.org/10.1016/j.biocon.2020.108926

Giroux, J.-F., Batt, B.D.J., Brault, S., Costanzo, G., Filion, B., Gauthier, G., Luszcz, D., Reed, A., 1998. Conclusions and management recommendations., in: Batt, B.D.J. (Ed.), The greater snow goose: Report of the arctic goose habitat working group. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service and Canadian Wildlife Service., Washington, DC and Ottawa, Canada.

Giroux, J.-F., Bedard, J., 1986. Sex-specific hunting mortality of greater snow geese along firing lines in Quebec. J. Wildl. Manage. 50, 416. https://doi.org/10.2307/3801097

Giroux, J.-F., Bergeron, R., 1996. Spring diets of sympatric greater snow geese and Canada geese in southern Quebec. Can. J. Zool. 74, 950–953. https://doi.org/10.1139/z96-107

Giroux, M.-A., Berteaux, D., Lecomte, N., Gauthier, G., Szor, G., Bêty, J., 2012. Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator: Spatio-temporal patterns in subsidization. J. Anim. Ecol. 81, 533–542. https://doi.org/10.1111/j.1365-2656.2011.01944.x

Grandmont, T., Fast, P., Grentzmann, I., Gauthier, G., Bêty, J., Legagneux, P., 2023. Should I breed or should I go? Manipulating individual state during migration influences breeding decisions in a long-lived bird species. Funct. Ecol. 37, 602–613. https://doi.org/10.1111/1365-2435.14256

Greenwood, R.J., Bair, W.C., 1974. Ice on waterfowl markers. Wildl. Soc. Bull. 2, 130–134.

Grzegorczyk, E., Caizergues, A., Eraud, C., Francesiaz, C., Le Rest, K., & Guillemain, M. (2024). Demographic and evolutionary consequences of hunting of wild birds. Biol. Rev. 13069, 1-16. https://doi.org/10.1111/brv.13069

Guillemain, M., Fritz, H., Johnson, A.R., Simon, G., 2007. What type of lean ducks do hunters kill? Weakest local ones rather than migrants. Wildlife Biol. 13, 102–107. https://doi.org/10.2981/0909-6396(2007)13[102:WTOLDD]2.0.CO;2

Gwinner, E., 1996. Circannual clocks in avian reproduction and migration. Ibis 138, 47–63. https://doi.org/10.1111/j.1474-919X.1996.tb04312.x

Hamel, S., Côté, S.D., Smith, K.G., Festa-Bianchet, M., 2006. Population dynamics and harvest potential of mountain goat herds in Alberta. J. Wildl. Manage. 70, 1044–1053. https://doi.org/10.2193/0022-541X(2006)70[1044:PDAHPO]2.0.CO;2

Hamel, S., Gaillard, J.-M., Festa-Bianchet, M., Côté, S.D., 2009. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. Ecology 90, 1981–1995. https://doi.org/10.1890/08-0596.1

Handa, I.T., Harmsen, R., Jefferies, R.L., 2002. Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. J. Ecol. 90, 86–99.

Haywood, S., Perrins, C.M., 1992. Is clutch size in birds affected by environmental conditions during growth? Proc. R. Soc. Lond. B 249, 195–197. https://doi.org/10.1098/rspb.1992.0103

Hentati-Sundberg, J., Berglund, P.-A., Hejdström, A., Olsson, O., 2021. COVID-19 lockdown reveals tourists as seabird guardians. Biol. Conserv. 254, 108950. https://doi.org/10.1016/j.biocon.2021.108950

Hessen, D.O., Tombre, I.M., van Geest, G., Alfsnes, K., 2017. Global change and ecosystem connectivity: How geese link fields of central Europe to eutrophication of Arctic freshwaters. Ambio 46, 40–47. https://doi.org/10.1007/s13280-016-0802-9

Hestbeck, J.B., Nichols, J.D., Malecki, R.A., 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72, 523–533. https://doi.org/10.2307/2937193

Holopainen, S., Arzel, C., Elmberg, J., Fox, A.D., Guillemain, M., Gunnarsson, G., Nummi, P., Sjöberg, K., Väänänen, V., Alhainen, M., Pöysä, H., 2018. Sustainable management of migratory European ducks: finding model species. Wildlife Biol. 2018, 1–11. https://doi.org/10.2981/wlb.00336

Hutchison, C., Guichard, F., Legagneux, P., Gauthier, G., Bêty, J., Berteaux, D., Fauteux, D., Gravel, D., 2020. Seasonal food webs with migrations: multi-season models reveal indirect species interactions in the Canadian Arctic tundra. Phil. Trans. R. Soc. A. 378, 20190354. https://doi.org/10.1098/rsta.2019.0354

IPCC, 2023. Climate Change 2022 – Impacts, adaptation and vulnerability: Working group II contribution to the sixth assessment report of the intergovernmental panel on climate change, 1st ed. Cambridge University Press. https://doi.org/10.1017/9781009325844

Jamieson, S.E., Gilchrist, H.G., Merkel, F.R., Diamond, A.W., Falk, K., 2006. Endogenous reserve dynamics of northern common eiders wintering in Greenland. Polar Biol. 29, 585–594. https://doi.org/10.1007/s00300-005-0093-2

Jano, A.P., Jefferies, R.L., Rockwell, R.F., 1998. The detection of vegetational change by multitemporal analysis of LANDSAT data: The effects of goose foraging. J. Ecol. 86, 93–99. https://doi.org/10.1046/j.1365-2745.1998.00232.x

Jefferies, R.L., Rockwell, R.F., 2002. Foraging geese, vegetation loss and soil degradation in an arctic salt marsh. Appl. Veg. Sci. 5, 7–16.

Jefferies, R.L., Rockwell, R.F., Abraham, K.F., 2003. The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands — a continuing saga. Environ. Rev. 11, 193–232. https://doi.org/10.1139/A04-002

Jensen, T.C., Walseng, B., Hessen, D.O., Dimante-Deimantovica, I., Novichkova, A.A., Chertoprud, E.S., Chertoprud, M.V., Sakharova, E.G., Krylov, A.V., Frisch, D., Christoffersen, K.S., 2019. Changes in trophic state and aquatic communities in high Arctic ponds in response to increasing goose populations. Freshw. Biol. 64, 1241–1254. https://doi.org/10.1111/fwb.13299

Johnsen, A., Lifjeld, J.T., Rohde, P.A., 1997. Coloured leg bands affect male mate-guarding behaviour in the bluethroat. Anim. Behav. 54, 121–130. https://doi.org/10.1006/anbe.1996.0437

Johnson, M.A., Padding, P.I., Gendron, M., Reed, E.T., Graber, D.A., 2012. Assessment of harvest from conservation actions for reducing midcontinent light geese and recommendations for future monitoring., in: Leafloor, J.O., Moser, T.J., Batt, B.D.J. (Eds.), Evaluation of special management measures for midcontinent lesser snow geese and Ross's geese. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington, D.C., and Ottawa, Canada., pp. 46–94.

Jolly, G.M., 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52, 225. https://doi.org/10.2307/2333826

Juillet, C., Choquet, R., Gauthier, G., Lefebvre, J., Pradel, R., 2012. Carry-over effects of spring hunt and climate on recruitment to the natal colony in a migratory species. J. Appl. Ecol. 49, 1237–1246. https://doi.org/10.1111/j.1365-2664.2012.02199.x

Juillet, C., Choquet, R., Gauthier, G., Pradel, R., 2011. A capture–recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss. J. Agric. Biol. Environ. Stat. 16, 88–104. https://doi.org/10.1007/s13253-010-0035-5

Kéry, M., Schaub, M., 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective, 1st ed. ed. Academic Press, Boston.

Kilgo, J.C., Labisky, R.F., Fritzen, D.E., 1998. Influences of hunting on the behavior of white-tailed deer: Implications for conservation of the florida panther. Conserv. Biol. 12, 1359–1364. https://doi.org/10.1111/j.1523-1739.1998.97223.x

Klaassen, M., Bauer, S., Madsen, J., Tombre, I., 2006. Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. J. Appl. Ecol. 43, 92–100. https://doi.org/10.1111/j.1365-2664.2005.01109.x

Klaassen, M., Hahn, S., Korthals, H., Madsen, J., 2017. Eggs brought in from afar: Svalbard-breeding pink-footed geese can fly their eggs across the Barents Sea. J. Avian Biol. 48, 173–179. https://doi.org/10.1111/jav.01364

Kleist, N.J., Guralnick, R.P., Cruz, A., Lowry, C.A., Francis, C.D., 2018. Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. Proc. Natl. Acad. Sci. U.S.A. 115, E648–E657. https://doi.org/10.1073/pnas.1709200115

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W.J., Bach, L.A., Coppack, T., Ergon, T., Gienapp, P., Gill, J.A., Gordo, O., Hedenström, A., Lehikoinen, E., Marra, P.P., Møller, A.P., Nilsson, A.L.K., Péron, G., Ranta, E., Rubolini, D., Sparks, T.H., Spina, F., Studds, C.E., Saether, S.A., Tryjanowski, P., Stenseth, N.C., 2011. Challenging claims in the study of migratory birds and climate change. Biol. Rev. 86, 928–946. https://doi.org/10.1111/j.1469-185X.2011.00179.x

Kokko, H., 2001. Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. Wildlife Biol. 7, 141–150. https://doi.org/10.2981/wlb.2001.018

Kokko, H., Lindström, J., 1998. Seasonal density dependence, timing of mortality, and sustainable harvesting. Ecol. Model. 110, 293–304. https://doi.org/10.1016/S0304-3800(98)00089-1

Kölzsch, A., Neefjes, M., Barkway, J., Müskens, G.J.D.M., van Langevelde, F., de Boer, W.F., Prins, H.H.T., Cresswell, B.H., Nolet, B.A., 2016. Neckband or backpack? Differences in tag design and their effects on GPS/accelerometer tracking results in large waterbirds. Anim. Biotelemetry 4, 1–14. https://doi.org/10.1186/s40317-016-0104-9

Koons, D.N., Aubry, L.M., Rockwell, R.F., 2019. Liberalized harvest regulations have not affected overabundant Snow Geese in Northern Manitoba. The Condor 121, duz006. https://doi.org/10.1093/condor/duz006

Koons, D.N., Iles, D.T., Schaub, M., Caswell, H., 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. Ecol. Lett. 19, 1023–1031. https://doi.org/10.1111/ele.12628

Koons, D.N., Rockwell, R.F., Aubry, L.M., 2014. Effects of exploitation on an overabundant species: the lesser snow goose predicament. J. Anim. Ecol. 83, 365–374. https://doi.org/10.1111/1365-2656.12133

Lamarre, J.-F., Legagneux, P., Gauthier, G., Reed, E.T., Bêty, J., 2017. Predator-mediated negative effects of overabundant snow geese on arctic-nesting shorebirds. Ecosphere 8, 1–13. https://doi.org/10.1002/ecs2.1788

Lameris, T.K., Tomkovich, P.S., Johnson, J.A., Morrison, R.I.G., Tulp, I., Lisovski, S., DeCicco, L., Dementyev, M., Gill, R.E., Ten Horn, J., Piersma, T., Pohlen, Z., Schekkerman, H., Soloviev, M., Syroechkovsky, E.E., Zhemchuzhnikov, M.K., Van Gils, J.A., 2022. Mismatch-induced growth reductions in a clade of Arctic-breeding shorebirds are rarely mitigated by increasing temperatures. Glob. Chang. Biol. 28, 829–847. https://doi.org/10.1111/gcb.16025

Lameris, T.K., Van Der Jeugd, H.P., Eichhorn, G., Dokter, A.M., Bouten, W., Boom, M.P., Litvin, K.E., Ens, B.J., Nolet, B.A., 2018. Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. Curr. Biol. 28, 2467-2473.e4. https://doi.org/10.1016/j.cub.2018.05.077

Lebreton, J., Nichols, J.D., Barker, R.J., Pradel, R., Spendelow, J.A., 2009. Chapter 3: Modeling individual animal histories with multistate capture–recapture models, in: Advances in ecological research. Elsevier, pp. 87–173. https://doi.org/10.1016/S0065-2504(09)00403-6

Lebreton, J.-D., 2005. Dynamical and statistical models for exploited populations. Aust. N. Z. J. Stat. 47, 49–63. https://doi.org/10.1111/j.1467-842X.2005.00371.x

Lebreton, J.-D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecol. Monogr. 62, 67–118. https://doi.org/10.2307/2937171

Lebreton, J.-D., Morgan, B.J.T., Pradel, R., Freeman, S.N., 1995. A simultaneous survival rate analysis of dead recovery and live recapture data. Biometrics 51, 1418. https://doi.org/10.2307/2533272

Lecomte, N., Gauthier, G., Giroux, J.-F., Milot, E., Bernatchez, L., 2009. Tug of war between continental gene flow and rearing site philopatry in a migratory bird: the sex-biased dispersal paradigm reconsidered. Mol. Ecol. 18, 593–602. https://doi.org/10.1111/j.1365-294X.2008.04067.x

Lefebvre, J., Gauthier, G., Giroux, J.-F., Reed, A., Reed, E.T., Bélanger, L., 2017. The greater snow goose Anser caerulescens atlanticus: Managing an overabundant population. Ambio 46, 262–274. https://doi.org/10.1007/s13280-016-0887-1

Legagneux, P., Fast, P.L.F., Gauthier, G., Bêty, J., 2012. Manipulating individual state during migration provides evidence for carry-over effects modulated by environmental conditions. Proc. R. Soc. Lond. B 279, 876–883. https://doi.org/10.1098/rspb.2011.1351

Legagneux, P., Simard, A.-A., Gauthier, G., Bêty, J., 2013. Effect of neck collars on the body condition of migrating greater snow geese. J. Field Ornithol. 84, 201–209. https://doi.org/10.1111/jofo.12019

Lemoine, V., 2003. Évaluation de la chasse de conservation printanière à la grande oie des neiges : comportement, succès des chasseurs et effet sur la survie des oies. Université du Québec à Montréal, Canada.

Lepage, D., Gauthier, G., Menu, S., 2000. Reproductive consequences of egg-laying decisions in snow geese. J. Anim. Ecol. 69, 414–427.

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

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2024. Evidence for seasonal compensation of hunting mortalities in a long-lived migratory bird. J. Appl. Ecol. 61: 2169-2179. https://doi.org/10.1111/1365-2664.14731

LeTourneux, F., Grandmont, T., Dulude-de Broin, F., Martin, M.-C., Lefebvre, J., Kato, A., Bêty, J., Gauthier, G., Legagneux, P., 2021. COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species. Biol. Conserv. 255, 108968. https://doi.org/10.1016/j.biocon.2021.108968

Leyrer, J., Lok, T., Brugge, M., Spaans, B., Sandercock, B.K., Piersma, T., 2013. Mortality within the annual cycle: seasonal survival patterns in Afro-Siberian Red Knots Calidris canutus canutus. J. Ornithol. 154, 933–943. https://doi.org/10.1007/s10336-013-0959-y

Li, Y., Jiao, Z., Zhao, K., Dong, Y., Zhou, Y., Zeng, Y., Xu, H., Zhang, X., Hu, T., Cui, L., 2021. Influence of varying solar zenith angles on land surface phenology derived from vegetation indices: A case study in the Harvard forest. Remote Sens. 13, 4126. https://doi.org/10.3390/rs13204126

Lindberg, M.S., 2012. A review of designs for capture–mark–recapture studies in discrete time. J. Ornithol. 152, 355–370. https://doi.org/10.1007/s10336-010-0533-9

Lindberg, M.S., Sedinger, J.S., Lebreton, J., 2013. Individual heterogeneity in black brant survival and recruitment with implications for harvest dynamics. Ecol. Evol. 3, 4045–4056. https://doi.org/10.1002/ece3.767

Lindén, M., Gustafsson, L., Part, T., 1992. Selection on fledging mass in the collared flycatcher and the great tit. Ecology 73, 336–343. https://doi.org/10.2307/1938745

Lindström, J., 1999. Early development and fitness in birds and mammals. Trends Ecol. Evol. 14, 343–348. https://doi.org/10.1016/S0169-5347(99)01639-0

Madsen, J., 1995. Impacts of disturbance on migratory waterfowl. Ibis 137, S67–S74. https://doi.org/10.1111/j.1474-919X.1995.tb08459.x

Madsen, J., Clausen, K.K., Christensen, T.K., Johnson, F.A., 2016. Regulation of the hunting season as a tool for adaptive harvest management — first results for pink-footed geese *Anser brachyrhynchus*. Wildlife Biol. 22, 204–208. https://doi.org/10.2981/wlb.00234

Madsen, J., Fox, A.D., 1995. Impacts of hunting disturbance on waterbirds - a review. Wildlife Biol. 1, 193–207. https://doi.org/10.2981/wlb.1995.0025

Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., Nyegaard, H., Cottaar, F., 2007. Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese Anser brachyrhynchus. Polar Biol. 30, 1363–1372. https://doi.org/10.1007/s00300-007-0296-9

Madsen, T., Shine, R., 2008. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. J. Anim. Ecol. 69, 952–958. https://doi.org/10.1111/j.1365-2656.2000.00477.x

Mainguy, J., Bêty, J., Gauthier, G., Giroux, J.-F., 2002. Are body condition and reproductive effort of laying greater snow geese affected by the spring hunt? Condor 104, 156–161.

Manenti, R., Mori, E., Di Canio, V., Mercurio, S., Picone, M., Caffi, M., Brambilla, M., Ficetola, G.F., Rubolini, D., 2020. The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: Insights from the first European locked down country. Biol. Conserv. 249. https://doi.org/10.1016/j.biocon.2020.108728

Manseau, M., Gauthier, G., 1993. Interactions between greater snow geese and their rearing habitat. Ecology 74, 2045–2055. https://doi.org/10.2307/1940850

Mantyka-pringle, C.S., Martin, T.G., Rhodes, J.R., 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Glob. Chang. Biol. 18, 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x

Marquis, O., Massot, M., Le Galliard, J.F., 2008. Intergenerational effects of climate generate cohort variation in lizard reproductive performance. Ecology 89, 2575–2583. https://doi.org/10.1890/07-1211.1

Massé, H., Rochefort, L., Gauthier, G., 2001. Carrying capacity of wetland habitats used by breeding greater snow geese. J. Wildl. Manage. 65, 271. https://doi.org/10.2307/3802906

McDuie, F., Lorenz, A.A., Klinger, R.C., Overton, C.T., Feldheim, C.L., Ackerman, J.T., Casazza, M.L., 2021. Informing wetland management with waterfowl movement and sanctuary use responses to human-induced disturbance. J. Env. Manage. 297, 113170. https://doi.org/10.1016/j.jenvman.2021.113170

McEwen, B.S., Wingfield, J.C., 2003. The concept of allostasis in biology and biomedicine. Horm. Behav. 43, 2–15. https://doi.org/10.1016/S0018-506X(02)00024-7

Menu, S., Gauthier, G., Reed, A., 2005. Survival of young greater snow geese (Chen caerulescens atlantica) during fall migration. Auk 122, 479–496.

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

Menu, S., Gauthier, G., Reed, A., 2001. Survival of Juvenile Greater Snow Geese Immediately after Banding. J. Field Ornithol. 72, 282–290.

Menu, S., Hestbeck, J.B., Gauthier, G., Reed, A., 2000. Effects of neck bands on survival of greater snow geese. J. Wildl. Manage. 64, 544–552. https://doi.org/10.2307/3803252

Møller, A.P., Rubolini, D., Lehikoinen, E., 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proc. Natl. Acad. Sci. U.S.A. 105, 16195–16200. https://doi.org/10.1073/pnas.0803825105

Morez, V., Gauthier, G., Reed, A., 2000. Effect of body condition on vulnerability of greater snow geese to hunting and capture. J. Wildl. Manage. 64, 875–886. https://doi.org/10.2307/3802758

Morrissette, M., Bêty, J., Gauthier, G., Reed, A., Lefebvre, J., 2010. Climate, trophic interactions, density dependence and carry-over effects on the population productivity of a migratory Arctic herbivorous bird. Oikos 119, 1181–1191. https://doi.org/10.1111/j.1600-0706.2009.18079.x

Mowbray, T.B., Cooke, F., Ganter, B., 2020. Snow Goose (Anser caerulescens) [WWW Document]. Birds of the World. URL https://birdsoftheworld.org/bow/species/snogoo/cur/introduction (accessed 8.18.23).

Muth, R.M., Ruppert, D.E., & Glass, R.J. (1987). Subsistence use of fisheries resources in Alaska: Implications for Great Lakes fisheries management. Trans. Am. Fish. Soc. 116(3), 510–518. https://doi.org/10.1577/1548-8659(1987)116<510:SUOFRI>2.0.CO;2

Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C.E., Bertram, M.G., Bijleveld, A.I., et al., 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. Science 375, eabg1780. https://doi.org/10.1126/science.abg1780

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, et al., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324

Newton, I., 2007. Weather-related mass-mortality events in migrants. Ibis 149, 453–467. https://doi.org/10.1111/j.1474-919X.2007.00704.x

Nichols, J.D., Sauer, J.R., Pollock, K.H., Hestbeck, J.B., 1992. Estimating transition probabilities for stage-based population projection matrices using capture-recapture data. Ecology 73, 306–312. https://doi.org/10.2307/1938741

Nicolau, P.G., Ims, R.A., Sørbye, S.H., Yoccoz, N.G., 2022. Seasonality, density dependence, and spatial population synchrony. Proc. Natl. Acad. Sci. U.S.A. 119, e2210144119. https://doi.org/10.1073/pnas.2210144119

Nishizawa, K., Deschamps, L., Maire, V., Bêty, J., Lévesque, E., Kitagawa, R., Masumoto, S., Gosselin, I., Morneault, A., Rochefort, L., Gauthier, G., Tanabe, Y., Uchida, M., Mori, A.S., 2021. Long-term consequences of goose exclusion on nutrient cycles and plant communities in the High-Arctic. Polar Sci. 14. https://doi.org/10.1016/j.polar.2020.100631

Nolet, B.A., Kölzsch, A., Elderenbosch, M., van Noordwijk, A.J., 2016. Scaring waterfowl as a management tool: how much more do geese forage after disturbance? J. Appl. Ecol. 53, 1413–1421. https://doi.org/10.1111/1365-2664.12698

Nolet, B.A., Schreven, K.H.T., Boom, M.P., Lameris, T.K., 2020. Contrasting effects of the onset of spring on reproductive success of Arctic-nesting geese. Auk 137, ukz063. https://doi.org/10.1093/auk/ukz063

Oberbauer, S.F., Elmendorf, S.C., Troxler, T.G., Hollister, R.D., Rocha, A.V., Bret-Harte, M.S., Dawes, M.A., Fosaa, A.M., Henry, G.H.R., Høye, T.T., Jarrad, F.C., Jónsdóttir, I.S., Klanderud, K., Klein, J.A., Molau, U., Rixen, C., Schmidt, N.M., Shaver, G.R., Slider, R.T., Totland, Ø., Wahren, C.-H., Welker, J.M., 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. Phil. Trans. R. Soc. B 368, 20120481. https://doi.org/10.1098/rstb.2012.0481

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S., Martínez-Abraín, A., 2013. Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. 16, 1501–1514. https://doi.org/10.1111/ele.12187

Osenberg, C.W., Schmitt, R.J., 1996. Detecting ecological impacts caused by human activities, in: Schmitt, R.J., Osenberg, C.W. (Eds.), Detecting Ecological Impacts. Academic Press, San Diego, pp. 3–16. https://doi.org/10.1016/B978-012627255-0/50003-3

Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. Ecosystems 1, 535–545. https://doi.org/10.1007/s100219900049

Pearse, A.T., Krapu, G.L., Cox, R.R., 2012. Spring snow goose hunting influences body composition of waterfowl staging in Nebraska. J. Wildl. Manage. 76, 1393–1400. https://doi.org/10.1002/jwmg.389

Pennycuick, C.J., Fast, P.L.F., Ballerstädt, N., Rattenborg, N., 2012. The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration. J. Ornithol. 153, 633–644. https://doi.org/10.1007/s10336-011-0781-3

Péron, G., 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. J. Anim. Ecol. 82, 408–417. https://doi.org/10.1111/1365-2656.12014

Peterson, S.L., Rockwell, R.F., Witte, C.R., Koons, D.N., 2014. Legacy effects of habitat degradation by lesser snow geese on nesting savannah sparrows. Condor 116, 527–537. https://doi.org/10.1650/CONDOR-14-45.1

Pfister, C.A., 1998. Patterns of variance in stage-structured populations: Evolutionary predictions and ecological implications. Proc. Natl. Acad. Sci. U.S.A. 95, 213–218. https://doi.org/10.1073/pnas.95.1.213

Piedboeuf, N., Gauthier, G., 1999. Nutritive quality of forage plants for greater snow goose goslings: when is it advantageous to feed on grazed plants? Can. J. Zool. 77.

Post, E., Stenseth, N.C., 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80, 1322–1339. https://doi.org/10.1890/0012-9658(1999)080[1322:CVPPAN]2.0.CO;2

Pot, M.T., Koning, S. de, Westerduin, C., de Boer, W.F., Shariati, M., Lameris, T.K., 2019. Wintering geese trade-off energetic gains and costs when switching from agricultural to natural habitats. Ardea 107, 183–196. https://doi.org/10.5253/arde.v107i2.a6

Pradel, R., 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics 61, 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Pradel, R., Wintrebert, C.M.A., Gimenez, O., 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. Biometrics 59, 43–53. https://doi.org/10.1111/1541-0420.00006

R Core Team, 2020. R: A language and environment for statistical computing.

Rantanen, M., Karpechko, A.Yu., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., Laaksonen, A., 2022. The Arctic has warmed nearly four times faster than the globe since 1979. Commun. Earth Environ. 3, 168. https://doi.org/10.1038/s43247-022-00498-3

Reed, A., Giroux, J.-F., Gauthier, G., 1998. Population size, productivity, harvest and distribution., in: Batt, B.D.J. (Ed.), The greater snow goose: Report of the arctic goose habitat working group. Canadian Wildlife Service and U.S. Fish and Wildlife Service, Ottawa, Ontario and Washington, D.C.

Reed, E.T., Calvert, A.M., 2007. Evaluation of the special conservation measures for greater snow geese: report of the greater snow goose working group, Arctic Goose Joint Venture special publication.

Reed, E.T., Gauthier, G., Giroux, F., 2004. Effects of spring conditions on breeding propensity of greater snow goose females. Anim. Behav. 27, 25–46.

Reed, E.T., Gauthier, G., Pradel, R., 2005. Effects of neck bands on reproduction and survival of female greater snow geese. J. Wildl. Manage. 69, 91–100.

Reed, T.E., Grøtan, V., Jenouvrier, S., Sæther, B.-E., Visser, M.E., 2013. Population growth in a wild bird is buffered against phenological mismatch. Science 340, 488–491. https://doi.org/10.1126/science.1232870

Reneerkens, J., Schmidt, N.M., Gilg, O., Hansen, J., Hansen, L.H., Moreau, J., Piersma, T., 2016. Effects of food abundance and early clutch predation on reproductive timing in a high Arctic shorebird exposed to advancements in arthropod abundance. Ecol. Evol. 6, 7375–7386. https://doi.org/10.1002/ece3.2361

Reséndiz-Infante, 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. Université Laval, Québec.

Reséndiz-Infante, C., Gauthier, G., 2024. Can arctic migrants adjust their phenology based on temperature encountered during the spring migration? The case of the greater snow goose. Front. Bird Sci. 3:1307628. doi: 10.3389/fbirs.2024.1307628

Rexstad, E.A., 1992. Effect of hunting on annual survival of Canada geese in Utah. J. Wildl. Manage. 56, 297–305. https://doi.org/10.2307/3808826

Reznick, D., Bryant, M.J., Bashey, F., 2002. r- and K-selection revisited: the role of population regulation in life-history evolution. Ecology 83, 1509–1520. https://doi.org/10.2307/3071970

Rhoads, C.L., Bowman, J.L., Eyler, B., 2013. Movements of female exurban white-tailed deer in response to controlled hunts. Wildl. Soc. Bull. 37, 631–638. https://doi.org/10.1002/wsb.298

Ricouard, A., Lehuta, S., & Mahévas, S. (2023). Are maximum yields sustainable? Effect of intra-annual time-scales on MSY, stability and resilience. Ecol. Modell. 479, 1-20. https://doi.org/10.1016/j.ecolmodel.2023.110321

Riecke, T.V., Lohman, M.G., Sedinger, B.S., Arnold, T.W., Feldheim, C.L., Koons, D.N., Rohwer, F.C., Schaub, M., Williams, P.J., Sedinger, J.S., 2022. Density-dependence produces spurious relationships among demographic parameters in a harvested species. J. Anim. Ecol. 91, 2261–2272. https://doi.org/10.1111/1365-2656.13807

Ripley, B., Venables, B., Bates, D.M., Hornik, K., Gebhardt, A., Firth, D., 2020. MASS: Support functions and datasets for Venables and Ripley's MASS.

Robinson, W.D., Bowlin, M.S., Bisson, I., Shamoun-Baranes, J., Thorup, K., Diehl, R.H., Kunz, T.H., Mabey, S., Winkler, D.W., 2010. Integrating concepts and technologies to advance the study of bird migration. Front. Ecol. Environ. 8, 354–361. https://doi.org/10.1890/080179

Romero, L.M., Wingfield, J.C., 2016. Tempests, poxes, predators, and people: stress in wild animals and how they cope, Oxford series in behavioral neuroendocrinology. Oxford University Press, Oxford ; New York.

Ross, M.V., Alisauskas, R.T., Douglas, D.C., Kellett, D.K., 2017. Decadal declines in avian herbivore reproduction: density-dependent nutrition and phenological mismatch in the Arctic. Ecology 98, 1869–1883. https://doi.org/10.1002/ecy.1856

Ross, M.V., Alisauskas, R.T., Douglas, D.C., Kellett, D.K., Drake, K.L., 2018. Density-dependent and phenological mismatch effects on growth and survival in lesser snow and Ross's goslings. J. Avian Biol. 49, jav.01748. https://doi.org/10.1111/jav.01748

Rotem, G., Berger, H., King, R., Kutiel, P.B., Saltz, D., 2011. The effect of anthropogenic resources on the space-use patterns of golden jackals. J. Wildl. Manage. 75, 132–136. https://doi.org/10.1002/jwmg.9

Rutz, C., Loretto, M.-C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R.B., Ropert-Coudert, Y., Tucker, M.A., Wikelski, M., Cagnacci, F., 2020. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. Nat. Ecol. Evol. 4, 1156–1159. https://doi.org/10.1038/s41559-020-1237-z

Saino, N., Romano, M., Ambrosini, R., Rubolini, D., Boncoraglio, G., Caprioli, M., Romano, A., 2012. Longevity and lifetime reproductive success of barn swallow offspring are predicted by their hatching date and phenotypic quality: Longevity and LRS of barn swallow offspring. J. Anim. Ecol. 81, 1004–1012. https://doi.org/10.1111/j.1365-2656.2012.01989.x

Samelius, G., Alisauskas, R.T., 2009. Habitat alteration by geese at a large arctic goose colony: Consequences for lemmings and voles. Can. J. Zool. 87, 95–101. https://doi.org/10.1139/Z08-140

Sandercock, B.K., Nilsen, E.B., Brøseth, H., Pedersen, H.C., 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan: Harvest and ptarmigan survival. J. Anim. Ecol. 80, 244–258. https://doi.org/10.1111/j.1365-2656.2010.01769.x

Saraux, C., Le Bohec, C., Durant, J.M., Viblanc, V.A., Gauthier-Clerc, M., Beaune, D., Park, Y.-H., Yoccoz, N.G., Stenseth, N.C., Le Maho, Y., 2011. Reliability of flipper-banded penguins as indicators of climate change. Nature 469, 203–206. https://doi.org/10.1038/nature09630

Sauve, A.M.C., Barraquand, F., 2020. From winter to summer and back: Lessons from the parameterization of a seasonal food web model for the Białowieża forest. J. Anim. Ecol. 89, 1628–1644. https://doi.org/10.1111/1365-2656.13227

Schaub, M., Lebreton, D., 2004. Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. Anim. Behav. 21, 73–85.

Schaub, M., Pradel, R., 2004. Assessing the relative importance of different sources of mortality from recoveries or marked animals. Ecology 85, 930–938. https://doi.org/10.1890/03-0012

Schmidt, N.M., Ims, R.A., Høye, T.T., Gilg, O., Hansen, L.H., Hansen, J., Lund, M., Fuglei, E., Forchhammer, M.C., Sittler, B., 2012. Response of an arctic predator guild to collapsing lemming cycles. Proc. R. Soc. B. 279, 4417–4422. https://doi.org/10.1098/rspb.2012.1490

Schmutz, J.A., Morse, J.A., 2000. Effects of neck collars and radiotransmitters on survival and reproduction of emperor geese. J. Wildl. Manage. 64, 231–237. https://doi.org/10.2307/3802995

Searcy, W.A., Peters, S., Nowicki, S., 2004. Effects of early nutrition on growth rate and adult size in song sparrows *Melospiza melodia*. J. Avian Biol. 35, 269–279. https://doi.org/10.1111/j.0908-8857.2004.03247.x

Seber, G.A.F., 1965. A note on the multiple-recapture census. Biometrika 52, 249. https://doi.org/10.2307/2333827

Sedinger, J.S., Flint, P.L., Lindberg, M.S., 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (Branta bernicla). Ecology 76, 2404–2414. https://doi.org/10.2307/2265816

Sedinger, J.S., Lindberg, M.S., Chelgren, N.D., 2001. Age-specific breeding probability in black brant: effects of population density. J. Anim. Ecol. 70:798-807. https://doi.org/10.1046/J.0021-8790.2001.00535.X

Sedinger, J.S., Raveling, D.G., 1986. Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. J. Anim. Ecol. 55, 1083. https://doi.org/10.2307/4435

Senner, N.R., Stager, M., Sandercock, B.K., 2017. Ecological mismatches are moderated by local conditions for two populations of a long-distance migratory bird. Oikos 126, 61–72. https://doi.org/10.1111/oik.03325

Seress, G., Sándor, K., Vincze, E., Pipoly, I., Bukor, B., Ágh, N., Liker, A., 2021. Contrasting effects of the COVID-19 lockdown on urban birds' reproductive success in two cities. Sci. Rep. 11, 17649. https://doi.org/10.1038/s41598-021-96858-8

Servanty, S., Choquet, R., Baubet, É., Brandt, S., Gaillard, J.-M., Schaub, M., Toïgo, C., Lebreton, J.-D., Buoro, M., Gimenez, O., 2010. Assessing whether mortality is additive using marked animals: a Bayesian state–space modeling approach. Ecology 91, 1916–1923. https://doi.org/10.1890/09-1931.1

Sharp, C.M., Abraham, K.F., Hobson, K.A., Burness, G., 2013. Allocation of nutrients to reproduction at high latitudes: Insights from two species of sympatrically nesting geese. Auk 130, 171–179. https://doi.org/10.1525/auk.2012.12016

Sheaffer, S.E., Kendall, W.L., Bowers, E.F., 2005. Impact of special early harvest seasons on subarctic-nesting and temperate-nesting Canada geese. J. Wildl. Manage. 69, 1494–1507. https://doi.org/10.2193/0022-541X(2005)69[1494:IOSEHS]2.0.CO;2

Sherfy, M.H., Kirkpatrick, R.L., 2003. Invertebrate response to snow goose herbivory on moist-soil vegetation. Wetlands 23, 236–249. https://doi.org/10.1672/3-20

Shields, A., 2021. Le dossier des cerfs de Longueuil toujours dans l'impasse. Le Devoir.

Sih, A., Englund, G., Wooster, D., 1998. Emergent impacts of multiple predators on prey. Trends Ecol. Evol. 13, 350–355. https://doi.org/10.1016/S0169-5347(98)01437-2

Sliwinski, S.M., Schummer, M.L., Alice Lindsay, K., Whipps, C.M., Dunn, D.A., Wagner, M.R., 2023. Morphological differences and migration patterns of greater and lesser snow geese in New York State. Wildl. Soc. Bull. 47, e1388. https://doi.org/10.1002/wsb.1388

Smith, A.C., Gendron, M., 2022. Spring snow goose hunt in eastern Canada. Unpublished annual reports (1999-2022). National Wildlife Research Centre, Canadian Wildlife Service, Environment and Climate Change Canada.

Sokos, C.K., Birtsas, P.K., Connelly, J.W., Papaspyropoulos, K.G., 2013. Hunting of migratory birds: disturbance intolerant or harvest tolerant? Wildlife Biol. 19, 113–125. https://doi.org/10.2981/12-032

Souchay, G., 2013. Aspects non-canalisés de la dynamique de population de la grande oie des neiges Probabilités de reproduction et de survie juvénile. Université Laval, Québec.

Souchay, G., Gauthier, G., Pradel, R., 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. https://doi.org/10.1890/13-1277.1

Srivastava, D.S., Jefferies, R.L., 1996. A positive feedback: Herbivory, plant growth, salinity, and the desertification of an arctic salt-marsh. J. Ecol. 84, 31–42. https://doi.org/10.2307/2261697

Stearns, S.C., Kawecki, T.J., 1994. Fitness sensitivity and the canalization of life-history traits. Evolution 48, 1438–1450. https://doi.org/10.1111/j.1558-5646.1994.tb02186.x

Steffen, W., Persson, Å., Deutsch, L., Zalasiewicz, J., Williams, M., Richardson, K., Crumley, C., Crutzen, P., Folke, C., Gordon, L., Molina, M., Ramanathan, V., Rockström, J., Scheffer, M., Schellnhuber, H.J., Svedin, U., 2011. The Anthropocene: From global change to planetary stewardship. Ambio 40, 739–761. https://doi.org/10.1007/s13280-011-0185-x

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., Lima, M., 2002. Ecological effects of climate fluctuations. Science 297, 1292–1296. https://doi.org/10.1126/science.1071281

Sullivan, J.D., Ditchkoff, S.S., Collier, B.A., Ruth, C.R., Raglin, J.B., 2018. Recognizing the danger zone: response of female white-tailed to discrete hunting events. Wildlife Biol. 2018, 1–8. https://doi.org/10.2981/wlb.00455

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Høye, T.T., Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I., Winfield, I.J., Wanless, S., 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature 535, 241–245. https://doi.org/10.1038/nature18608

Therrien, J.-F., Gauthier, G., Korpimäki, E., Bêty, J., 2014. Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic. Ecology 95, 56–67. https://doi.org/10.1890/13-0458.1

Thornburg, D.D., 1973. Diving duck movements on Keokuk pool, Mississippi River. J. Wildl. Manage. 37, 382–389. https://doi.org/10.2307/3800129

Tombre, I.M., Eythórsson, E., Madsen, J., 2013. Towards a solution to the goose-agriculture conflict in North Norway, 1988–2012: The interplay between policy, stakeholder influence and goose population dynamics. PLoS ONE 8, e71912. https://doi.org/10.1371/journal.pone.0071912

Tombre, I.M., Høgda, K.A., Madsen, J., Griffin, L.R., Kuijken, E., Shimmings, P., Rees, E., Verscheure, C., 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*. J. Avian Biol. 39, 691–703. https://doi.org/10.1111/j.1600-048X.2008.04440.x

Traylor, J.J., Alisauskas, R.T., Slattery, S.M., Drake, K.L., 2012. Comparative survival and recovery of Ross's and lesser snow geese from Canada's central arctic. J. Wildl. Manage. 76, 1135–1144. https://doi.org/10.1002/jwmg.375

Turcotte, Y., Bédard, J., 1989. Shared parental investment, parent-offspring conflict and brood size in greater snow geese. Anim. Behav. 38, 703–706. https://doi.org/10.1016/S0003-3472(89)80016-8

Valéry, L., Cadieux, M.-C., Gauthier, G., 2010. Spatial heterogeneity of primary production as both cause and consequence of foraging patterns of an expanding greater snow goose colony. Écoscience 17, 9–19. https://doi.org/10.2980/17-1-3279

van der Jeugd, H.P., Kwak, A., 2017. Management of a Dutch resident barnacle goose Branta leucopsis population: How can results from counts, ringing and hunting bag statistics be reconciled? Ambio 46, 251–261. https://doi.org/10.1007/s13280-017-0900-3

van Oudenhove, L., Gauthier, G., Lebreton, J.-D., 2014. Year-round effects of climate on demographic parameters of an arctic-nesting goose species. J. Anim. Ecol. 83, 1322–1333. https://doi.org/10.1111/1365-2656.12230

Vardi, R., Berger-Tal, O., Roll, U., 2021. iNaturalist insights illuminate COVID-19 effects on large mammals in urban centers. Biol. Conserv. 254, 108953. https://doi.org/10.1016/j.biocon.2021.108953

Venables, W.N., Ripley, B.D., 2002. Modern applied statistics with S, 4th ed. ed, Statistics and computing. Springer, New York.

Verhulst, S., Nilsson, J.-Å., 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Phil. Trans. R. Soc. B 363, 399–410. https://doi.org/10.1098/rstb.2007.2146

Vermote, E., 2022. NOAA climate data record (CDR) of VIIRS Normalized Difference Vegetation Index (NDVI), Version 1. https://doi.org/10.25921/GAKH-ST76

Vermote, E., 2018. NOAA climate data record (CDR) of AVHRR Normalized Difference Vegetation Index (NDVI), Version 5. https://doi.org/10.7289/V5ZG6QH9

Visser, M.E., Gienapp, P., 2019. Evolutionary and demographic consequences of phenological mismatches. Nat. Ecol. Evol. 3, 879–885. https://doi.org/10.1038/s41559-019-0880-8

Vitousek, P.M., D'Antonio, C.M.V., Loope, L.L., Westbrooks, R., 1996. Biological invasions as global environmental change. Am. Sci. 84, 468–478.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of earth's ecosystems. Science 277, 494–499. https://doi.org/10.1126/science.277.5325.494

Wagner, F.H., Seal, U.S., 1992. Values, problems, and methodologies in managing overabundant wildlife populations: An overview., in: Wildlife 2001: Populations. Presented at the Wildlife 2001: Populations, Elsevier Science Publishers Ltd, Oakland, CA, pp. 279–293.

Wagner, G.P., Booth, G., Bagheri-Chaichian, H., 1997. A population genetic theory of canalization. Evolution 51, 329–347. https://doi.org/10.1111/j.1558-5646.1997.tb02420.x

Weimerskirch, H., Clobert, J., Jouventin, P., 1987. Survival in five southern albatrosses and its relationship with their life history. J. Anim. Ecol. 56, 1043. https://doi.org/10.2307/4965

White, E.F.G., Lewis, H., 1937. The greater snow goose in Canada. Auk 54, 440–444. https://doi.org/10.2307/4078135

White, E.R., Hastings, A., 2020. Seasonality in ecology: Progress and prospects in theory. Ecol. Complex. 44, 100867. https://doi.org/10.1016/j.ecocom.2020.100867

Wickham, H., 2016. ggplot2: Elegant graphics for data analysis, 2nd ed. 2016. ed, Use R! Springer International Publishing : Imprint: Springer, Cham. https://doi.org/10.1007/978-3-319-24277-4

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. J. Open Source Soft. 4, 1686. https://doi.org/10.21105/joss.01686

Witmer, G., 2022. Rodents in agriculture: A broad perspective. Agronomy 12, 6. https://doi.org/10.3390/agronomy12061458

Yparraguirre, D.R., Sanders, T.A., Weaver, M.L., Skalos, D.A., 2020. Abundance of Tule geese Anser albifrons elgasi in the Pacific flyway 2003–2019. Wildfowl 70, 27.

Zhemchuzhnikov, M.K., Versluijs, T.S.L., Lameris, T.K., Reneerkens, J., Both, C., Van Gils, J.A., 2021. Exploring the drivers of variation in trophic mismatches: A systematic review of long-term avian studies. Ecol. Evol. 11, 3710–3725. https://doi.org/10.1002/ece3.7346

Zicus, M.C., Schultz, D.F., Cooper, J.A., 1983. Canada goose mortality from neckband icing. Wildl. Soc. Bull. 11, 286–290.

Annexe S1 – **Documentation supplémentaire pour le Chapitre 1**

Annexe S1.1 **– Dates of data acquisition**

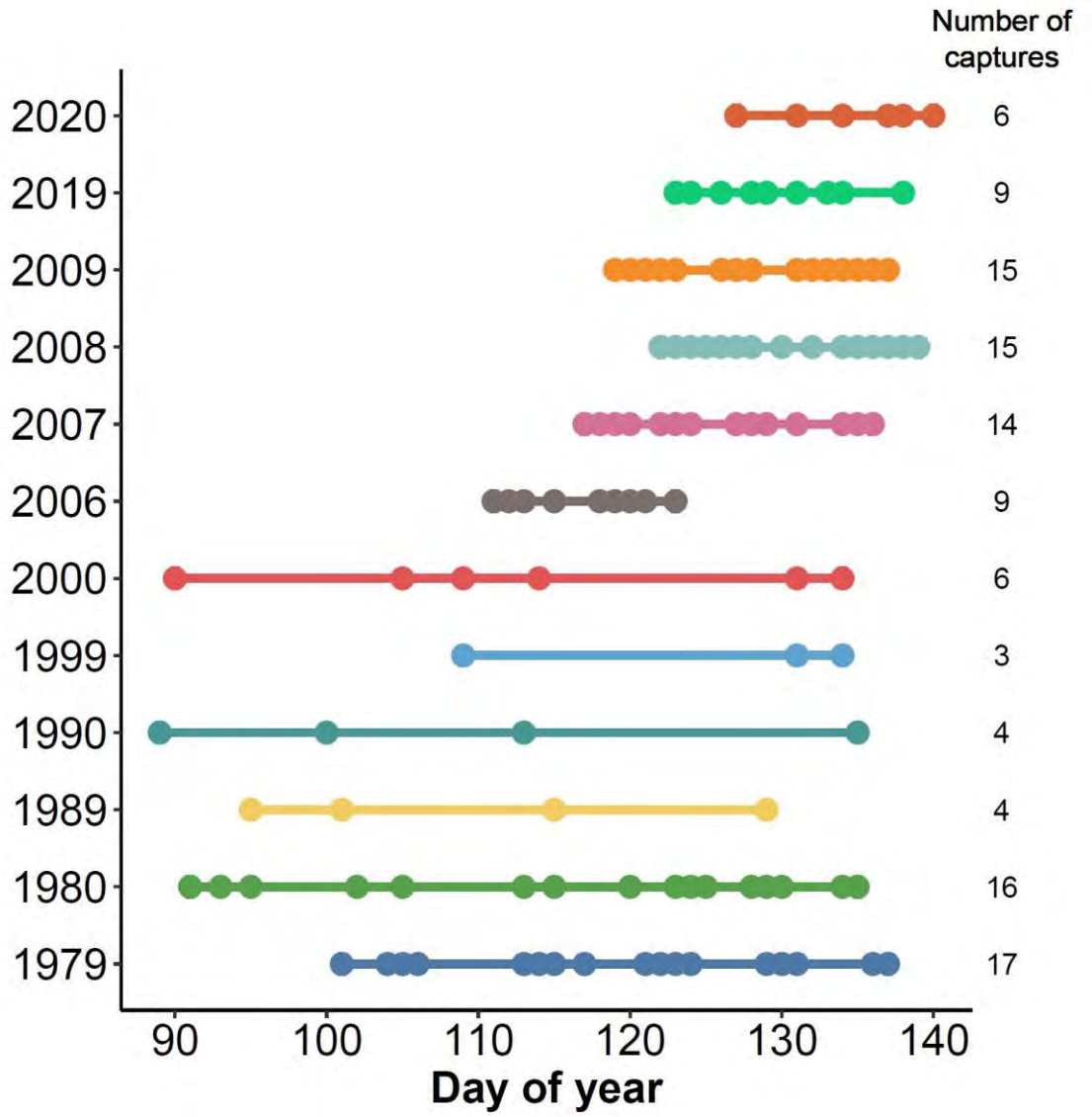

Figure S1.1 Period for which body condition data were available between 1979 and 2020. Each dot represents a day when geese were captured (i.e. one cannon-netting event). The line shows the time period between the first and the last goose captures every year.

Annexe S1.2 **– Selected model to adjust mass for the effect of date**

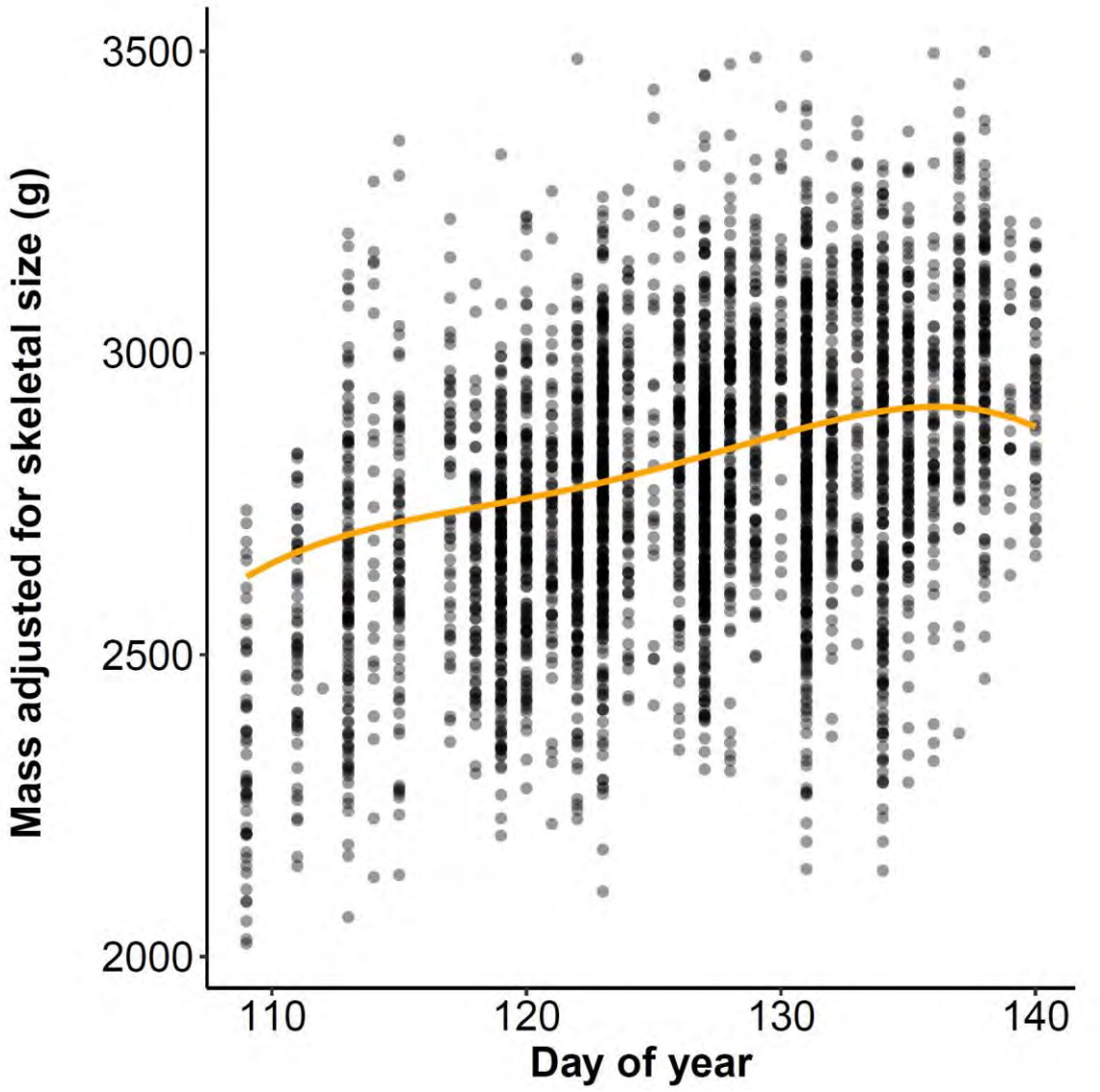

Figure S1.2 Body mass adjusted for skeletal size in relation with day of year in greater snow geese weighed between 1979 and 2020. Points represent individual body masses corrected for skeletal size. The line represents the prediction of the best polynomial regression of mass on day of year.

Annexe S1.3 **– Weather data**

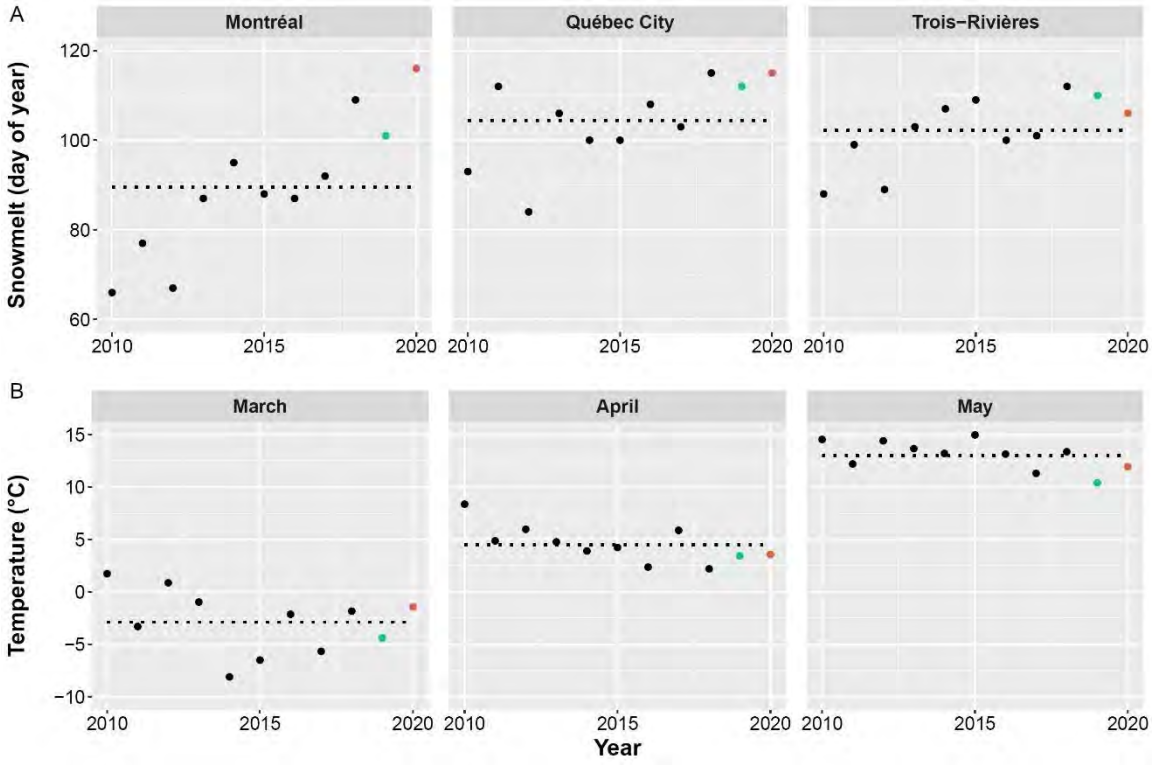

Figure S1.3 Spring weather data from three meteorological stations located in the staging area used by greater snow geese in southern Québec for 2010-2020. Years 2019 and 2020 are highlighted in green and orange, respectively. Horizontal dotted lines represent the 10-year mean. A: Annual variation in snowmelt date for three cities located along the staging area used by geese between 2010 and 2020. B: Annual variation in mean monthly temperatures of three cities located along the staging area used by geese for March, April and May. Source: https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Annexe S1.4 **– Hunting pressure metrics**

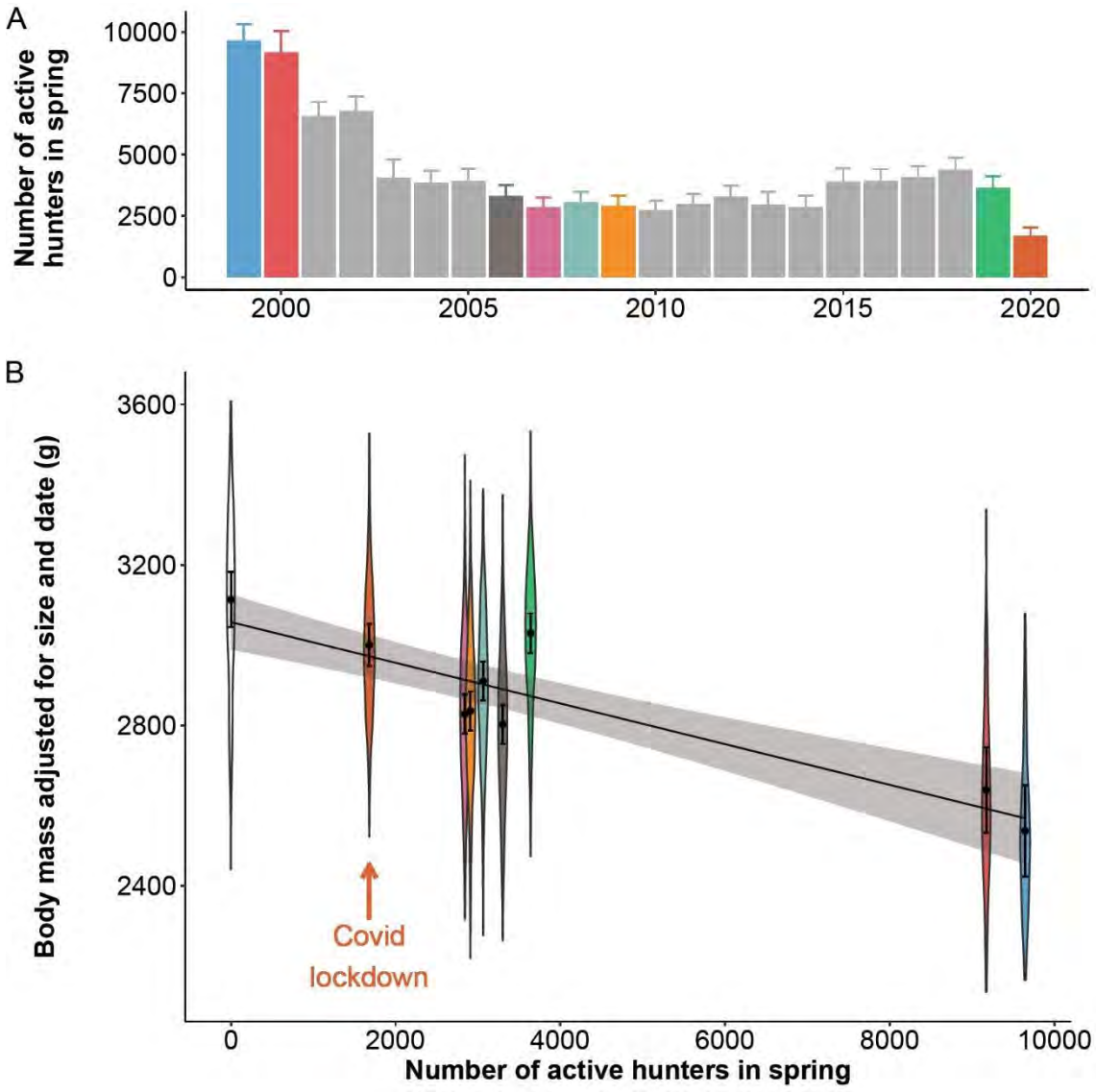

Figure S1.4 Effect of hunting pressure on goose spring body condition using number of active spring hunters. A: Annual numbers of active greater snow goose hunters in spring from 1999 to 2020. Error bars represent 95% confidence intervals. Colored bars represent years for which data on body condition is available. B: Spring body condition of geese at the end of the staging period in relation to annual number of active hunters in spring. Values at 0 active hunters (white violin) correspond to years without a spring Conservation Harvest (before 1999). The black line represents the mean model predictions based on individual data points with its 95% CI (shaded; regression slope [95%CI]: -0.05 g/active hunter [-0.07, -0.03], n = 3460). Black dots and error bars are the mean body mass with its 95% CI for each number of active hunter level and color shading represents the density distribution of individual data points. Source of hunting statistics: Smith and Gendron 2020.

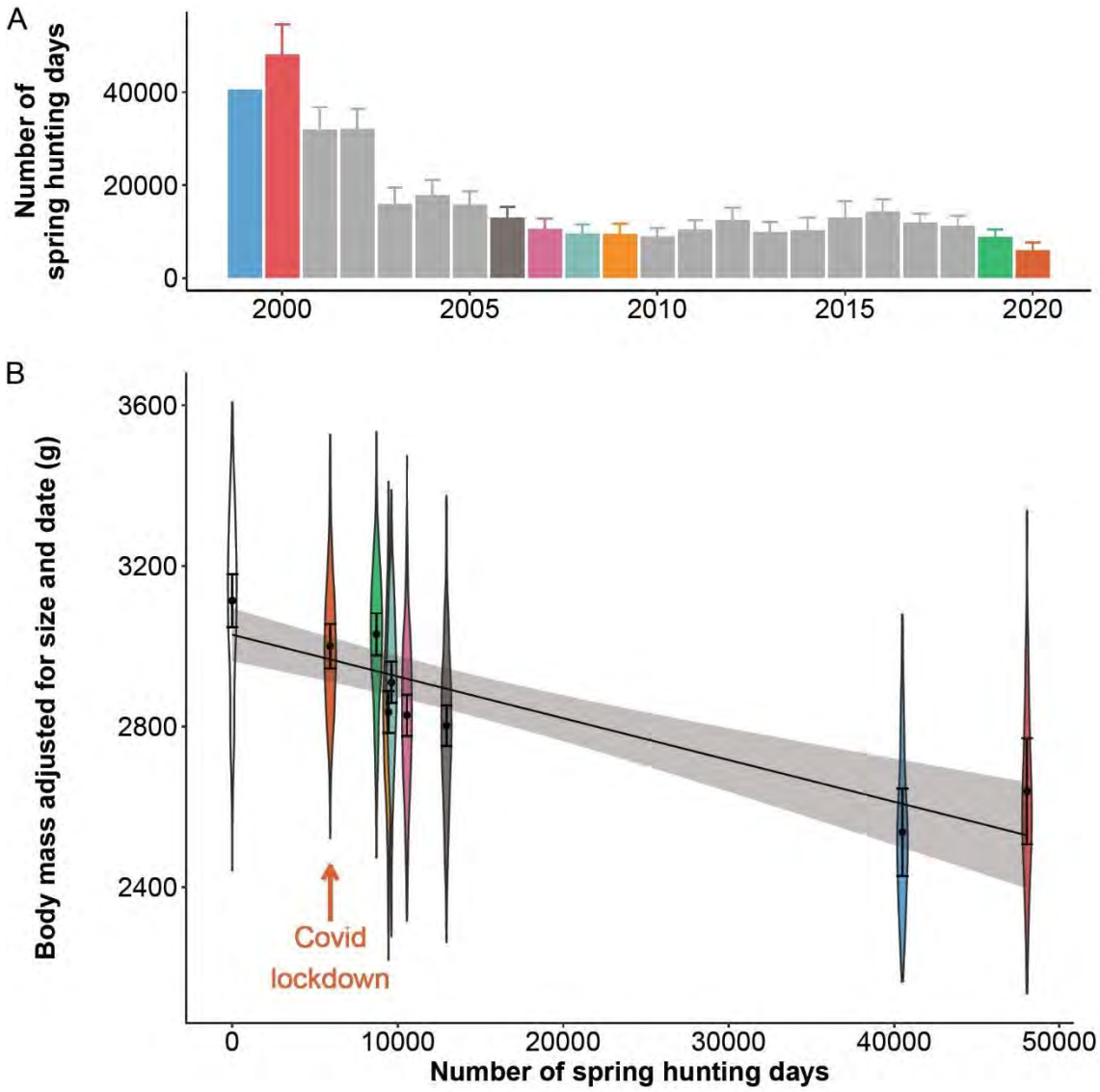

Figure S1.5 Effect of hunting pressure on goose spring body condition using number of spring hunting days. A: Annual numbers of greater snow goose hunting days in spring from 1999 to 2020. Error bars represent 95% confidence intervals. Colored bars represent years for which data on body condition is available. B: Spring body condition of geese at the end of the staging period in relation to annual number of spring hunting days. Values at 0 hunting days (white violin) correspond to years without a spring Conservation Harvest (before 1999). The black line represents the mean model predictions based on individual data points with its 95% CI (shaded; regression slope [95%CI]: -0.010[-0.014, -0.007] g/hunting day, n = 3460). Black dots and error bars are the mean body mass with its 95% CI for each number of hunting days level and color shading represents the density distribution of individual data points. Source of hunting statistics: Smith and Gendron 2020.

Bibliography

Smith, A.C., Gendron, M., 2020. Spring Snow Goose Hunt in Eastern Canada. Unpublished annual reports (1999-2020). National Wildlife Research Centre, Canadian Wildlife Service, Environment and Climate Change Canada.

Annexe S1.5 – **Analysis of habitat use for all GPS-marked birds**

When all GPS-marked geese were used (*n* = 15), the relative use of agricultural fields by geese was 0.52 [0.59, 0.44] in 2019 compared to 0.22 [0.37, 0.12] during the COVID lockdown in 2020 (Fig. S1.6).

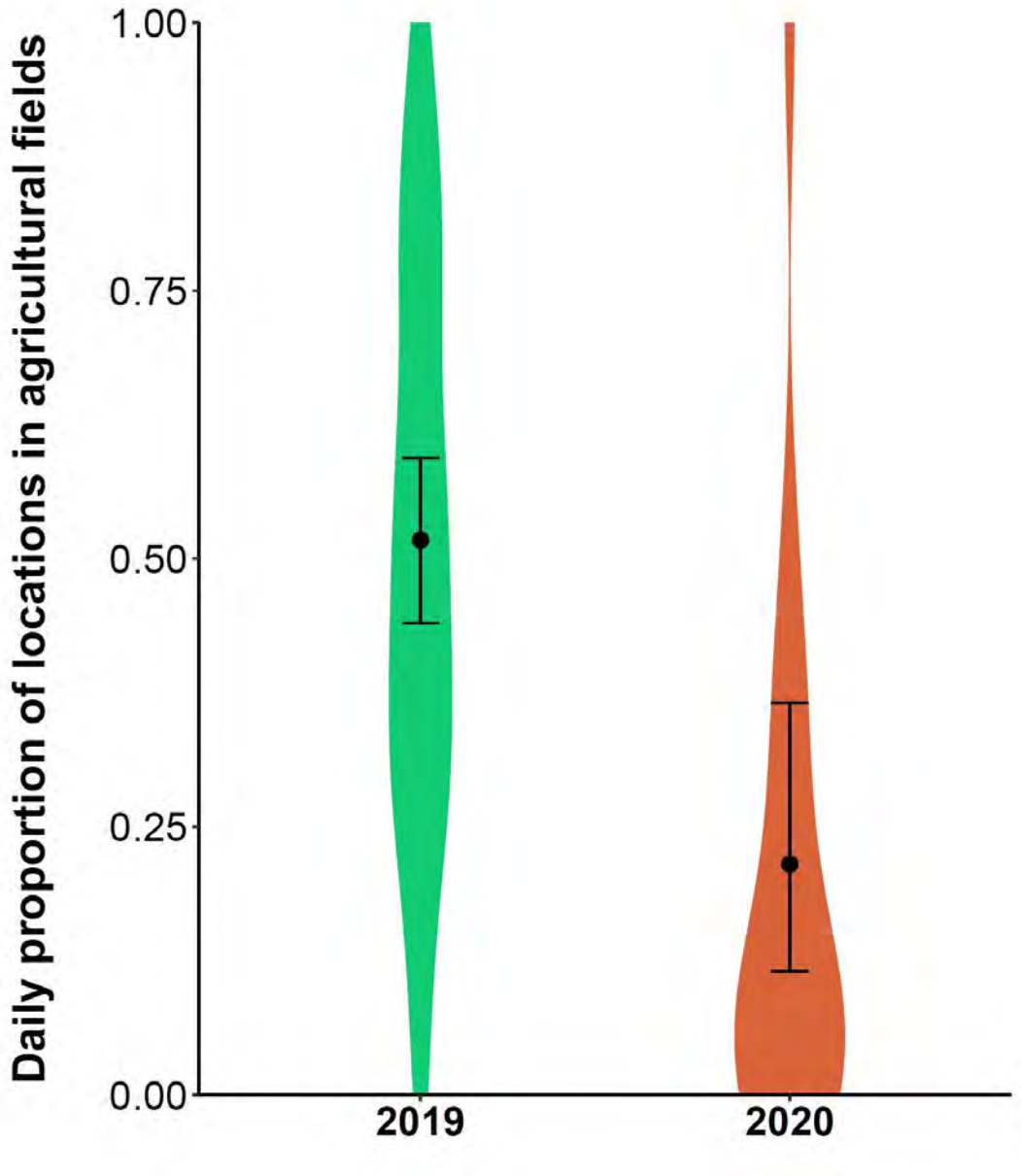

Figure S1.6 Average daily proportion of locations recorded in fields by GPS-marked geese in 2019 (*n*=10) and 2020 (*n*=5) near the end of the staging period. Error bars are 95% CI and colored shading represents the density distribution of data points.

Annexe S1.6 **– Abdominal profile scores**

S1.6.1 Methods for abdominal profile scores

In 2020, we estimated body condition of geese by scoring the shape of their abdominal profile from a distance. As geese fatten up, their abdomen bulges and this can be detected with a spotting scope at a distance. Although much coarser than body mass, abdominal profiles are non-invasive and easy to obtain which allow for larger sample size over longer sampling period. This technique was calibrated by Féret et al. (2005) for snow geese and provide a rough, but reliable index of body condition. Three observers regularly visited sites used by staging geese in southern Québec and used 20x-60x spotting scope to classify goose abdominal profiles in 11 categories based on the protocol developed by Féret et al. (2005). The three observers calibrated their scoring of abdominal profiles against each other to ensure consistency in data collection. Abdominal profile scores increased markedly in 2020 between mid-April and mid-May confirming that geese arrived in Québec in low body condition and fattened on the staging ground during the COVID19 lockdown period.

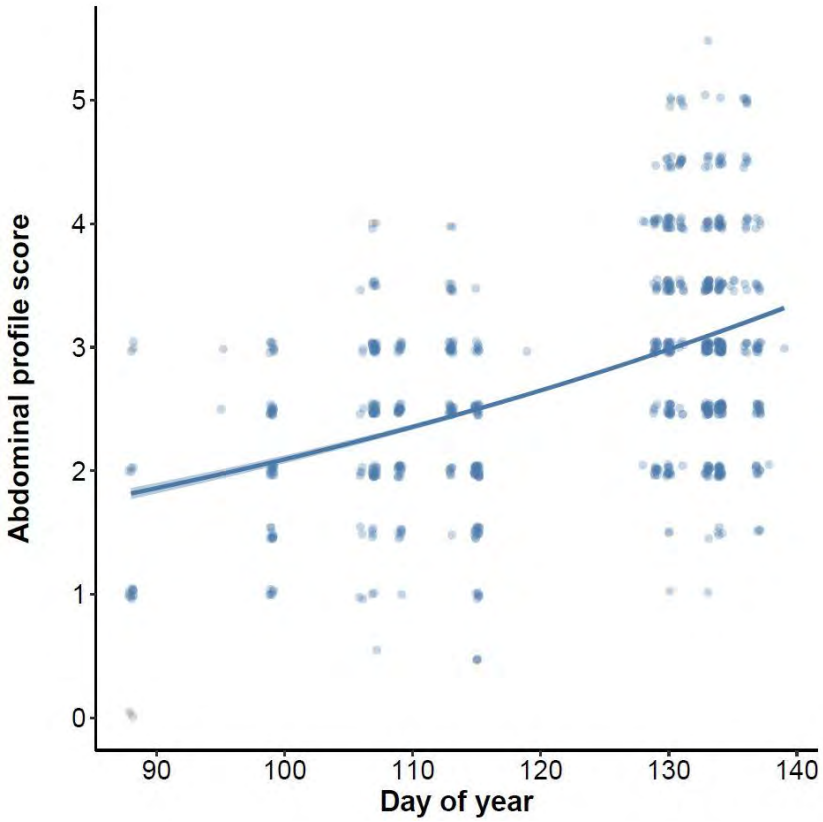

Figure S1.7 Abdominal profile scores of greater snow geese in relation with day of year during spring staging in southern Québec in 2020. Profile score increased exponentially with days (Poisson regression; day-effect estimate [95%CI] = 1.012 [1.010, 1.014]) going from an average score of 2 in early April to an average score of 3.5 in early May.

Bibliography

Féret, M., Bêty, J., Gauthier, G., Giroux, J.-F., Picard, G., 2005. Are abdominal profiles useful to assess body condition of spring staging greater snow geese? Condor 107, 694–702.

Annexe S2 – **Documentation supplémentaire pour le Chapitre 2**

Annexe S2.1 **– Supplementary figures**

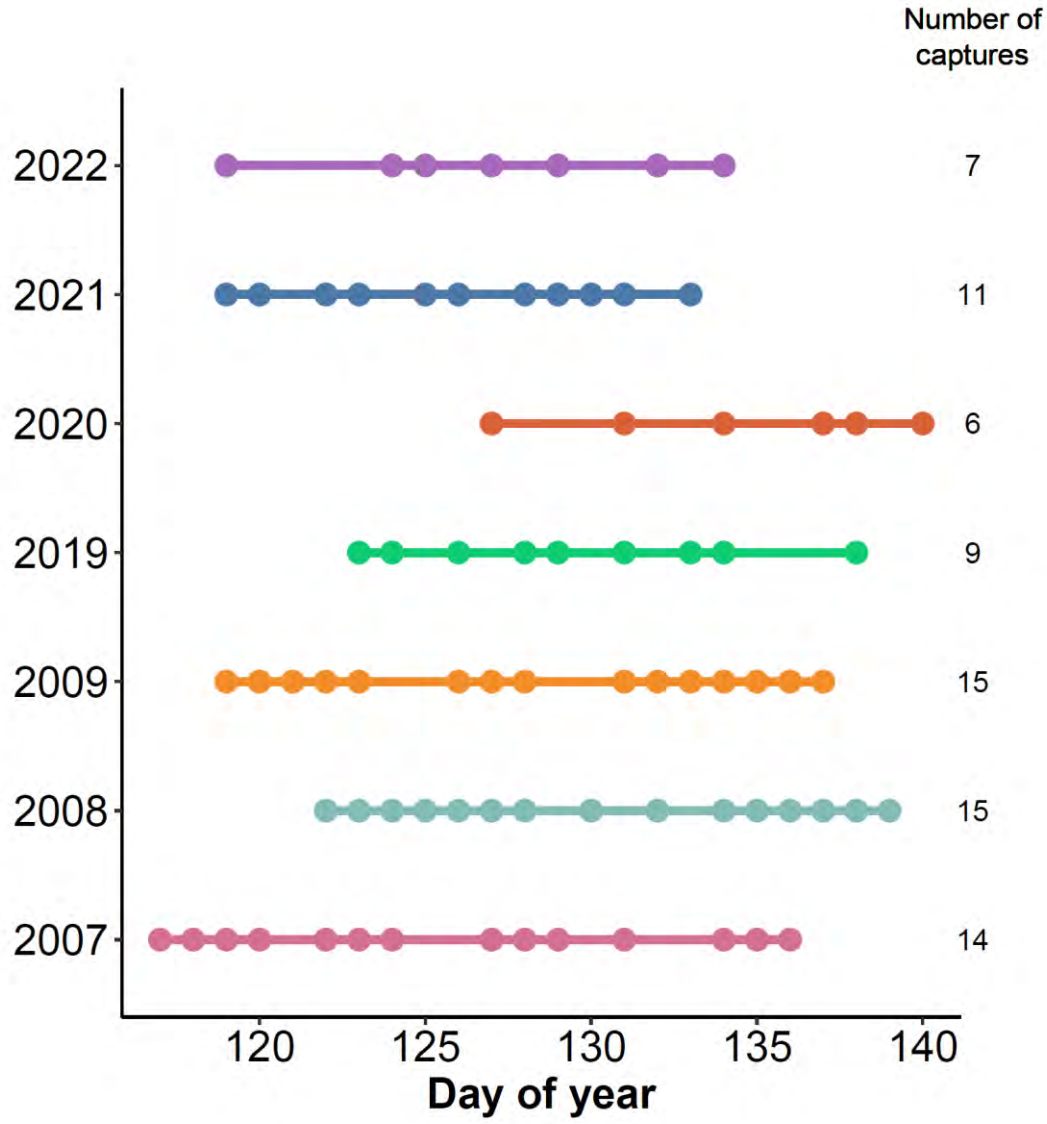

Figure S2.1 Dates when goose body condition data are available each year between 2007 and 2022. Points represent days when goose captures occurred at Île-aux-Oies, Québec, Canada. The line represents the period covered by goose captures every year.

Annexe S2.2 – Calculation of hunting effect on average annual body condition

To determine the overall effect of hunting pressure on average annual body condition of greater snow geese at the population level (i.e., excluding individual variation), we used a normal linear regression between average annual spring body condition estimates (see main text) and harvest estimates, our proxy of hunting pressure (Fig. S2.2). We accounted for uncertainty in average annual body condition and harvest estimates using a bootstrap approach. We generated 10,000 datasets of average annual body condition and spring harvest by sampling values from normal distributions defined by each annual body condition and harvest estimate and their standard errors. Mean and standard error for body condition were obtained through the analysis of our data (see main text), while mean harvest estimates and their standard errors were obtained from Smith and Gendron (2022). We ran a linear regression between annual average condition and spring harvest values derived from each simulated dataset and we calculated the mean slope and its 95% confidence interval from the distribution of the 10,000 slope estimates obtained. We used the same procedure to obtain a coefficient of determination (R^2) value along with its 95% C.I. that accounted for uncertainty in the condition and harvest estimates. We visually assessed the linear model assumption of normality of residuals.

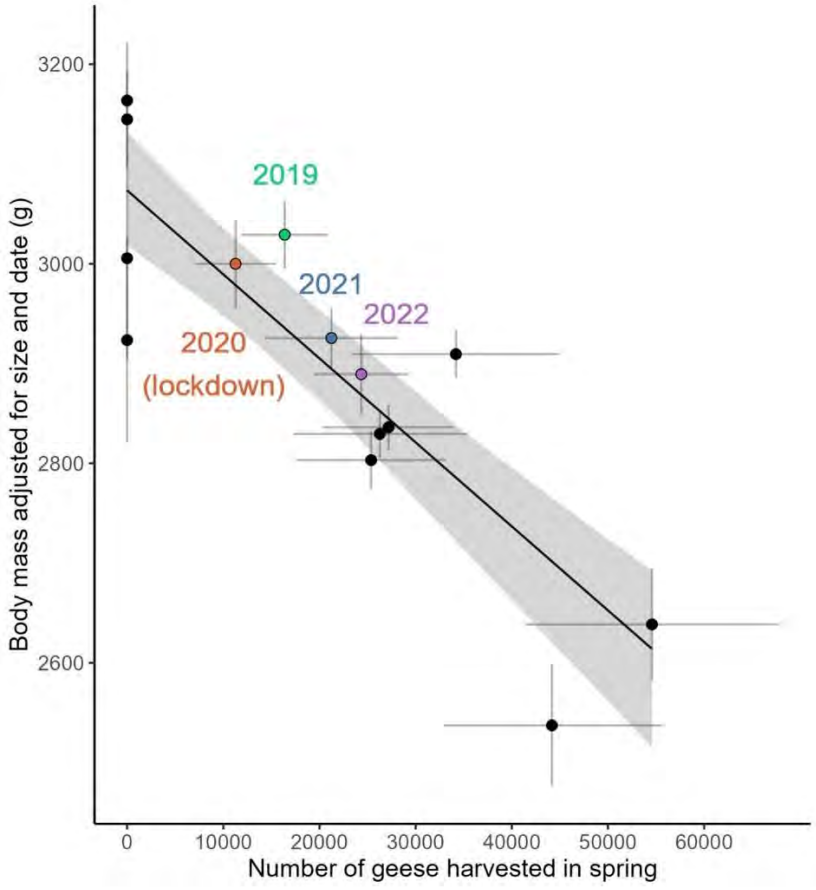

Figure S2.2 Relationship between average annual body condition of greater snow geese captured at the end of staging and yearly harvest by hunters between 1979 and 2022. Points are the average yearly condition estimates with their 95% C.I. The line represents the mean bootstrapped slope estimated from 10,000 simulations. The gray shading represents the central 95% of the bootstrapped relationships. Slope: -0.008 [-0.010, -0.006], R^2 = 0.68 [0.51, 0,83]. See above text for details on calculation of the slope value, coefficient of determination (R^2) and their respective 95% C.I. Values at 0 on the X axis correspond to years without spring hunting, before 1999.

Annexe S3 – Documentation supplémentaire pour le Chapitre 3

Annexe S3.1 – **Multievent model definition**

In multi-event capture-mark-recapture models, observations are decoupled from biological processes through events describing the different types of encounters (Pradel, 2005). In our model, there are 4 possible types of encounters that can occur at a given occasion. '1', a ringed (non-collared) individual can be physically captured; '2', a collared individual can be physically captured or sighted; '3' a marked bird can have its ring reported by a hunter; and '0', when individuals are not encountered at a given occasion. These events make up the encounter histories and the 'hidden' biological states of individuals are inferred based on these observations. We considered 7 and 9 states in our two analyses, respectively, as described below.

S3.1.1 Overall survival analysis

Seven states were considered in this analysis. 'ARH': alive with ring only and highly observable; 'ARW': alive with ring only and weakly observable; 'ACH' alive with collar and ring, and highly observable; 'ACW': alive with collar and ring, and weakly observable; 'NDR': newly dead with ring only; 'NDC': newly dead with collar and ring; 'D': dead. The distinction made between 'ARH (or ACH)' and 'ARW (or ACW)' is necessary to take into account heterogeneity in live-encounter probability (see Appendix S3.2 for details). A distinction is also made between individuals dead in the current interval from those dead earlier because the latter are no longer available to be recovered (Gauthier and Lebreton, 2008). In transition matrices, the rows are departure states and the columns represent the arrival states. There are two biological processes of interest for this model, and they are separated into two transition matrices. The first step describes collar loss, which allows accounting for heterogeneity in reporting rate due to collar loss (Juillet et al., 2011). This step involves the probability that an individual loses their collar (*C*) between year *i* and year *i+1*.

$$C^i = \begin{array}{c} \\ ARH \\ ARW \\ ACH \\ ACW \\ NDR \\ NDC \\ D \end{array} \begin{array}{c} \begin{array}{ccccccc} ARH & ARW & ACH & ACW & NDR & NDC & D \end{array} \\ \begin{bmatrix} \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 \\ \boldsymbol{C} & 0 & \mathbf{1}-\boldsymbol{C} & 0 & 0 & 0 & 0 \\ 0 & \boldsymbol{C} & 0 & \mathbf{1}-\boldsymbol{C} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{1} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \end{bmatrix} \end{array}$$

In this step, an individual wearing a collar can lose it and become a non-collared individual. Upon loss of their collars, individuals remain highly or weakly observable depending on their initial state.

The second step is the transition matrix describing survival:

$$S^i = \begin{array}{c} \\ ARH \\ ARW \\ ACH \\ ACW \\ NDR \\ NDC \\ D \end{array} \begin{array}{c} \begin{array}{ccccccc} ARH & ARW & ACH & ACW & NDR & NDC & D \end{array} \\ \begin{bmatrix} \boldsymbol{S} & 0 & 0 & 0 & \mathbf{1}-\boldsymbol{S} & 0 & 0 \\ 0 & \boldsymbol{S} & 0 & 0 & \mathbf{1}-\boldsymbol{S} & 0 & 0 \\ 0 & 0 & \boldsymbol{S}' & 0 & 0 & \mathbf{1}-\boldsymbol{S}' & 0 \\ 0 & 0 & 0 & \boldsymbol{S}' & 0 & \mathbf{1}-\boldsymbol{S}' & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \end{bmatrix} \end{array}$$

Here we note that the survival probability is independent of whether an individual is highly- or weakly-observable. However, a distinct survival probability is estimated for collared (*S'*) and non-collared birds (*S*). Also, individuals

dying during the previous interval ('newly dead'; NDR or NDC) transition into the absorbing 'dead' state (D), becoming unavailable for further encounter.

Finally, the event matrix (E) links the underlying states (rows) to the observations (columns). A bird can be physically recaptured (1) with probabilities *p* in state 'Alive with ring only and highly observable (ARH)' or *p** in state 'Alive with ring only and weakly observable (ARW)'. Similarly, a collared bird can be physically recaptured or re-sighted during the breeding season (2) with probabilities *p'* in state 'Alive with collar and ring, and highly observable (ACH)' or *p'** in state 'Alive with collar and ring, and weakly observable (ACW)'. Finally, a bird can be recovered with probability *r* in the state 'newly dead with ring only (NDR)' or *r'* in the state 'newly dead with collar and ring (NDC)'.

$$E^i = \begin{array}{c} \\ ARH \\ ARW \\ ACH \\ ACW \\ NDR \\ NDC \\ D \end{array} \begin{array}{c} \begin{array}{cccc} 0 & 1 & 2 & 3 \end{array} \\ \begin{bmatrix} \mathbf{1-p} & \mathbf{p} & 0 & 0 \\ \mathbf{1-p^*} & \mathbf{p^*} & 0 & 0 \\ \mathbf{1-p'} & 0 & \mathbf{p'} & 0 \\ \mathbf{1-p'^*} & 0 & \mathbf{p'^*} & 0 \\ \mathbf{1-r} & 0 & 0 & \mathbf{r} \\ \mathbf{1-r'} & 0 & 0 & \mathbf{r'} \\ \mathbf{1} & 0 & 0 & 0 \end{bmatrix} \end{array}$$

S3.1.2 Partitioning of mortality between hunting and natural sources

In the second analysis, we separated our 'newly dead' states into 'newly dead from hunting' (NDHR – rings only, and NDHC – collars) and 'newly dead from natural causes' (NDNR and NDNC). This required adding a third step in the transition matrices. The first step was again to estimate collar loss (*C*). In the second step, we estimate the hunting mortality probability and finally, the third step describes the non-hunting mortality process, which represents mortality from sources other than hunting.

With the addition of the two new states, the collar loss transition matrix is now as follows.

$$C^i = \begin{array}{c} \\ ARH \\ ARW \\ ACH \\ ACW \\ NDNR \\ NDNC \\ NDHR \\ NDHC \\ D \end{array} \begin{array}{c} \begin{array}{ccccccccc} ARH & ARW & ACH & ACW & NDNR & NDNC & NDHR & NDHC & D \end{array} \\ \begin{bmatrix} \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \mathbf{1} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \boldsymbol{C} & 0 & \mathbf{1-C} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \boldsymbol{C} & 0 & \mathbf{1-C} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \end{bmatrix} \end{array}$$

The second step now represents the hunting mortality process, with a different probability for birds with rings only (*h*) and those with a collar (*h'*):

$$HM^i = \begin{array}{c} \\ ARH \\ ARW \\ ACH \\ ACW \\ NDNR \\ NDNC \\ NDHR \\ NDHC \\ D \end{array} \begin{array}{c} \begin{array}{ccccccccc} ARH & ARW & ACH & ACW & NDNR & NDNC & NDHR & NDHC & D \end{array} \\ \begin{bmatrix} \mathbf{1-h} & 0 & 0 & 0 & 0 & 0 & \mathbf{h} & 0 & 0 \\ 0 & \mathbf{1-h} & 0 & 0 & 0 & 0 & \mathbf{h} & 0 & 0 \\ 0 & 0 & \mathbf{1-h'} & 0 & 0 & 0 & 0 & \mathbf{h'} & 0 \\ 0 & 0 & 0 & \mathbf{1-h'} & 0 & 0 & 0 & \mathbf{h'} & 0 \\ 0 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \end{bmatrix} \end{array}$$

Finally, the third transition step describes the process for mortality from sources other than hunting, again with a different probability for birds with rings only (*n*) and those with a collar (*n*'):

$$NM^i = \begin{array}{c} \\ ARH \\ ARW \\ ACH \\ ACW \\ NDNR \\ NDNC \\ NDHR \\ NDHC \\ D \end{array} \begin{array}{c} \begin{array}{ccccccccc} ARH & ARW & ACH & ACW & NDNR & NDNC & NDHR & NDHC & D \end{array} \\ \begin{bmatrix} \mathbf{1-n} & 0 & 0 & 0 & \mathbf{n} & 0 & 0 & 0 & 0 \\ 0 & \mathbf{1-n} & 0 & 0 & \mathbf{n} & 0 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{1-n'} & 0 & 0 & \mathbf{n'} & 0 & 0 & 0 \\ 0 & 0 & 0 & \mathbf{1-n'} & 0 & \mathbf{n'} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \\ 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \mathbf{1} \end{bmatrix} \end{array}$$

Here, individuals that have survived to hunters have a probability n (or *n*') of dying from sources other than hunting.

Finally, the event matrix linking the observations to the states for this model is:

$$E^i = \begin{array}{c} \\ ARH \\ ARW \\ ACH \\ ACW \\ NDNR \\ NDNC \\ NDHR \\ NDHC \\ D \end{array} \begin{array}{c} \begin{array}{cccc} 0 & 1 & 2 & 3 \end{array} \\ \begin{bmatrix} \mathbf{1-p} & \mathbf{p} & 0 & 0 \\ \mathbf{1-p^*} & \mathbf{p^*} & 0 & 0 \\ \mathbf{1-p'} & 0 & \mathbf{p'} & 0 \\ \mathbf{1-p^{*\prime}} & 0 & \mathbf{p^{*\prime}} & 0 \\ \mathbf{1} & 0 & 0 & 0 \\ \mathbf{1} & 0 & 0 & 0 \\ \mathbf{1-r} & 0 & 0 & \mathbf{r} \\ \mathbf{1-r'} & 0 & 0 & \mathbf{r'} \\ \mathbf{1} & 0 & 0 & 0 \end{bmatrix} \end{array}$$

Here, we note that birds that die from non-hunting causes can never be observed because we have no information about individuals that died except for hunter-shot birds whose rings were recovered.

Bibliography

Gauthier, G., Lebreton, J.-D., 2008. Analysis of band-recovery data in a multistate capture-recapture framework. Can. J. Stat. 36, 59–73. https://doi.org/10.1002/cjs.5550360107

Juillet, C., Choquet, R., Gauthier, G., Pradel, R., 2011. A capture–recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss. J. Agric. Biol. Environ. Stat. 16, 88–104. https://doi.org/10.1007/s13253-010-0035-5

Pradel, R., 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics 61, 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Annexe S3.2 **– Harvest rate estimation**

Greater snow geese are hunted during the regular hunting season in eastern Canada in fall and in the USA in winter. The number of geese harvested annually during these regular seasons is estimated through a standard hunter survey conducted in both countries. In Canada, it is estimated with the Harvest Questionnaire Survey and the Species Composition Survey conducted by the Canadian Wildlife Service, and in the USA with the Migratory Bird Harvest Information Program conducted by the US Fish and Wildlife Service (Lefebvre et al., 2017). We used the total number of snow geese harvested in eastern Ontario and Quebec for Canada and in the Atlantic Flyway states for the USA. A special hunter survey was implemented by the Canadian Wildlife Service starting in 1999 to estimate the number of snow geese harvested during the spring hunting season (the Conservation Harvest) in Quebec. Similarly, the Atlantic Flyway Committee implemented a special hunter survey starting in 2009 to estimate the number of snow geese harvested during the Conservation Order in the USA. The estimated number of geese harvested during these special hunting seasons were added to those harvested during the regular hunting season in order to estimate the total annual harvest.

The population size estimate used in the calculation of the harvest rate came from the aerial spring survey of the greater snow goose population conducted annually in Quebec. The survey is conducted when the whole population is concentrated along the St. Lawrence River staging area in Quebec. The whole staging area is overflown on a single day and all flocks encountered are photographed. Geese are subsequently counted on these photos, which yields a highly accurate survey (see details in Béchet et al., 2004). To estimate the adult fall population size, we multiplied the spring population estimate by 0.96, the estimated survival rate during summer (Gauthier et al., 2001). Fall population size, which excluded young of the year produced during the summer, was used as the denominator in our calculation of annual harvest rate.

Bibliography

Béchet, A., Reed, A., Plante, N., Giroux, J.-F., Gauthier, G., 2004. Estimating the size of the greater snow goose population. J. Wildl. Manage. 68, 639–649. https://doi.org/10.2193/0022-541X(2004)068[0639:ETSOTG]2.0.CO;2

Gauthier, G., Pradel, R., Menu, S., Lebreton, J.-D., 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology 82, 3105–3119. https://doi.org/10.2307/2679838

Lefebvre, J., Gauthier, G., Giroux, J.-F., Reed, A., Reed, E.T., Bélanger, L., 2017. The greater snow goose Anser caerulescens atlanticus: Managing an overabundant population. Ambio 46, 262–274. https://doi.org/10.1007/s13280-016-0887-1

Annexe S3.3 **– Goodness-of-fit tests**

S3.3.1 Goodness-of-fit test results

In our goodness-of-fit (GOF) tests, we found that both test 3G (mostly associated with survival or transience effects) and test M (mostly associated with a trap dependence effect) were highly significant (Table S3.1). A detailed analysis of the contingency tables associated to the test M revealed that, on average, individuals missed (i.e. not captured) at a given occasion were generally less re-encountered alive at subsequent occasions than individuals that were captured on that occasion. This suggests heterogeneity in live-encounter probability in our dataset (i.e. some individuals are more capturable or observable than others), something that can be explained by our marking scheme. Since females exhibit fidelity to nesting and brood-rearing sites (Lecomte et al., 2008), individuals that regularly nest or rear their young in the core of the area covered by our ringing activity should be more likely to be observed and recaptured than those on the edge of this area.

Test 3G was also highly significant but Jeyam et al. (2018) have shown that the presence of heterogeneity in live-encounter probabilities can lead to a significant Test 3 even in the absence of heterogeneity in survival or transience effects. To verify this hypothesis, we simulated ten 30-year capture-recapture datasets with heterogeneity in live-encounter probability. We simulated two unbalanced groups with a different live-encounter probability but with the same probabilities of survival (0.85) and recovery (0.3). We simulated 1000 individuals marked annually with 80 % of individuals exhibiting a low live-encounter probability (0.25) and the remaining 20% a high live-encounter probability (0.5). GOF for these datasets were subsequently conducted in U-CARE (Choquet et al., 2009). Similarly to our original data, we found that the Test 3G was significant for all simulated datasets despite an absence of survival or transience effect in the simulated datasets. We conclude that the transient effect detected by test 3G in our original data is likely an artifact of the heterogeneity in live-encounter probabilities among birds.

S3.3.2 Accounting for heterogeneity in live-encounter probability

To account for heterogeneity in live-encounter probability, we split the state 'Alive with ring only' of Juillet et al. (2011) into 'Alive with ring only and highly encounterable' and 'Alive with ring only and weakly encounterable' (states ARH and ARW in Appendix S3.1). The same was done for bird marked with collars, which were split into states ACH and ACW (Appendix S3.1). This allowed us to estimate a different live-encounter probability for birds belonging to each group. Although we have no a-priori information on which group, highly or weakly encounterable, a bird belongs to when it is originally captured, the multievent framework used in this study is a natural tool to analyze such a dataset. This framework was developed by Pradel (2005) precisely for assigning individuals to groups when this information is unknown at the time of encounter (i.e., uncertainty in state assignment).

S3.3.3 $\hat{c}$ calculation

Our overall variance inflation factor ($\hat{c}$) can be calculated by dividing the overall χ^2 statistic from our GOF tests by the degrees of freedom associated to this test ($\hat{c}$ = 2087.37/1299 = 1.607, Table S3.1). However, this value needed to be adjusted for the added complexity of our model structure (i.e., introduction of highly and weakly observable states), which captured overdispersion linked to heterogeneity in live-encounter probabilities. To do so, we conducted a Likelihood Ratio Test (LRT) between two versions of our most general model, one including heterogeneity in live-encounter probabilities (model M1 in Table 3.1) and the other without. The LRT between models with and without heterogeneity is simply the difference in their deviance. It follows an approximated chi-square distribution with the difference in number of parameters between models as its degrees of freedom. A GOF test for the heterogeneity model can then be obtained by discounting the LRT statistic from the GOF of the model without heterogeneity. Its number of degrees of freedom is similarly obtained by subtracting the number of degrees of freedom of the LRT from that of the original GOF test. The calculation of our adjusted $\hat{c}$ was thus:

$$\hat{c}_{adj} = \frac{{\chi^2}_0 - (DEV_0 - DEV_g)}{df_0 - (np_g - np_0)}$$

Where: ${\chi^2}_0$ is the overall χ^2 test statistic from the GOF test of the most general model without heterogeneity,

DEV_0 is the deviance of the most general model without heterogeneity,

DEV_g is the deviance of the most general model with heterogeneity,

df_0 is the degrees of freedom of the χ^2 from the GOF test of the model without heterogeneity,

np_g is the number of parameters of the most general model with heterogeneity and,

np_0 is the number of parameters of the most general model without heterogeneity.

The statistics of two models used for this calculation (deviance and np) are presented in Table S3.2. This yielded an adjusted *ĉ* of 1.256 (1556.08/1239), which was used for our modelling.

Table S3.1 Multi-state goodness-of-fit test and variance inflation factors calculated for our dataset of adult female greater snow geese marked from 1990 to 2018 on Bylot Island. Test 3G examines homogeneity in survival between newly marked and previously marked individuals while test M verifies homogeneity of re-encounter between captured and missed individuals on each occasion. For each test component, chi-squared test statistic (χ^2), degrees of freedom (df) and p-values (*p*) are provided. *Overall ĉ* is the overall variance inflation factor and *Adjusted ĉ* is the variance inflation factor adjusted for inclusion of heterogeneity in live-encounter probabilities (see text).

Test component	χ^2	df	*p*
Test 3G.Sr	142.82	56	<0.001
Test 3G.Sm	623.91	435	<0.001
Test M.ITEC	529.05	788	<0.001
Test M.LTEC	772.87	592	<0.001
Overall test	2087.37	1299	<0.001
Overall ***ĉ***		1.607	
Adjusted ***ĉ***		1.256	

Table S3.2 Results of the general model with and without heterogeneity in live-encounter probabilities. Both models have the same structure for collar loss, survival, live-encounter and dead recovery probabilities than model M1 (Table 3.1) except for heterogeneity on live-encounters.

Model	NP	Deviance
With heterogeneity in live-encounter probabilities (M1)	237	118119.73
Without heterogeneity in live-encounter probabilities	177	118651.02

Bibliography

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., Pradel, R., 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. Ecography 32, 1071–1074. https://doi.org/10.1111/j.1600-0587.2009.05968.x

Jeyam, A., McCrea, R.S., Bregnballe, T., Frederiksen, M., Pradel, R., 2018. A test of positive association for detecting heterogeneity in capture for capture–recapture data. J. Agric. Biol. Environ. Stat. 23, 1–19. https://doi.org/10.1007/s13253-017-0315-4

Juillet, C., Choquet, R., Gauthier, G., Pradel, R., 2011. A capture–recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss. J. Agric. Biol. Environ. Stat. 16, 88–104. https://doi.org/10.1007/s13253-010-0035-5

Lecomte, N., Gauthier, G., Giroux, J.-F., 2008. Breeding dispersal in a heterogeneous landscape: the influence of habitat and nesting success in greater snow geese. Oecologia 155, 33–41. https://doi.org/10.1007/s00442-007-0860-6

Pradel, R., 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics 61, 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Annexe S3.4 **– Encounter probabilities**

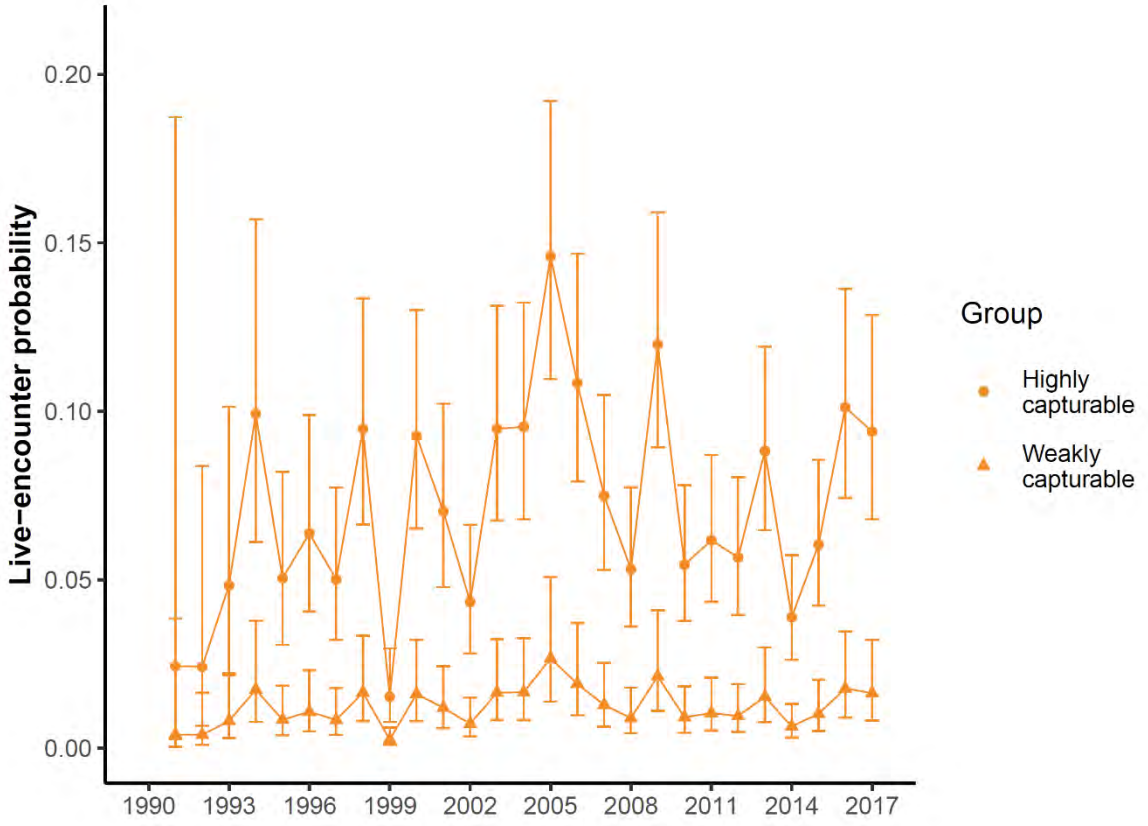

Figure S3.1 Point estimates of encounter probabilities (physical recaptures) of non-collared adult female greater snow geese marked between 1990 and 2016 and encountered from 1991 to 2017 on Bylot Island, Nunavut. Error bars are 95% C.I. Estimates were obtained from model M14 (Table 3.1).

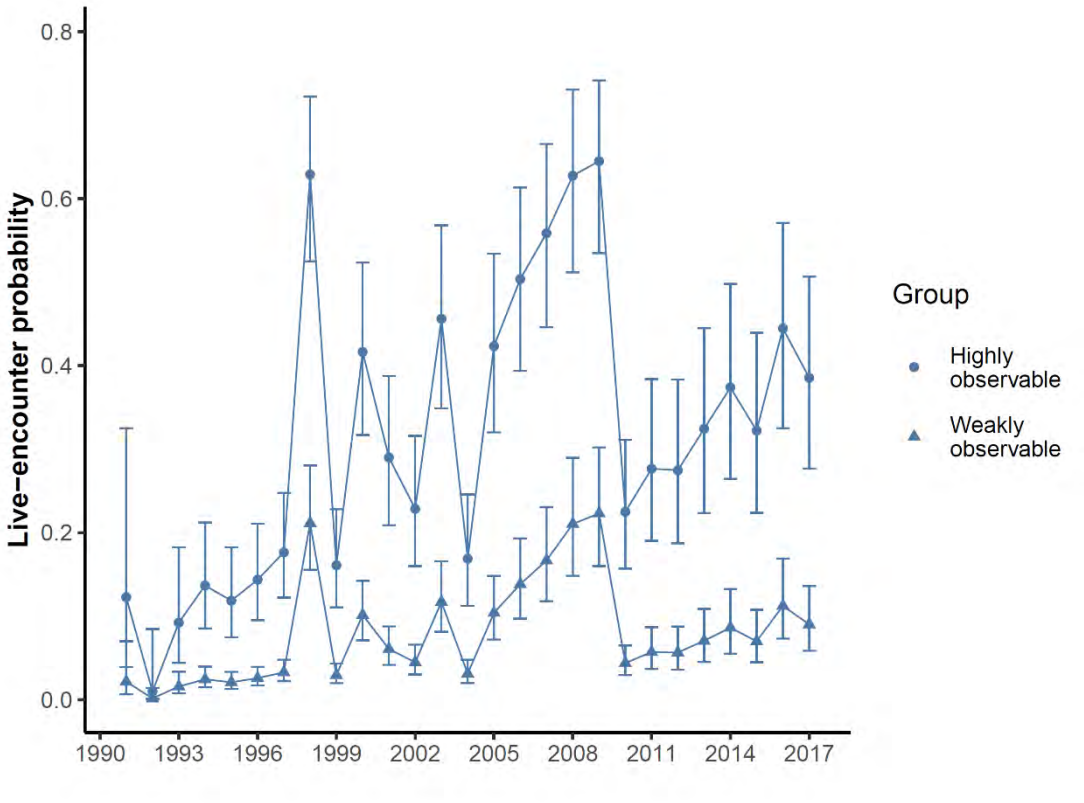

Figure S3.2 Point estimates of encounter probabilities (physical recaptures and resighting) of adult female greater snow geese marked with collars between 1990 and 2016 and encountered from 1991 to 2017 on Bylot Island, Nunavut. Error bars are 95% C.I. Estimates were obtained from model M14 (Table 3.1).

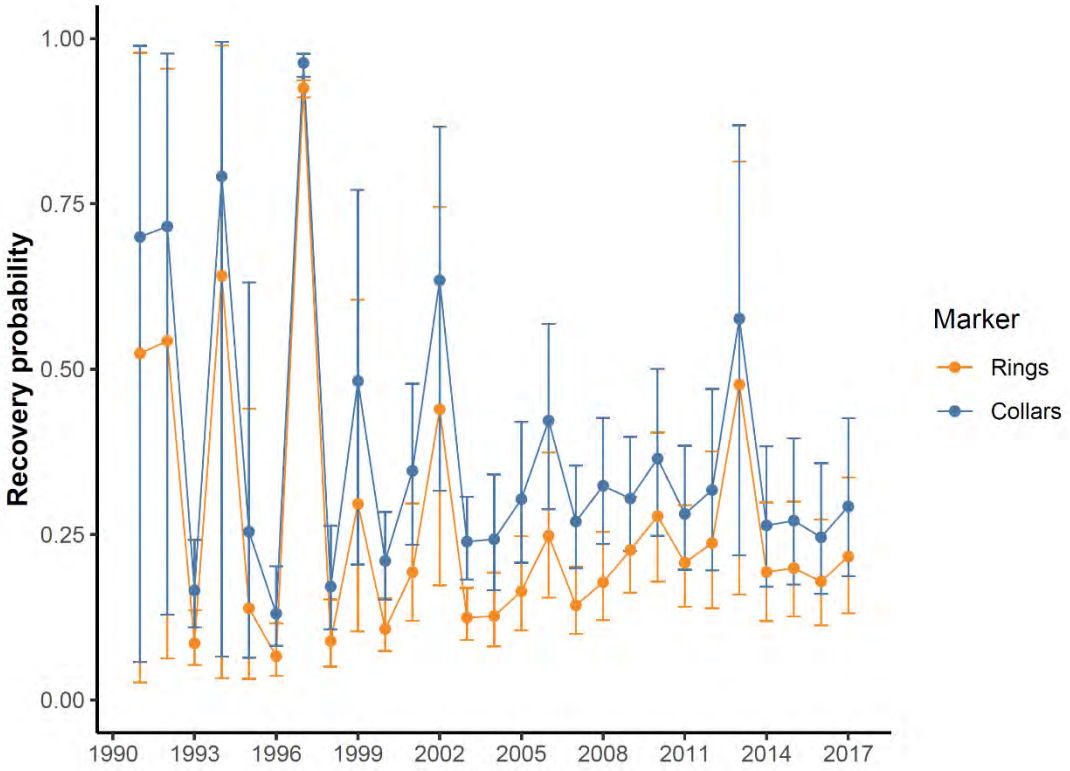

Figure S3.3 Point estimates of hunting recovery probabilities of adult female greater snow geese marked between 1990 and 2016 on Bylot Island, Nunavut and recovered from 1990 to 2017. Error bars are 95% C.I. Estimates were obtained from model M14 (Table 3.1).

Annexe S3.5 **– E-SURGE syntax for model M14 (Table 3.1)**

Initial settings – Data
Number of occasions: 30
Number of states: 7
Number of events: 4
Number of groups: 1
Number of age classes: 4

Initial settings – Options
Link function = Generalized Logit
Overdispersion coefficient = 1.256

Model matrices – Gepat file

```
%%%% VERSION 2.0 %%%%%%
3
%%%% Initial state %%%%%%
1
1 6 IS
p p p * - -
%%%% Transition %%%%%%
2
7 7 C
* - - - - - -
- * - - - - -
y - * - - - -
y y - * - - -
- - - - * - -
- - - - - * -
- - - - - - *
7 7 S
S - - - * - -
- S - - * - -
- - S - - * -
- - - S - * -
- - - - - - *
- - - - - - *
- - - - - - *
%%%% Event  %%%%%%
1
7 4 E
* b - -
* b - -
* - b -
* - b -
* - - b
* - - b
* - - -
```

Model Definition – GEMACO

Initial state (3 parameters)

```
to
```

Transition

- STEP 1 (collar loss) *(3 parameters)*

```
a(1,2:3,4)
```

- STEP 2 (Survival) *(31 parameters)*

```
t+t(9:18,19:27).f(3 4)
```

Event (93 parameters)

```
firste+nexte.[f(1 2).[f(2)+t]+f(3 4).[f(4)+t]+f(5 6).t+
f(6).t(2:9,10:19,20:30)]
```

IVFV (Initial Values and Fixed Values)

Fixed values: Event

```
Beta #38 = 1
```

Annexe S3.6 **– Complete model selection tables**

Table S3.3 Complete set of models tested for the analysis of collar loss, survival, and live- and dead-encounter probabilities in adult female greater snow geese marked between 1990 and 2018. For each model, deviance, number of estimated parameters (NP) and difference in QAIC (ΔQAIC) with the most parsimonious model (M13) are provided. Models already present in Table 3.1 are identified by their names in column 'Name'.

#	Name	Collar loss	Survival	Encounter			NP	Deviance	ΔQAIC
				Ring	Collar	Dead			
1	M1	a	t . col	t . g	t . g	t . col	237	118119.73	97.52
2		a	t . col	t . g	t . g	t	209	118218.20	119.92
3	M2	a	t . col	t . g	t . g	$t + col$	210	118161.02	76.39
4		a	t . col	t . g	t	$t + col$	181	118418.98	223.78
5		a	t . col	t	t . g	$t + col$	180	118260.05	95.24
6	M3	a	t . col	$t + g$	t . g	$t + col$	183	118193.30	48.09
7	M4	a	t . col	$t + g$	$t + g$	$t + col$	156	118237.61	27.37
8	M5	i	t . col	$t + g$	$t + g$	$t + col$	152	118267.49	45.16
9		$a_{1,2:4}$	t . col	$t + g$	$t + g$	$t + col$	153	118265.80	45.82
10	M6	$a_{1,2:3,4}$	t . col	$t + g$	$t + g$	$t + col$	154	118237.77	25.50
11		$a_{1:3,4}$	t . col	$t + g$	$t + g$	$t + col$	153	118244.93	29.20
12	M7	$a_{1,2:3,4}$	t	$t + g$	$t + g$	$t + col$	125	118388.79	87.74
13	M8	$a_{1,2:3,4}$	$t + col$	$t + g$	$t + g$	$t + col$	126	118307.25	24.82
14	M9	$a_{1,2:3,4}$	$t + d$. col	$t + g$	$t + g$	$t + col$	128	118279.72	6.90
15	M10	$a_{1,2:3,4}$	$t + d_3$. col	$t + g$	$t + g$	$t + col$	126	118311.04	27.83
16	M11	$a_{1,2:3,4}$	$t + d_{2:3}$. col	$t + g$	$t + g$	$t + col$	126	118295.74	15.65
17		$a_{1,2:3,4}$	$d_1 + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	103	118371.72	30.15
18	M12	$a_{1,2:3,4}$	d . col	$t + g$	$t + g$	$t + col$	104	118371.72	32.15
19		$a_{1,2:3,4}$	d	$t + g$	$t + g$	$t + col$	101	118471.00	105.19
20	M13	$a_{1,2:3,4}$	$t + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	127	118280.80	5.75
21		$a_{1,2:4,5}$	$t + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	127	118284.93	9.05
22		$a_{1,2:5,6}$	$t + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	127	118288.63	11.99
23		$a_{1,2:6,7}$	$t + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	127	118293.36	15.76
24		$a_{1,2:3,4}$	$t + d_{2,3}$. col	t	$t + g$	$t + col$	125	118353.20	59.40
25		$a_{1,2:3,4}$	$t + d_{2,3}$. col	$t + g$	t	$t + col$	126	118502.21	180.04
26		$a_{1,2:3,4}$	$t + d_{2,3}$. col	$t + g$	$t + g$	t	126	118394.61	94.37
27		$a_{1,2:3,4}$	$t + d_{2,3}$. col	$t + g$	$t + g$	col	99	118393.67	39.62
28		a - 4 classes	$t + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	128	118280.68	7.66
29		a - 5 classes	$t + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	129	118279.80	8.96
30		a - 6 classes	$t + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	130	118279.02	10.34
31		a - 7 classes	$t + d_{2,3}$. col	$t + g$	$t + g$	$t + col$	131	118278.78	12.15
32	**M14**	$\boldsymbol{a_{1,2:3,4}}$	$\boldsymbol{t + d_{2,3}}$ **.** $\boldsymbol{col}$	$\boldsymbol{t + g}$	$\boldsymbol{t + g}$	$\boldsymbol{t + col}$ **.** $\boldsymbol{d}$	**129**	**118268.54**	**0.00**
33	M15	$a_{1,2:3,4}$	$t + d$. col	$t + g$	$t + g$	$t + col$. d	130	118266.82	0.63

34	M16	$a_{1,2:3,4}$	*t + col*	*t + g*	*t + g*	*t + col . d*	128	118295.31	21.31
35	M17	$a_{1,2:3,4}$	*d . col*	*t + g*	*t + g*	*t + col . d*	106	118360.19	26.97
36	M18	$a_{1,2:3,4}$	$d_1 + d_{2,3}$ *. col*	*t + g*	*t + g*	*t + col . d*	105	118360.23	25.00

Note: *a*, age effect; *t*, time effect; *col*, collar effect; *g*, heterogeneity in encounter probability (groups with high and low encounter probability); *i*, constant; *d,* time effect reduced to three periods (1: before special hunting regulations; 2: special hunting regulations in Canada only; 3: special hunting regulations in Canada and the USA); '+', additive effect; '.', interaction. Notation for indices: ':' denotes a parameter constrained equal for two periods or age classes; ',' denotes a parameter varying between periods or age classes.

Table S3.4 Complete set of models tested for the analysis of hunting and natural mortality probabilities in adult female greater snow geese marked between 1990 and 2018. Constraints on collar loss were identical to model M14 in Table 3.1. For each model, deviance, number of estimated parameters (NP) and difference in QAIC (ΔQAIC) with the most parsimonious model (P10) are provided.

Name	Mortality		Encounter			NP	Deviance	ΔQAIC
	Hunting	Non-hunting	Ring	Collar	Dead			
P24	*HR + $d_{2:3}$. col*	*t + d_3 . col*	*t + g*	*t + g*	*t + col . d*	132	118267.86	0.00
P10	***HR + $d_{2:3}$. col***	***t + d_3 . col***	***t + g***	***t + g***	***t + col***	**129**	**118276.33**	**0.74**
P23	*HR + $d_{2:3}$. col*	*t + $d_{2,3}$. col*	*t + g*	*t + g*	*t + col . d*	133	118267.72	1.89
P9	*HR + $d_{2:3}$. col*	*t + $d_{2,3}$. col*	*t + g*	*t + g*	*t + col*	130	118276.09	2.56
P15	*HR + $d_{2,3}$. col*	*t + $d_{2,3}$. col*	*t + g*	*t + g*	*t + col*	131	118273.61	2.58
P25	*HR + $d_{2,3}$. col*	*t + $d_{2,3}$. col*	*t + g*	*t + g*	*t + col . d*	134	118266.10	3.31
P5	*HR + d . col*	*t + d . col*	*t + g*	*t + g*	*t + col*	133	118270.30	3.95
P11	*HR + col*	*t + d_3 . col*	*t + g*	*t + g*	*t + col*	129	118281.18	4.61
P22	*HR + d . col*	*t + d . col*	*t + g*	*t + g*	*t + col . d*	136	118264.86	5.61
P12	*HR + col*	*t + d . col*	*t + g*	*t + g*	*t + col*	131	118279.44	7.22
P20	*HR + $d_{2:3}$. col*	*t + d_3 . col*	*t + g*	*t + g*	*t*	128	118297.96	15.97
P7	*HR*	*t + d . col*	*t + g*	*t + g*	*t + col*	130	118296.48	18.79
P4	*HR + d . col*	*t + col*	*t + g*	*t + g*	*t + col*	131	118294.20	18.97
P8	*HR + $d_{2,3}$. col*	*t + $d_{2,3}$. col*	*t + g*	*t + g*	*t*	130	118296.88	19.10
P13	*HR*	*t + $d_{2,3}$. col*	*t + g*	*t + g*	*t + col*	129	118303.69	22.52
P1	*HR + d . col*	*t . col*	*t + g*	*t + g*	*t + col*	159	118237.24	29.62
P14	*HR + $d_{2,3}$. col*	*t*	*t + g*	*t + g*	*t + col*	129	118314.54	31.17
P6	*HR + d . col*	*t*	*t + g*	*t + g*	*t + col*	130	118313.95	32.70
P3	*HR + d . col*	*t . col*	*t + g*	*t + g*	*t*	158	118250.49	38.17
P17	*HR + d . col*	*i*	*t + g*	*t + g*	*t + col*	102	118392.49	39.23
P2	*HR + d . col*	*t . col*	*t + g*	*t + g*	*t . col*	182	118207.91	52.27
P18	*HR + $d_{2:3}$. col*	*t + d_3 . col*	*t*	*t + g*	*t + col*	127	118352.00	56.99
P16	*HR + $d_{2,3}$. col*	*t + $d_{2,3}$. col*	*t + g*	*t + g*	*col*	103	118492.57	120.91
P21	*HR + $d_{2:3}$. col*	*t + d_3 . col*	*t + g*	*t + g*	*col*	101	118533.36	149.39

Note: *HR*, harvest rate covariate; *d,* time effect reduced to three periods (1: before special hunting regulations; 2: special hunting regulations in Canada only; 3: special hunting regulations in Canada and the USA); *col*, collar effect; *t*, time effect; *g*, heterogeneity in encounter probability (groups with high and low encounter probability); *i*, constant; '+', additive effect; '.', interaction; notation for indices: ':' denotes a parameter constrained equal for two periods; ',' denotes a parameter varying for two periods.

Annexe S4 – Documentation supplémentaire pour le Chapitre 4

Annexe S4.1 **– Multievent model definition**

In multi-event capture-mark-reencounter models, the biological states of individuals are decoupled from their observations, allowing the assignment of one or more biological states to a same observation 'event' (or encounter; Pradel, 2005). LeTourneux et al. (2022) developed a model that took into account differences in catchability of individuals on the summer breeding grounds (i.e., heterogeneity in encounter probability) observed in this species. Here, we expand this model to account for heterogeneity in live encounter in multiple seasons, which was detected in our dataset (see Appendix S4.2). We consider 4 types of encounters in our model, with some that can occur only in particular seasons. '1' is for a leg-ringed-only bird physically captured on the breeding grounds during the summer only. '2' is for a collared bird observed in any season or physically captured on the breeding grounds during the summer. '3' is for a bird shot and reported by hunters, which can happen in fall, winter and, after 1999, in the spring season as well. Finally, '0' is for a bird that is not encountered.

S4.1.1 Modelling heterogeneity in live-encounter probability

The model of LeTourneux et al. (2022) considered 7 distinct states. A bird Alive with Ring only can be Highly encounterable (state ARH) or Weakly encounterable (ARW). Similarly, and a bird Alive with a Collar can also be Highly (ACH) or Weakly encounterable (ACW). Birds that died in the interval between occasions *t* and *t+1* are in the states Newly Dead with Ring only or Newly Dead with Collar at occasion *t+1* (states NDR and NDC, respectively). At the next occasion, all newly dead birds transition to an absorbing Dead state (state D), which is unobservable and ensures that individuals encountered dead are not contributing to the likelihood beyond the occasion when they are recovered (Gauthier and Lebreton, 2008). In the case of collared individuals that can be encountered alive at all seasons, we cannot assume that individuals highly observable in one season will also be highly observable in other seasons as well (see Appendix S4.3). We account for this by splitting the ACH and ACW states in summer into two new states each for birds highly and weakly observable during fall. Thus, Highly observable collared birds during summer are split into 'Alive with Collar, Highly observable summer, Highly observable fall' (ACHH) and 'Alive with Collar, Highly observable summer, Weakly observable fall' (ACHW). Similarly, weakly observable birds during summer are split into two groups, one highly observable in fall and one weakly observable in fall, yielding the states ACWH and ACWW. Each of these four states are then split in two more states for birds that are highly and weakly observable in winter, and the same is subsequently done for the spring season, yielding at the end 16 states 'Alive with Collar'.

The live-encounter probabilities of the 8 states representing individuals with a high encounter probability in a given season are constrained equal regardless of their previous history. For instance, in winter, we group the following states: ACHHHH, ACHHHW, ACHWHH, ACHWHW, ACWHHH, ACWHHW, ACWWHH, ACWWHW, or all those that have the letter 'H' in the 5th position of the state abbreviation. They represent a group of birds that is highly encounterable in winter but can either be highly or weakly encounterable in the other 3 seasons. In the state abbreviations, the letters in positions 3 to 6 represent the observability group an individual belongs to in summer, fall, winter and spring, respectively. For the sake of simplicity, we assume that the proportion of birds transitioning to either the highly or weakly observable state in the following season is independent of their observability in the current season (i.e., probabilities (*l*) of the initial state matrices below are constant across departure states). Furthermore, we do not allow transitions between these encounterability states between years, thereby forcing individuals belonging to an observability class in a given season to remain in that class for that season over the whole study period. This applies only to collared birds as ringed-only individuals can only be encountered alive during the summer occasion.

The multievent framework developed by Pradel (2005) accommodates datasets where state assignation is uncertain as is the case here (i.e. there is no a-priori information on whether an individual belongs to the highly or weakly observable category in each season). In multievent models, there are three types of matrices, each defining different processes. The first type is the initial state matrix (δ), which defines the states of individuals when initially marked. In our model, the probability that individuals belong to each 'encounterability' group (*l*) is

determined through the initial state matrix. The four steps of that matrix define the probability that individuals belonging to a high or low encounter group become part of a high or low encounter group at each subsequent season. Hence, the first step defines the probabilities that individuals belong to the high or low encounter group in the summer for leg-ringed-only birds (l_{su} and l^*_{su}, respectively) and collared birds (l'_{su} and $1 - (l_{su} + l^*_{su} + l'_{su})$), the second step the probability for fall (l'_f), the third step for winter (l'_w) and the fourth step for spring (l'_{sp}). Steps 2 to 4 define these probabilities for collared birds only because leg-ringed-only birds can not be observed alive outside of the summer occasion. Matrices for these four steps are defined as follow:

(Note that to simplify the presentation, only Alive with collar states are shown in matrix δ_4 since transitions between the other states (ARH, ARW, NDR, NDC and D) are identical to those of matrix δ_3).

$$\delta_1 = \begin{array}{cccccccc} ARH & ARW & ACH & ACW & NDR & NDC & D \\ I_{su} & I^*_{su} & I'_{su} & 1-(I_{su}+I^*_{su}+I'_{su}) & 0 & 0 & 0 \end{array}$$

$$\delta_2 = \begin{array}{c|ccccccccc} & ARH & ARW & ACH\boldsymbol{H} & ACH\boldsymbol{W} & ACW\boldsymbol{H} & ACW\boldsymbol{W} & NDR & NDC & D \\ ARH & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ARW & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ AC\boldsymbol{H} & 0 & 0 & I'_f & 1-I'_f & 0 & 0 & 0 & 0 & 0 \\ AC\boldsymbol{W} & 0 & 0 & 0 & 0 & I'_f & 1-I'_f & 0 & 0 & 0 \\ NDR & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ NDC & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ D & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

$$\delta_3 = \begin{array}{c|ccccccccccccc} & ARH & ARW & ACHH\boldsymbol{H} & ACHH\boldsymbol{W} & ACHW\boldsymbol{H} & ACHW\boldsymbol{W} & ACWH\boldsymbol{H} & ACWH\boldsymbol{W} & ACWW\boldsymbol{H} & ACWW\boldsymbol{W} & NDR & NDC & D \\ ARH & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ARW & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACH\boldsymbol{H} & 0 & 0 & I'_w & 1-I'_w & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACH\boldsymbol{W} & 0 & 0 & 0 & 0 & I'_w & 1-I'_w & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACW\boldsymbol{H} & 0 & 0 & 0 & 0 & 0 & 0 & I'_w & 1-I'_w & 0 & 0 & 0 & 0 & 0 \\ ACW\boldsymbol{W} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I'_w & 1-I'_w & 0 & 0 & 0 \\ NDR & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ NDC & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ D & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

$$\delta_4 = \begin{array}{c|cccccccccccccccc} & ACHHH\boldsymbol{H} & ACHHH\boldsymbol{W} & ACHHW\boldsymbol{H} & ACHHW\boldsymbol{W} & ACHWH\boldsymbol{H} & ACHWH\boldsymbol{W} & ACHWW\boldsymbol{H} & ACHWW\boldsymbol{W} & ACWHH\boldsymbol{H} & ACWHH\boldsymbol{W} & ACWHW\boldsymbol{H} & ACWHW\boldsymbol{W} & ACWWH\boldsymbol{H} & ACWWH\boldsymbol{W} & ACWWW\boldsymbol{H} & ACWWW\boldsymbol{W} \\ ACHH\boldsymbol{H} & I'_{sp} & 1-I'_{sp} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACHH\boldsymbol{W} & 0 & 0 & I'_{sp} & 1-I'_{sp} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACHW\boldsymbol{H} & 0 & 0 & 0 & 0 & I'_{sp} & 1-I'_{sp} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACHW\boldsymbol{W} & 0 & 0 & 0 & 0 & 0 & 0 & I'_{sp} & 1-I'_{sp} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACWH\boldsymbol{H} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I'_{sp} & 1-I'_{sp} & 0 & 0 & 0 & 0 & 0 & 0 \\ ACWH\boldsymbol{W} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I'_{sp} & 1-I'_{sp} & 0 & 0 & 0 & 0 \\ ACWW\boldsymbol{H} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I'_{sp} & 1-I'_{sp} & 0 & 0 \\ ACWW\boldsymbol{W} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I'_{sp} & 1-I'_{sp} \end{array}$$

The second type of matrix is the transition matrix, which describes ecological processes of interest, in our case the probabilities of collar loss and survival. The transition matrix is decomposed in two steps, one for each of these processes. The collar loss matrix defines the probability that an individual wearing a collar and a leg-ring loses its collar (*C*), which allows heterogeneity in reporting rate due to collar loss (Juillet et al., 2011). This matrix is:

$$C^t = \begin{array}{c|cccccccccccccc} & ARH & ARW & ACHHHH & ACHHHW & ACHHWH & ACHHWW & \dots & ACWWHH & ACWWHW & ACWWWH & ACWWWW & NDR & NDC & D \\ ARH & 1 & 0 & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ARW & 0 & 1 & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACHHHH & C & 0 & 1-C & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACHHHW & C & 0 & 0 & 1-C & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACHHWH & C & 0 & 0 & 0 & 1-C & 0 & & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ ACHHWW & C & 0 & 0 & 0 & 0 & 1-C & & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \vdots & \vdots & & & & & & \ddots & & & & & & & \vdots \\ ACWWHH & 0 & C & 0 & 0 & 0 & 0 & & 1-C & 0 & 0 & 0 & 0 & 0 & 0 \\ ACWWHW & 0 & C & 0 & 0 & 0 & 0 & & 0 & 1-C & 0 & 0 & 0 & 0 & 0 \\ ACWWWH & 0 & C & 0 & 0 & 0 & 0 & & 0 & 0 & 1-C & 0 & 0 & 0 & 0 \\ ACWWWW & 0 & C & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 1-C & 0 & 0 & 0 \\ NDR & 0 & 0 & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ NDC & 0 & 0 & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ D & 0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Here, a bird that loses its collar remains highly- or weakly-encounterable during summer based on whether they were initially highly- or weakly-encounterable during the summer occasion, regardless of their encounterability in the other seasons. This is because birds wearing only a leg-ring can only be encountered alive during the summer occasion. The second step of the transition matrix defines survival probabilities (*S*) between *t* and *t+1*.

Survival differs between collared individuals (*S*') and leg-ringed-only birds (*S*) but is independent of whether a bird is highly- or weakly-encounterable. Ringed-only and collared birds dying between *t* and *t+1* enter the NDR and NDC states, respectively. All newly dead birds transition to the permanent dead absorbing state (D) at the next interval where they become unavailable for encounter.

$$S^t = \begin{array}{c|cccccccccccccc} & ARH & ARW & ACHHHH & ACHHHW & ACHHWH & ACHHWW & \dots & ACWWHH & ACWWHW & ACWWWH & ACWWWW & NDR & NDC & D \\ ARH & S & 0 & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 1-S & 0 & 0 \\ ARW & 0 & S & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 1-S & 0 & 0 \\ ACHHHH & 0 & 0 & S' & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 1-S' & 0 \\ ACHHHW & 0 & 0 & 0 & S' & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 1-S' & 0 \\ ACHHWH & 0 & 0 & 0 & 0 & S' & 0 & & 0 & 0 & 0 & 0 & 0 & 1-S' & 0 \\ ACHHWW & 0 & 0 & 0 & 0 & 0 & S' & & 0 & 0 & 0 & 0 & 0 & 1-S' & 0 \\ \vdots & \vdots & & & & & & \ddots & & & & & & & \vdots \\ ACWWHH & 0 & 0 & 0 & 0 & 0 & 0 & & S' & 0 & 0 & 0 & 0 & 1-S' & 0 \\ ACWWHW & 0 & 0 & 0 & 0 & 0 & 0 & & 0 & S' & 0 & 0 & 0 & 1-S' & 0 \\ ACWWWH & 0 & 0 & 0 & 0 & 0 & 0 & & 0 & 0 & S' & 0 & 0 & 1-S' & 0 \\ ACWWWW & 0 & 0 & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & S' & 0 & 1-S' & 0 \\ NDR & 0 & 0 & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ NDC & 0 & 0 & 0 & 0 & 0 & 0 & & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\ D & 0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

Finally, the third type of matrix is the event matrix (Ω), which links the observations (events, columns) to the states of individuals (rows). This matrix is also implemented in two steps to allow a different recovery probability for ringed and collared birds. The first step contains the observation probabilities of individuals that are encountered alive with a leg-ring (*p*) or a collar (*p'*), and the recovery probabilities of collared birds encountered dead (*r*). Asterisks denote live encounter probabilities of weakly-encounterable individuals (*p**, *p'**). Constraints are used on observation probabilities of matrix Ω_1 so that all groups that are highly or weakly encounterable in one season share the same observation probability. For the sake of simplicity, we only show two versions of this matrix, one for the summer and one for the winter, but matrices for the fall and spring are adjusted accordingly.

$$\Omega^1_{summer} = \begin{array}{c|ccccc} & '0' & '1' & '2' & NDR & '3' \\ ARH & 1-p & p & 0 & 0 & 0 \\ ARW & 1-p^* & p^* & 0 & 0 & 0 \\ AC\boldsymbol{H}HHH & 1-p' & 0 & p' & 0 & 0 \\ AC\boldsymbol{H}HHW & 1-p' & 0 & p' & 0 & 0 \\ AC\boldsymbol{H}HWH & 1-p' & 0 & p' & 0 & 0 \\ AC\boldsymbol{H}HWW & 1-p' & 0 & p' & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \\ AC\boldsymbol{W}WHH & 1-p'^* & 0 & p'^* & 0 & 0 \\ AC\boldsymbol{W}WHW & 1-p'^* & 0 & p'^* & 0 & 0 \\ AC\boldsymbol{W}WWH & 1-p'^* & 0 & p'^* & 0 & 0 \\ AC\boldsymbol{W}WWW & 1-p'^* & 0 & p'^* & 0 & 0 \\ NDR & 1-r & 0 & 0 & r & 0 \\ NDC & 1-r & 0 & 0 & 0 & r \\ D & 1 & 0 & 0 & 0 & 0 \end{array}$$

$$\Omega^1_{winter} = \begin{array}{c|ccccc} & '0' & '1' & '2' & NDR & '3' \\ ARH & 1 & 0 & 0 & 0 & 0 \\ ARW & 1 & 0 & 0 & 0 & 0 \\ ACHH\boldsymbol{H}H & 1-p' & 0 & p' & 0 & 0 \\ ACHH\boldsymbol{H}W & 1-p' & 0 & p' & 0 & 0 \\ ACHH\boldsymbol{W}H & 1-p'^* & 0 & p'^* & 0 & 0 \\ ACHH\boldsymbol{W}W & 1-p'^* & 0 & p'^* & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \\ ACWW\boldsymbol{H}H & 1-p' & 0 & p' & 0 & 0 \\ ACWW\boldsymbol{H}W & 1-p' & 0 & p' & 0 & 0 \\ ACWW\boldsymbol{W}H & 1-p'^* & 0 & p'^* & 0 & 0 \\ ACWW\boldsymbol{W}W & 1-p'^* & 0 & p'^* & 0 & 0 \\ NDR & 1-r & 0 & 0 & r & 0 \\ NDC & 1-r & 0 & 0 & 0 & r \\ D & 1 & 0 & 0 & 0 & 0 \end{array}$$

A second and last step of the event matrix is introduced to fully define the recovery probability of ringed-only individuals, while other encounter probabilities remain identical. In this step, parameter *b* is introduced to ensure that recovery probability of leg-ringed-only birds (*r*) do not exceed that of collared birds. Recovery probability for leg-ringed-only birds is obtained by the product *r* * *b* (see Appendix S4.4 for details).

$$\Omega_2 = \begin{array}{c|cccc} & '0' & '1' & '2' & '3' \\ '0' & 1 & 0 & 0 & 0 \\ '1' & 0 & 1 & 0 & 0 \\ '2' & 0 & 0 & 1 & 0 \\ NDR & 1-b & 0 & 0 & b \\ '3' & 0 & 0 & 0 & 1 \end{array}$$

The capture histories, E-SURGE model definition and initial values for our most parsimonious model are publicly available on Dryad, along with R scripts and associated data to reproduce all figures. (LeTourneux F, Gauthier G, Pradel R, Lefebvre J, Legagneux P. 2024. Data from: Evidence for seasonal compensation of hunting mortalities in a long-lived migratory bird [Dataset]. Dryad. https://doi.org/10.5061/dryad.x95x69pt7).

Bibliography

Gauthier, G., Lebreton, J.-D., 2008. Analysis of band-recovery data in a multistate capture-recapture framework. Can. J. Stat. 36, 59–73. https://doi.org/10.1002/cjs.5550360107

Juillet, C., Choquet, R., Gauthier, G., Pradel, R., 2011. A capture–recapture model with double-marking, live and dead encounters, and heterogeneity of reporting due to auxiliary mark loss. J. Agric. Biol. Environ. Stat. 16, 88–104. https://doi.org/10.1007/s13253-010-0035-5

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

Pradel, R., 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics 61, 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Annexe S4.2 **– Discrete analysis of continuous live encounter data**

One assumption of CMR models is that live encounters occur during discrete encounter occasions separated by relatively long intervals (Hargrove and Borland, 1994). The condition of no or negligible mortality over the course of relatively short encounter occasions is then reasonable. However, when encounter occasions are spread out over longer periods (e.g., a few months), this increases the risk of introducing heterogeneity in live encounter probabilities because individuals that die during an encounter occasion are no longer available to be encountered alive for the same period of time compared to individuals that survive the until the end. Therefore, individuals dying during the encounter "occasion" are not exposed to being observed for the whole period of time, which reduces their live encounter probability compared to individuals that survive. Although this can theoretically bias survival estimates, studies have found that using continuous live encounter data for periods up to 6 months did not significantly bias survival estimations and actually increased their precision (O'Brien et al., 2005). In our dataset, another potential issue with lengthy encounter occasions is that individuals do not all migrate at the same time, creating a situation where, for short periods, some individuals can be encountered at a certain location (i.e., an encounter occasion in our sampling scheme) while others have migrated and left the area and thus cannot be encountered there anymore. This could also lead to heterogeneous encounter probabilities between individuals because again they are not all exposed to being encountered for the same amount of time at a given occasion.

We examined if these violations of assumptions could bias our estimates using simulations. More specifically, we tested whether the introduction of heterogeneity in live encounter probabilities from either (1) the use of continuous and relatively long live encounter occasions or (2) different migration schedules between individuals could bias our survival estimates. We generated 200 datasets where the observation and survival processes were simulated on a weekly basis, allowing individuals to be observed and subsequently die during the same season (i.e., occasion). We also introduced a migration process where individuals had an increasing probability of migrating to the next location (i.e., occasion) as they came closer to the end of the current occasion. We adjusted the weekly migration and survival probabilities so that the seasonal distribution of simulated collar observations and recoveries was similar to our real dataset (Figure S4.1). Finally, we also introduced individual heterogeneity in live encounter probabilities (see Appendices S4.1 and S4.3) by simulating half the dataset as individuals with high, and the other half as individuals with low encounter probabilities. For the sake of simplicity, this was only done for collared individuals. Each dataset contained 900 marked individuals per summer (300 rings, 600 collars, mimicking the number of females marked with each marker) for 10 years. Average seasonal survival of leg-ringed-only birds in simulations was set at 0.99, 0.92, 0.95 and 0.96 for summer, fall, winter and spring seasons, respectively, and for collared birds at 0.99, 0.92, 0.87 and 0.92. Physical recapture probability during summer was simulated at 0.05. Finally, collar resighting probabilities varied among seasons and heterogeneous groups and were set for the high (low) observation groups at 0.27 (0.06), 0.48 (0.18), 0.25 (0.06), 0.27 (0.08) for summer, fall, winter, and spring, respectively. Simulations were done with `E-Surge` (Choquet et al., 2009), using the `R2Esurge` package in `R` to repeat analyses multiple times.

Results showed that survival and encounter probabilities estimated from the simulated data were similar to those used to generate the simulations (Fig. S4.2). Mean bias in survival probability was small (<0.01) at all seasons and bias did not exceed 0.04 for 95% of individual simulations. Moreover, estimated bias was normally distributed around the mean value (Fig S4.2). Thus, we conclude that the violation of the discrete encounter occasion assumption of CMR models did not induce significant biases in our survival estimates.

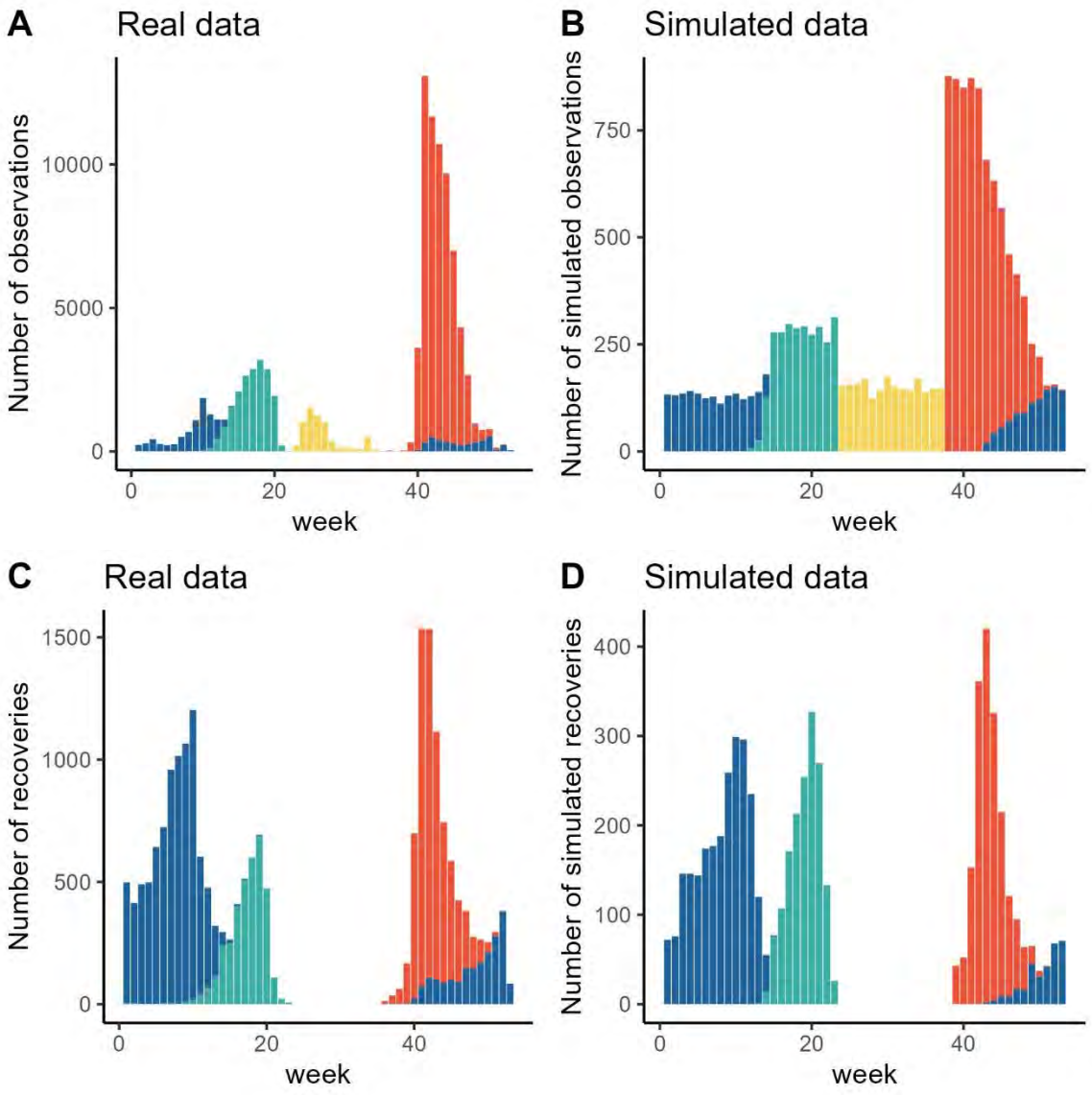

Figure S4.1 Comparison of the distribution of greater snow goose encounters in the real and simulated datasets according to week of the year. Annual distribution of A: observations of birds marked with neck collars between 1990 and 2019, B: observation of collared birds from simulated datasets, C: recoveries of birds shot between 1990 and 2019, D: recoveries from simulated datasets. Yellow is used for encounters occurring during the summer seasons, orange during the fall, blue during winter and green during spring.

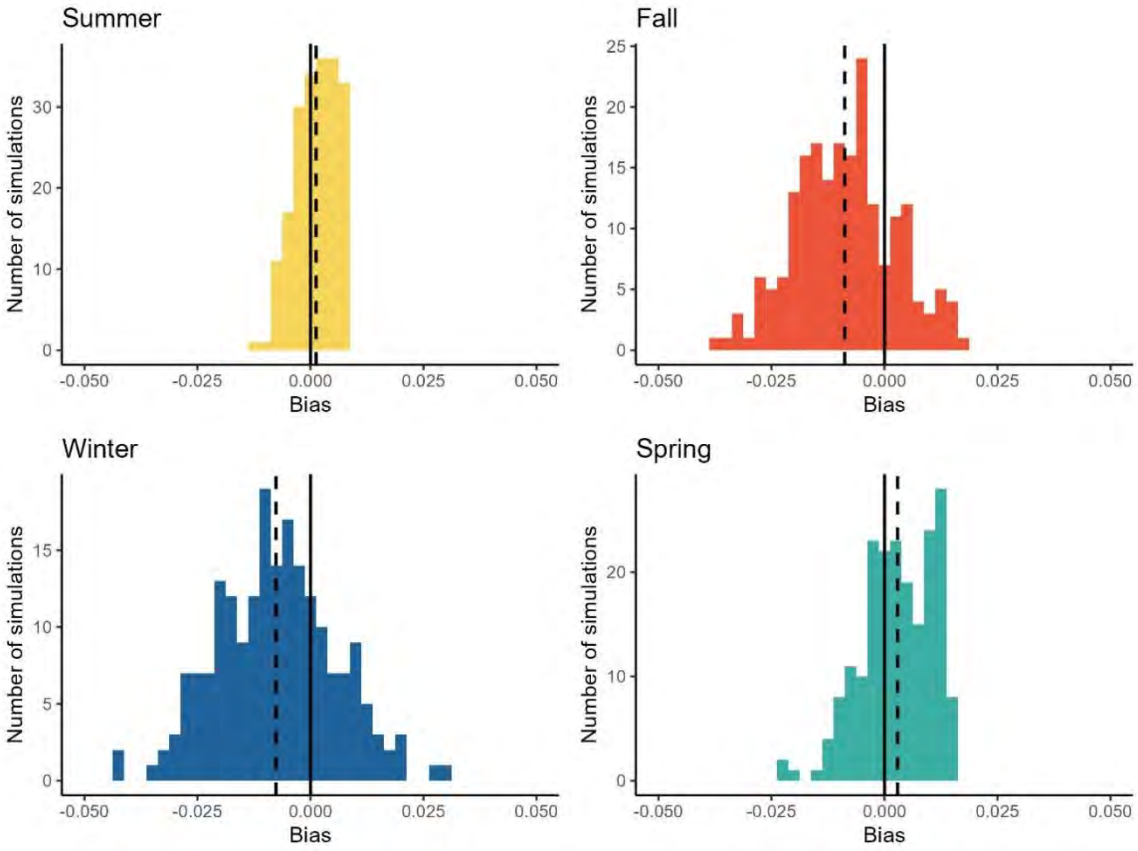

Figure S4.2 Frequency distribution of bias in average seasonal survival estimated for 200 datasets simulated and subsequently analyzed with E-Surge for summer, fall, winter, and spring. Bias is the difference between estimated survival in each simulation and the 'true' survival used to generate simulated datasets. The dashed lines are the mean bias over all simulations for each season.

Bibliography

Choquet, R., Rouan, L., Pradel, R., 2009. Program E-Surge: A software application for fitting multievent models, in: Thomson, D.L., Cooch, E.G., Conroy, M.J. (Eds.), Modeling demographic processes in marked populations. Springer US, Boston, MA, pp. 845–865. https://doi.org/10.1007/978-0-387-78151-8_39

Hargrove, J.W., Borland, C.H., 1994. Pooled population parameter estimates from mark-recapture data. Biometrics 50, 1129. https://doi.org/10.2307/2533449

O'Brien, S., Robert, B., Tiandry, H., 2005. Consequences of violating the recapture duration assumption of mark-recapture models: a test using simulated and empirical data from an endangered tortoise population: *Bias from lengthy mark-recapture occasions*. J. Appl. Ecol. 42, 1096–1104. https://doi.org/10.1111/j.1365-2664.2005.01084.x

Annexe S4.3 **– Goodness-of-fit tests**

The goodness-of-fit (GOF) tests revealed significant overdispersion in our dataset (Table S4.1). Test M (homogeneity in live encounter probability, trap dependence) and Test 3G (homogeneity in survival, transience) were highly significant for both leg-ringed-only and collared birds. As previously found in this dataset on an annual basis (LeTourneux et al., 2022), a detailed examination of the contingency tables of Test M revealed that individuals not encountered in a given occasion are subsequently less re-encountered alive compared to those encountered in that occasion. This suggests the presence of heterogeneity in live-encounter probabilities among individuals, which can be explained, at least in summer, by our sampling scheme and the biology of the species (LeTourneux et al., 2022). Indeed, because geese exhibit some nesting and brood rearing site fidelity (Lecomte et al., 2008), those that nest or rear a brood in the central area of our monitoring and ringing operations may be more likely to be encountered than other birds. Similarly, because collar observations on the staging and wintering grounds tend to occur at the same sites year after year, birds exhibiting fidelity to those sites may also be encountered more often than others. Tests of models with heterogeneity in collar observation probabilities confirmed that a model with heterogeneity at all seasons fitted the data much better than a model without any heterogeneity or when present only in summer (Table S4.2).

Test 3G was also highly significant for collared females and marginally significant for leg-ringed-only birds (Table S4.1). However, the presence of heterogeneity in live-encounter probabilities (Test M) can lead to a significant Test 3 even in the absence of transience effects or heterogeneity in survival probabilities (Jeyam et al., 2018), and this was demonstrated for our dataset with simulations (Appendix S3.3). Although we cannot entirely exclude the presence of some transient birds in our dataset, this possibility is minimized by our marking scheme. Indeed, geese are marked at the end of the brood-rearing period when only successful breeders are still present because most failed and non-breeders have left the area to moult elsewhere (Reed et al., 2003). Consequently, the transience-like effect identified in our dataset by Test 3G is probably largely an artifact of heterogeneity in live-encounter probabilities.

S4.3.1 **ĉ** calculation

The overall variance inflation factor for a CMR dataset can be calculated by dividing the Chi-squared statistic of the GOF test by its corresponding degrees of freedom (in our case, $\hat{c}$ = 12,595.66 / 4,234 = 2.97, Table S4.1). However, this statistic must be adjusted because the inclusion of heterogeneity in live-encounter probability in the model structure increases the fit to the data. We used the method implemented in LeTourneux et al. (2022) and conducted a Likelihood Ratio Test (LRT) between two versions of our most general model, one including heterogeneity in live-encounter probabilities at all seasons (our model M0 in Table 4.1) and one without. The calculation of our adjusted ĉ was thus:

$$\hat{c}_{adj} = \frac{{\chi^2}_{tot} - (DEV_i - DEV_g)}{df_{tot} - (np_g - np_i)}$$

Where ${\chi^2}_{tot}$ and df_{tot} are the chi-squared statistic and degrees of freedom of the overall GOF test (Table S4.1), DEV_i and np_i are the deviance and number of parameters of the initial model (i.e., without heterogeneity in live-encounter probabilities; model 3, Table S4.2), and DEV_g and np_g are the deviance and number of parameters of the model with heterogeneity in live-encounter probabilities at all seasons (model 1, Table S4.2), respectively. Applying this formula yielded an *Adjusted ĉ* of 2.0, which was used to adjust models in the main analysis.

Table S4.1 Results of the goodness-of-fit test for multi-state models and variance inflation factors computed for encounter histories of adult greater snow geese marked between 1990 and 2018. Tests were conducted separately for leg-ringed-only males and females (because their live encounter probabilities are estimated separately in all models) and for collared females (because they can be observed during all encounter occasions unlike birds wearing only a leg-ring). For leg-ringed-only birds, GOF tests were conducted on an annual dataset because Test M fails when individuals are not detectable in all occasions. For all groups and all test components, the chi-squared statistic (χ^2), degrees of freedom (df) and p-values (p) are provided. *Overall ĉ* is the variance inflation factor calculated from overall GOF tests and *Adjusted ĉ* is the inflation factor corrected for the inclusion of heterogeneity in live-encounter probability in our model (see text for calculation).

Group	Test component	χ^2	df	p
Collars - Females (seasonal)	Test 3G.Sr	54.788	29	0.003
	Test 3G.Sm	439.398	264	<0.001
	Test M.ITEC	2,779.483	288	<0.001
	Test M.LTEC	7,279.543	2,591	<0.001
Rings – Males (annual)	Test 3G.Sr	44.104	28	0.027
	Test 3G.Sm	108.231	103	0.343
	Test M.ITEC	445.849	81	<0.001
	Test M.LTEC	677.988	362	<0.001
Rings – Females (annual)	Test 3G.Sr	31.207	28	0.308
	Test 3G.Sm	123.961	96	0.029
	Test M.ITEC	193.356	79	<0.001
	Test M.LTEC	417.753	285	<0.001
All birds	Overall test	12,595.66	4,234	<0.001
Overall $\hat{c}$		2.97		
Adjusted $\hat{c}$		2.00		

Table S4.2 Number of parameter and deviances of models with the same constraints except for the presence of heterogeneity in live-encounter probabilities (K = number of parameters).

Model	K	Deviance
1. With heterogeneity in live-encounter probabilities at all seasons (model M0, Table 1)	370	377,865.108
2. With heterogeneity in live-encounter probabilities in summer only	364	381,149.217
3. Without heterogeneity in live-encounter probabilities	360	382,010.523

Bibliography

Jeyam, A., McCrea, R.S., Bregnballe, T., Frederiksen, M., Pradel, R., 2018. A test of positive association for detecting heterogeneity in capture for capture–recapture data. J. Agric. Biol. Environ. Stat. 23, 1–19. https://doi.org/10.1007/s13253-017-0315-4

Lecomte, N., Gauthier, G., Giroux, J.-F., 2008. Breeding dispersal in a heterogeneous landscape: the influence of habitat and nesting success in greater snow geese. Oecologia 155, 33–41. https://doi.org/10.1007/s00442-007-0860-6

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

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

Annexe S4.4 **– Additional modelling considerations**

S4.4.1 Initial parameter values

The complexity of our model required us to specify realistic initial parameter values (i.e. close to the expected values) to converge on a global maximum likelihood. To avoid local maxima, we ran the two preferred models 5 times with random starting values, but this systematically resulted in high deviances. We also ran these models 5 more times with random values in the vicinity of the parameter estimates and this systematically yielded identical deviances among themselves.

S4.4.2 Constraints on ring recovery probabilities of collared birds

In CMR models, encounter and survival probabilities are linked because they are estimated from the same dataset. Therefore, changes in the former can sometimes be compensated by changes in the latter and yield different mathematical solutions with similar likelihoods. This is especially true when estimating a large number of parameters, which can lead to instability in the model. Recovery probabilities are particularly challenging to estimate because a dead bird that is not recovered can never be re-observed later, as opposed to live birds not encountered in a particular occasion, which can eventually be encountered later. Early in our modelling selection process, some models converged on recovery probabilities that were higher for ringed birds than for collared birds. We consider this effect to be biologically unrealistic and likely to be an artefact due to parameter instability for several reasons. First, estimated recovery probabilities of collared birds are systematically higher or equivalent to those of birds with only a leg ring in other goose studies (Caswell et al., 2012; Reed et al., 2005; Samuel et al., 1990). Second, in our analyses some models would find a positive effect of collar on recoveries while others with very similar parameter constraints would find the opposite. Third, LeTourneux et al. (2022) systematically found a higher annual recovery rate for collars using the same dataset on an annual basis, using a simpler and more stable model.

We must also consider that the recovery probability in our model is defined as the probability that a bird dies from hunting, is retrieved and has its marker reported among birds that died between *t* and *t+1* (i.e. conditional on death). LeTourneux et al. (2022) found that hunting mortality was higher in collared than leg-ringed-only birds, providing little support for the hypothesis that leg-ringed birds would die proportionately more from hunting than collared birds. Finally, collars are a large and conspicuous marker that can not be missed when the bird is retrieved, which should increase the probability that it is reported by hunters compared to leg rings. Consequently, because recovery probabilities should be positively affected by the presence of a collar, we concluded that these discrepancies between models were an artefact of model instability, and we constrained recovery probabilities of leg-ringed-only birds to be lower or equal to that of collared birds in all models.

This was achieved by introducing parameter *b* in a second step of the event matrix (Ω_2; see Appendix S4.1 for details). When multiplying the two steps of the event matrix (Ω_1 and Ω_2), the recovery probability of a collared bird remains *r* while the recovery probability of a bird with only a leg ring becomes $r * b$. Because *b* is on the probability scale, this parameter is constrained to the [0,1] interval, effectively constraining $r * b \leq r$.

Bibliography

Caswell, J.H., Alisauskas, R.T., Leafloor, J.O., 2012. Effect of neckband color on survival and recovery rates of Ross's geese. J. Wildl. Manage. 76, 1456–1461. https://doi.org/10.1002/jwmg.392

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

Reed, E.T., Gauthier, G., Pradel, R., 2005. Effects of neck bands on reproduction and survival of female greater snow geese. J. Wildl. Manage. 69, 91–100.

Samuel, M.D., Rusch, D.H., Craven, S., 1990. Influence of neck bands on recovery and survival rates of Canada geese. J. Wildl. Manage. 54, 45. https://doi.org/10.2307/3808899

Annexe S4.5 – Survival of collared geese and encounter probabilities for all birds

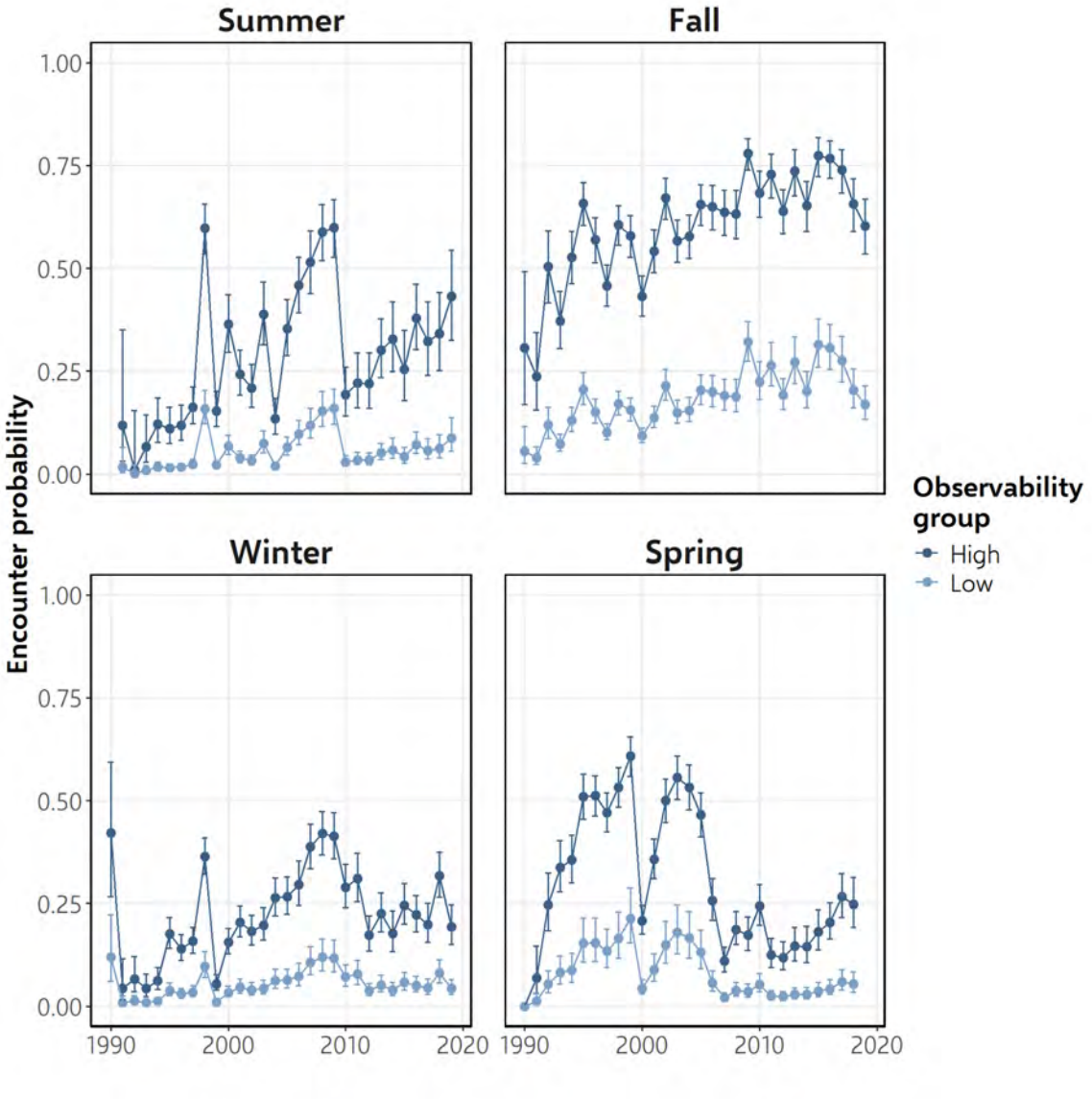

Figure S4.3 Seasonal live encounter estimates of collared greater snow geese for highly- and weakly-observable groups between 1990 and 2019 from model M10 (Table 4.1). Summer live encounters pool physical recaptures and observations while only observations are available in the other seasons. Points represent annual estimates with their 95% confidence intervals (error bars).

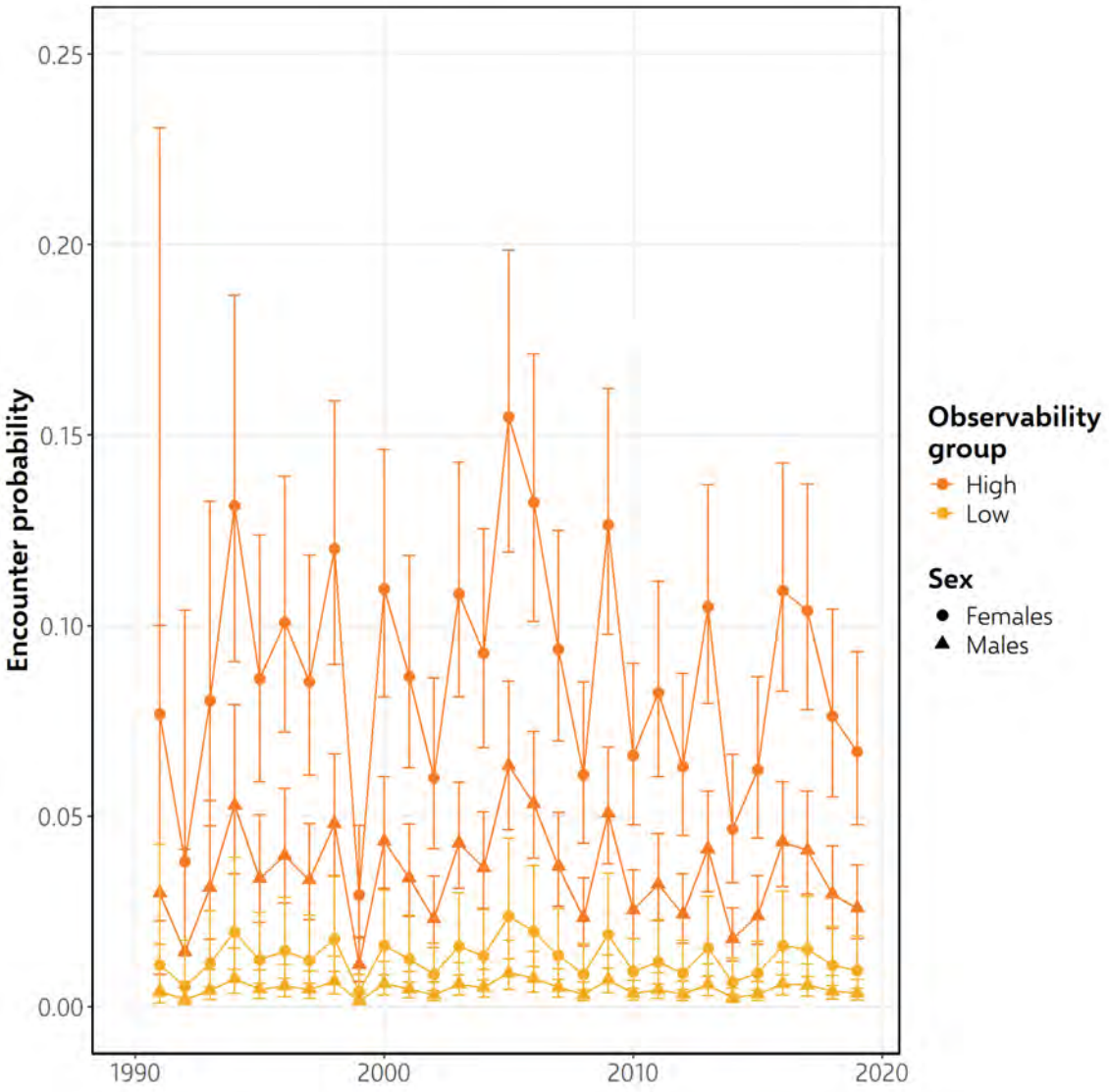

Figure S4.4 Summer live encounter estimates (physical recapture) of male and female leg-ringed-only greater snow geese for highly- and weakly-observable groups between 1990 and 2019 from model M10 (Table 4.1). Points represent annual estimates with their 95% confidence intervals (error bars).

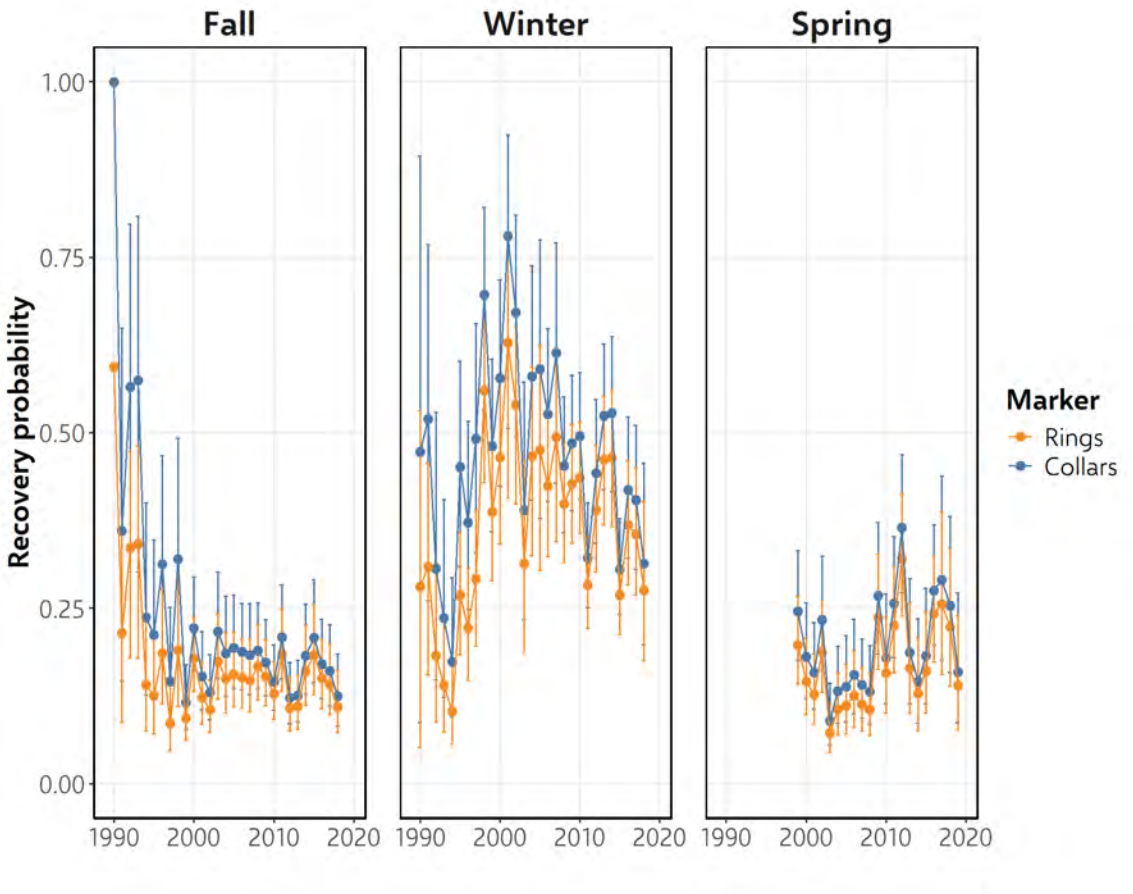

Figure S4.5 Seasonal recovery estimates of leg-ringed only and collared greater snow geese between 1990 and 2019 from model M10 (Table 4.1). Points represent annual estimates with their 95% confidence intervals (vertical bars).

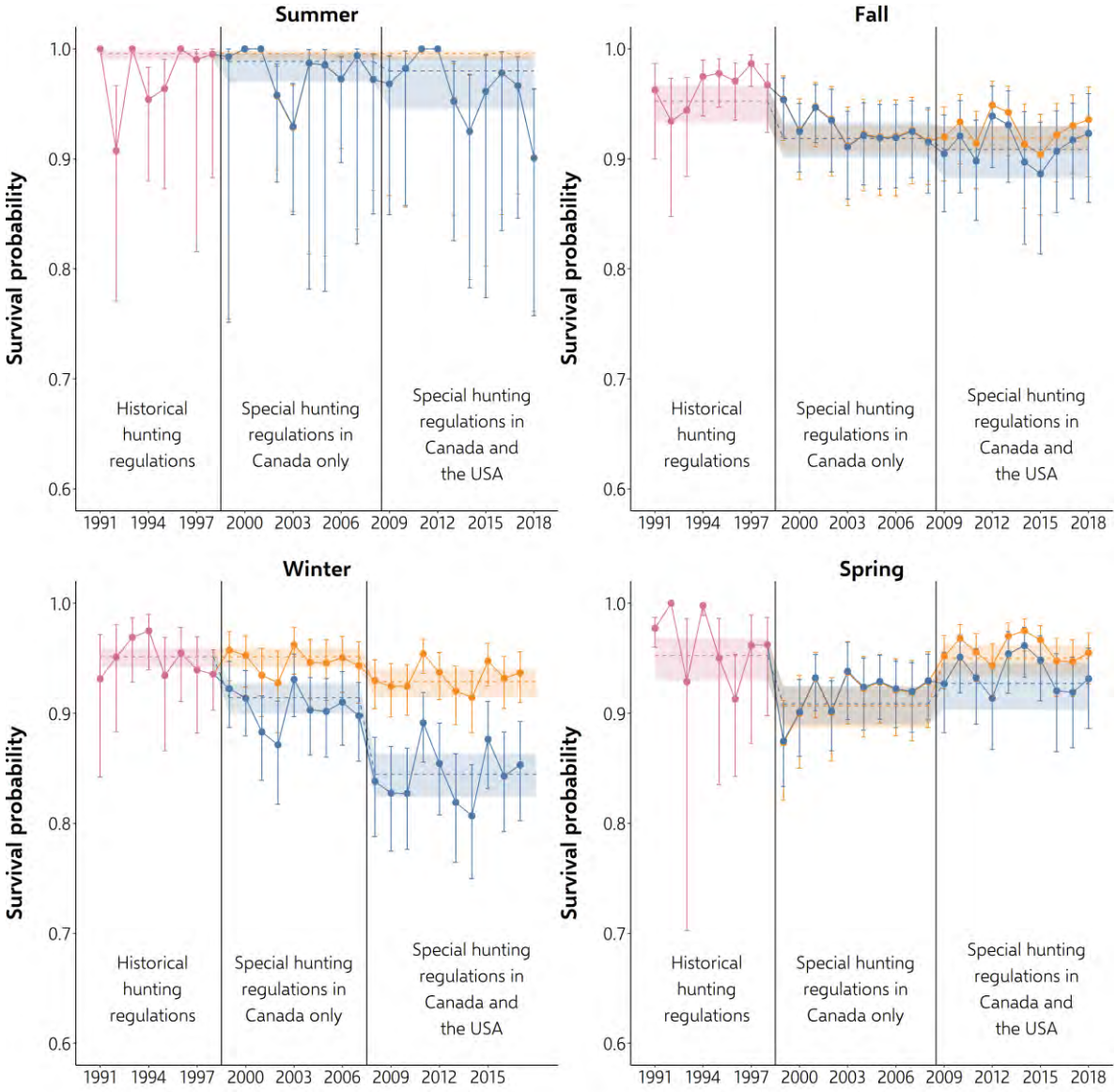

Figure S4.6 Seasonal survival estimates of greater snow geese between 1990 and 2019 from model M6, Table 4.1 (yellow: leg-ringed-only males and females, blue: collared females; pink: both groups combined). The shaded area represents the 95% C.I. of survival estimates from the most parsimonious model, where survival is constrained equal for time periods with similar hunting regulations (model M10, Table 4.1). Points represent annual survival estimates with their 95% confidence intervals (error bars).

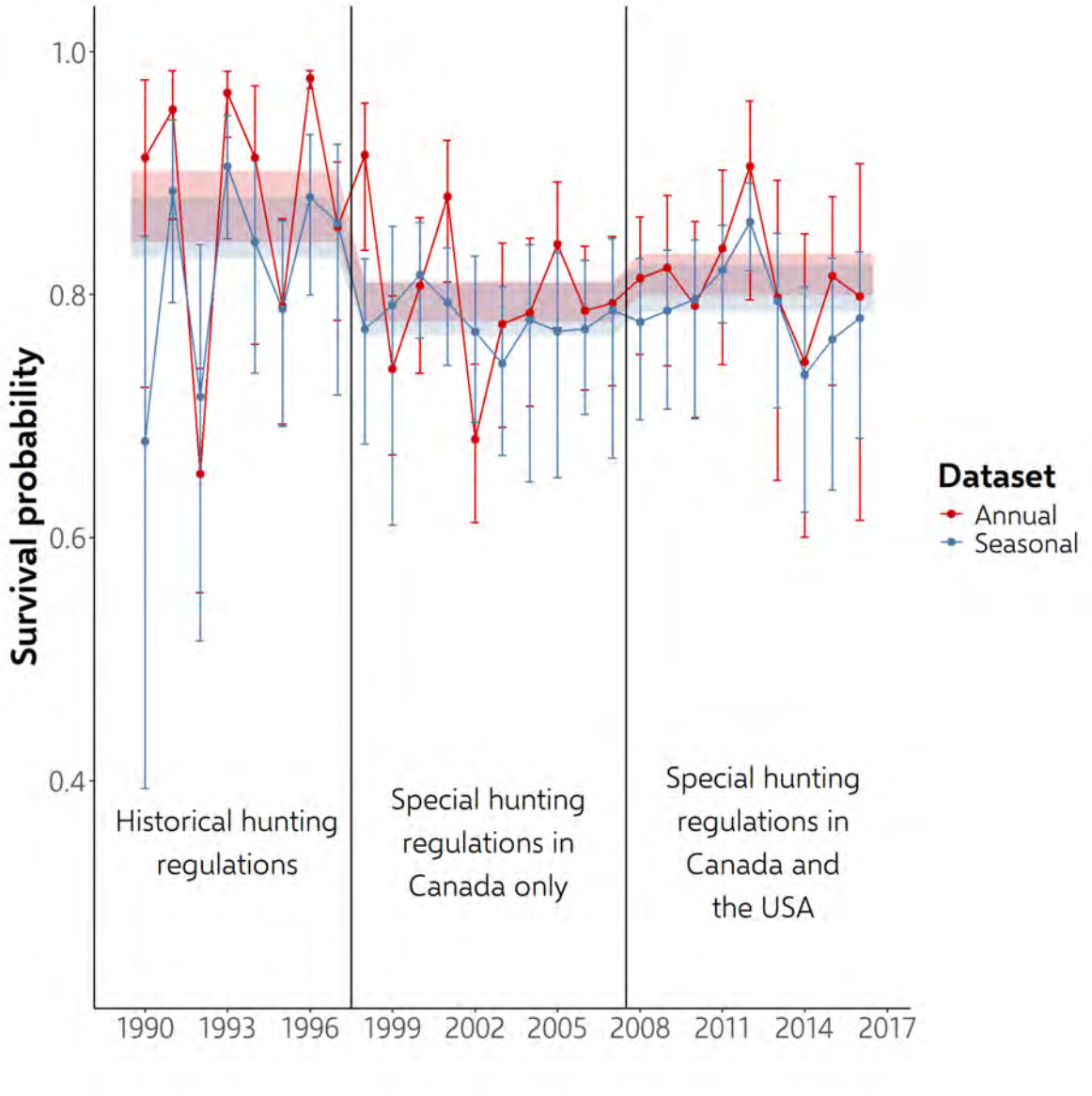

Figure S4.7 Comparison of annual survival estimates of leg-ringed-only adult greater snow geese obtained from the annual dataset (red; from LeTourneux et al., 2022) and reconstructed from the seasonal estimates (blue; this study, see Fig. 4.4). Points represent annual survival estimates with their 95% confidence intervals (red: model M14 in Table 3.1 (Chapter 3); blue: model M6 in Table 4.1, this study). The shaded area represents the 95% C.I. of survival estimates for models where survival is constrained equal for time periods with similar hunting regulations (red: model M17, Table 3.1 (Chapter 3); blue: model M5, Table 4.1, this study).

Bibliography

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

Annexe S4.6 **– Compensation relationships**

S4.6.1 Relationships between seasonal mortality for other seasons with hunting

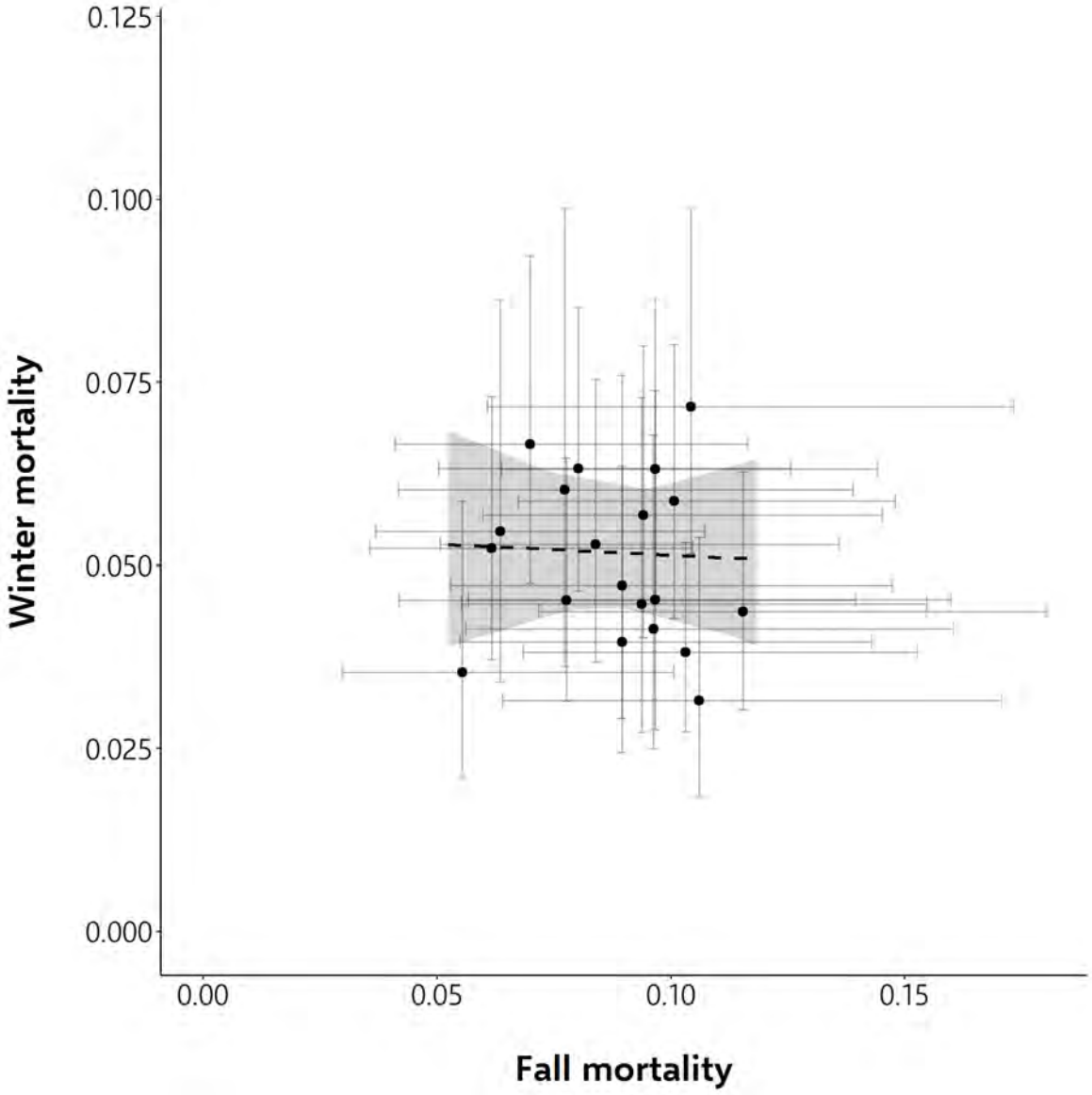

Figure S4.8 Relationship between winter and fall mortality estimates of adult greater snow geese between 1999 and 2018, after implementation of special hunting seasons in Canada only (spring, 1999-2008, closed dots) and in Canada and USA (spring and winter, 2008-2019, open dots). Error bars are 95% C.I. of seasonal survival estimates computed as 1-survival from model M6 (Table 4.1). The dashed line represents the mean bootstrapped slope estimated from 10 000 simulations (see methods; β [95%CI] = -0.03 [-0.27, 0.21]). The gray shading represents the central 95% of the bootstrapped relationships.

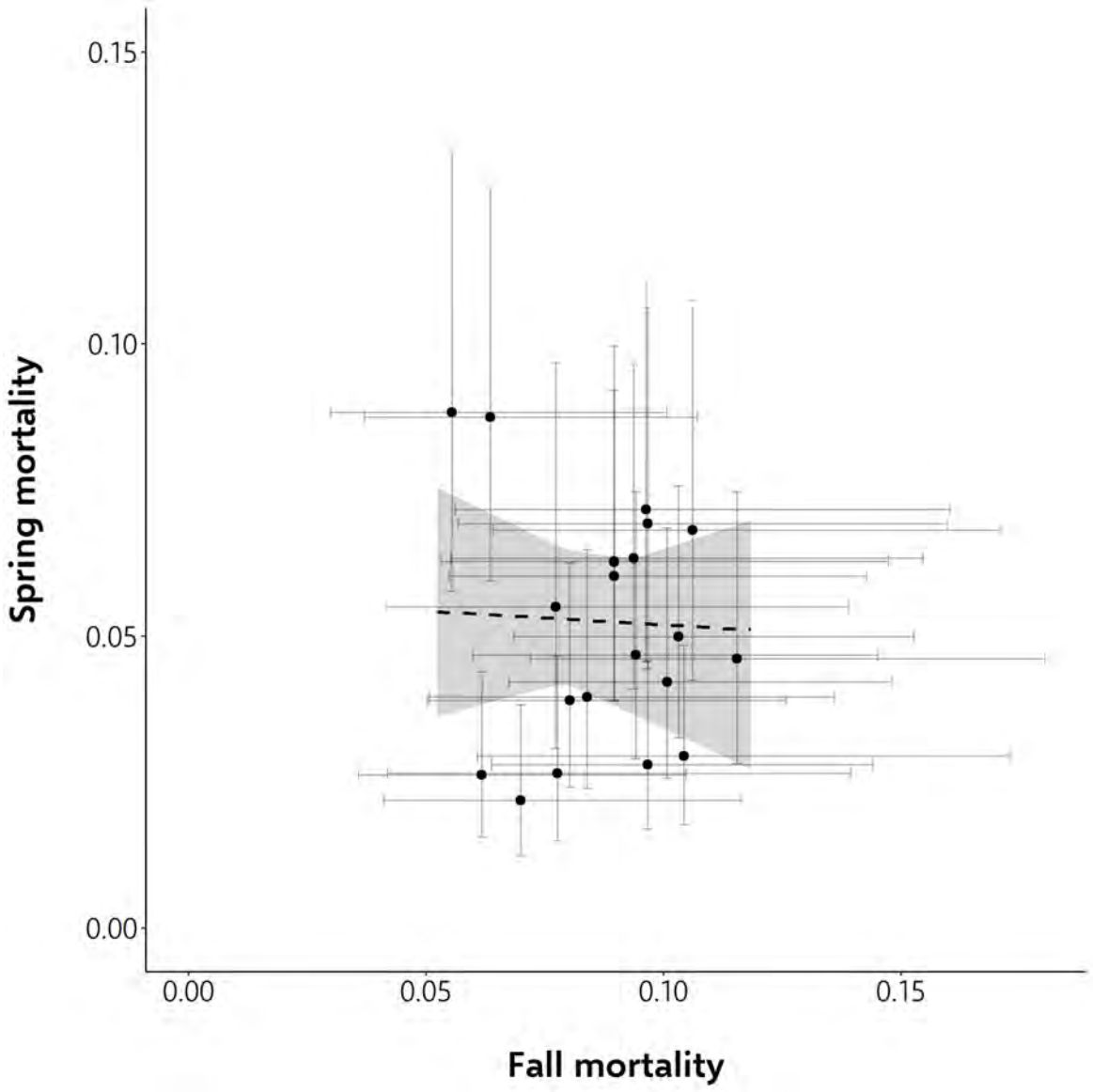

Figure S4.9 Relationship between spring and fall mortality estimates of adult greater snow geese between 1999 and 2018, after implementation of special hunting seasons in Canada only (spring, 1999-2008, closed dots) and in Canada and USA (spring and winter, 2008-2019, open dots). Error bars are 95% C.I. of seasonal survival estimates computed as 1-survival from model M6 (Table 4.1). The dashed line represents the mean bootstrapped slope estimated from 10 000 simulations (see methods; β [95%CI] = -0.05 [-0.41, 0.31]). The gray shading represents the central 95% of the bootstrapped relationships.

S4.6.2 Relationship between annual survival probability and harvest rate

We used a normal linear regression to determine the relationship between annual survival probability of adult greater snow geese and an independent estimate of annual adult harvest rate between 1999 and 2018. Annual harvest rates were obtained by dividing the number of adult geese harvested annually (estimated by national hunter surveys) by the fall population size (estimated by an aerial photographic census; see Appendix S3.2 for details on harvest rate calculation). We accounted for uncertainty in annual survival estimates in this regression using a bootstrap approach similar to the one used to determine the relationship between mortality estimates between seasons. Namely, we generated 10,000 datasets of annual survival by sampling values from logit-normal distributions defined by each seasonal survival estimate and its standard error, which were obtained from the relevant CMR model. The four seasonal survival estimates for each dataset were then multiplied to obtain annual survival estimates. We ran linear regressions between annual survival values derived from each simulated dataset and we calculated the mean slope and its 95% confidence interval from the distribution of the 10,000 slope estimates obtained. We visually assessed the linear model assumption of normality of residuals and made sure there were no outliers. Effects and estimates are reported with their 95% confidence intervals.

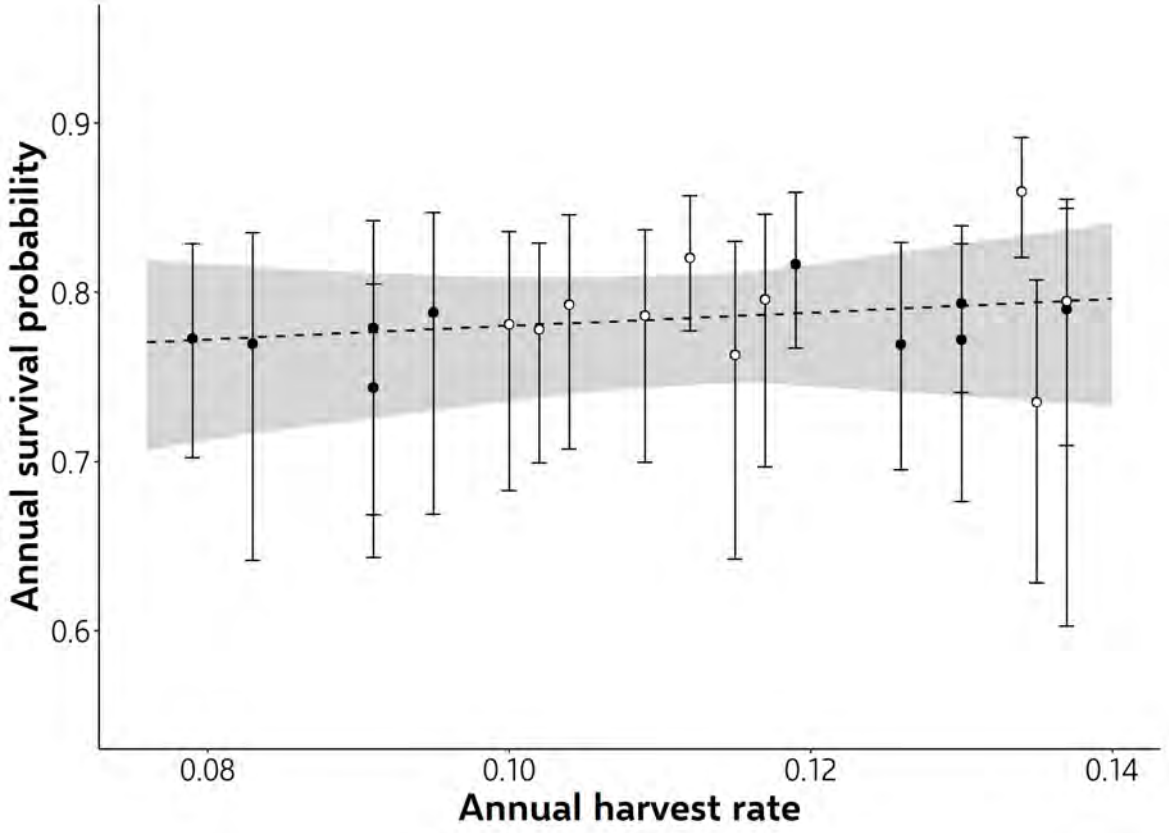

Figure S4.10 Relationship between annual survival probability estimates and harvest rate of adult greater snow geese between 1999 and 2018, after implementation of special hunting seasons in Canada only (spring, 1999-2008, closed dots) and in Canada and USA (spring and winter, 2008-2019, open dots). Error bars are 95% C.I. of annual survival estimates computed from seasonal estimates of model M6 (Table 4.1). The dashed line represents the mean bootstrapped slope estimated from 10,000 simulations (see text above; β [95%CI] = 0.4 [-0.6, 1.5]). The gray shading represents the central 95% of the bootstrapped relationships.

Annexe S4.7 **– Complete model selection table**

Table S4.3 Complete results of model selection for the analysis of seasonal survival and dead encounter (recovery) probabilities of adult greater snow geese marked between 1990 and 2018. For each model, model number from Table 4.1 in the main text, number of estimated parameters (K) and difference in QAIC (ΔQAIC) between the current and the most parsimonious model (M10) are provided. Full time variation and heterogeneity in observation in interaction with seasons was applied to live encounter probabilities of collared birds in all models. Similarly, full time variation for summer occasions, heterogeneity in live encounter probability and a sex effect were applied to live encounter of leg-ringed-only birds in all models, except for model M1 where the sex effect was absent.

Model No.	Survival	Recovery	K	ΔQAIC
M10	d . *spring* + *summer* + $d_{1:2,3}$. *winter* + $d_{1,2:3}$. *fall* + *col* . *seas* . $d_{2,3}$	t + *col* . d	259	0.00
M11	d . *spring* + *summer* + *winter* + $d_{1,2:3}$. *fall* + *col* . *seas* . $d_{2,3}$	t + *col* . d	258	0.98
M9	d . *seas* $_{\text{fall, spring}}$ + *summer* + $d_{1:2,3}$. *winter* + *col* . *seas* . $d_{2,3}$	t + *col* . d	260	2.00
-	d . *seas* $_{\text{fall, spring}}$ + *summer* + *winter* + *col* . *seas* . $d_{2,3}$	t + *col* . d	259	2.69
M13	d . *seas* $_{\text{summer, fall, spring}}$ + *winter* + *col* . *seas* . $d_{2,3}$	t + *col* . d	261	5.87
M8	d . *seas* $_{\text{summer, fall, spring}}$ + $d_{1:2,3}$. *winter* + *col* . *seas* . $d_{2,3}$	t + *col* . d	262	5.99
-	$d_{1,2:3}$. *spring* + *summer* + $d_{1:2,3}$. *winter* + $d_{1,2:3}$. *fall* + *col* . *seas* . $d_{2,3}$	t + *col* . d	258	6.83
M6	t + *col* . *seas* . $d_{2,3}$	d . (*seas* + *col*)	297	7.13
M7	d . *seas* + *col* . *seas* . $d_{2,3}$	t + *col* . d	263	7.45
M14	d . *seas* $_{\text{summer, fall, spring}}$ + $d_{1,2:3}$. *winter* + *col* . *seas* . $d_{2,3}$	t + *col* . d	262	7.85
-	d . *seas* + *col* . *seas* . d	t + *col*	264	8.59
-	d . *seas* $_{\text{summer, fall, winter}}$ + $d_{1,2:3}$. *spring* + *col* . *seas* . $d_{2,3}$	t + *col* . d	262	9.75
-	d . *seas* $_{\text{summer, fall, winter}}$ + *spring* + *col* . *seas* . $d_{2,3}$	t + *col* . d	261	10.41
-	d . *seas* $_{\text{summer, fall, winter}}$ + $d_{1:2,3}$. *spring* + *col* . *seas* . $d_{2,3}$	t + *col* . d	262	10.76
M5	d . *seas* + *col* . *seas* . d	t + *col* . d	266	10.73
M12	$d_{1:2,3}$. *spring* + *summer* + $d_{1:2,3}$. *winter* + $d_{1,2:3}$. *fall* + *col* . *seas* . $d_{2,3}$	t + *col* . d	258	10.80
-	t + *col* . *seas* . d	d . (*seas* + *col*)	300	11.66
M4	d . *seas* + *col* . *seas* . $d_{2,3}$	t + *col*	261	11.79
-	d . *seas* + *col* . *seas* . $d_{2,3}$	t + *col* . *seas*	263	11.89
-	d . *seas* + *col* . *seas* . d	t + *col* . *seas*	266	12.31
-	*spring* + *summer* + $d_{1:2,3}$. *winter* + $d_{1,2:3}$. *fall* + *col* . *seas* . $d_{2,3}$	t + *col* . d	257	13.33
-	d . *seas* + *col* . *seas* . d	t + *col* . *seas* . d	271	19.11
M0	t + *col* . *seas* . d	t + *col*	370	73.91
M2	t + *col* . *seas* . $d_{2,3}$	t + *col*	367	74.45
M3	t + *col* . $d_{2,3}$	t + *col*	361	136.20
M1	t + *col* . *seas* . d	t + *col*	369	296.37

Note: *t*, full time effect (seasons x years); *d*, year effect reduced to three periods (1: before special hunting regulations, 1990-19998; 2: special hunting regulations in Canada only, 1999-2008; 3: special hunting regulations in Canada and the USA, 2009-2019); *seas*, full seasonal effect (all seasons differ); *summer*, *fall*, *winter* or *spring*, seasonal effect present in the specified season; *col*, collar effect; '+', additive effect; '.', interaction. Notation for indices: ':' denotes a parameter constrained equal for two periods; ',' denotes a parameter varying between periods.

Annexe S5 – **Documentation supplémentaire pour le Chapitre 5**

Annexe S5.1 **– Multievent model definition**

Multievent models differentiate the true state of individuals from their observations, from which the true states can be inferred (Pradel, 2005). LeTourneux et al. (2022) developed a model that accounts for heterogeneity in live encounter probabilities for this population. Based on this model, we developed a new parameterization to allow permanent emigration from the study area. In the current model, we considered 3 types of encounters: '1' captured alive on the breeding grounds at time *t*, '2': shot by a hunter and recovered dead between *t - 1* and *t*, and '3' not encountered. These encounters can link individuals to one of 6 states that describe their status (alive/dead), age (juvenile/adult) and affiliation to one of 3 capturability groups (highly capturable, weakly capturable, emigrated – not capturable). These states are: Alive Juvenile (AJ), Alive Adult and Highly capturable (AAH), Alive Adult and Weakly capturable (AAW), Alive Adult permanently Emigrated (AAE), Newly Dead (ND) and Dead (D). Newly dead birds represent birds that just died, and the distinction between this state and an absorbing and unobservable dead state is needed to avoid individuals contributing to the recovery probability beyond the occasion in which they were recovered (Gauthier and Lebreton, 2008).

Multievent models are based on three type of matrices that describe different processes. The initial state matrix (δ) defines the states of individuals when they are initially marked. In this case, all juvenile birds are in the state AJ when they are initially captured. Adults are alive when first captured and can belong to either a group that is highly or weakly encounterable (AAH and AAW, respectively, see Appendix S3.1 for details). The initial state matrix defines the probability (*g*) that adults captured belong to either of these groups. No individual can initially be in the state permanently emigrated (AAE) as all birds were initially captured on Bylot Island. This matrix is defined as follow for juveniles and adults:

$$\delta^i_{juv.} = \begin{matrix} AJ & AAH & AAW & AAE & ND & D \\ 1 & 0 & 0 & 0 & 0 & 0 \end{matrix}$$

$$\delta^i_{ad.} = \begin{matrix} AJ & AAH & AAW & AAE & ND & D \\ 0 & g & (1-g) & 0 & 0 & 0 \end{matrix}$$

The second type of matrix is the transition matrix (Γ), which describes ecological processes of interest, that is survival (*S*) and emigration (*E*) probabilities. Adults that survive between year *t* and *t+1* (probability S_a) can emigrate from the breeding area (probability *E*) or remain breeders on Bylot Island in their initial state with a probability (*1-E*). However, adult birds cannot transition between encounterability groups, and emigration is permanent (i.e. emigrated birds remain in the state AAE once they have emigrated). In the case of juveniles, this matrix also defines the probabilities of transitioning to the high (AAH) or low (AAW) encounterability group as adults (probabilities *H* and *L*, respectively), conditional on their survival (S_j). Because surviving juveniles can only transition to either of those groups or to the Alive Adult and permanently Emigrated group, the probability that a juvenile emigrates, conditional on its survival between *t* and *t+1*, is (*1-H-L*). Survival probabilities of adults are constrained equal for all three states. The transition matrix is thus defined as follows:

$$\Gamma^i = \begin{array}{r|cccccc} & AJ & AAH & AAW & AAE & ND & D \\ AJ & 0 & S_j * H & S_j * L & S_j * (1-H-L) & 1-S_j & 0 \\ AAH & 0 & S_a * (1-E) & 0 & S_a * E & 1-S_a & 0 \\ AAW & 0 & 0 & S_a * (1-E) & S_a * E & 1-S_a & 0 \\ AAE & 0 & 0 & 0 & S_a & 1-S_a & 0 \\ ND & 0 & 0 & 0 & 0 & 0 & 1 \\ D & 0 & 0 & 0 & 0 & 0 & 1 \end{array}$$

The third and last type of matrix is the encounter matrix (Ω). This matrix links the different types of observations (events) to the biological states of interest. The model is conditional on the first capture, meaning that all individuals have a first capture probability of 1. This matrix thus defines encounter probabilities for occasions following the initial capture. Because juvenile birds automatically transition to the adult states if they survive their first year, they can not be encountered in that state at any point in their capture history, which is why all encounter probabilities are set to 0 for this state. This matrix contains capture probabilities for adults that are highly or weakly capturable (*p* and *p**, respectively). Similarly, newly dead birds can be encountered with probability *r*, which differs between adults and juveniles in our model. The event matrix is defined as follows:

$$\Omega^i = \begin{array}{c} \\ AJ \\ AAH \\ AAW \\ AAE \\ ND \\ D \end{array} \begin{array}{c} '1' \\ 0 \\ p \\ p^* \\ 0 \\ 0 \\ 0 \end{array} \begin{array}{c} '2' \\ 0 \\ 0 \\ 0 \\ 0 \\ r \\ 0 \end{array} \begin{array}{c} '3' \\ 0 \\ (1-p) \\ (1-p^*) \\ 1 \\ (1-r) \\ 1 \end{array}$$

Note that because of parameter estimation issues linked to MCMC sampling that are beyond the scope of this appendix, recovery probabilities in the model code provided along with this paper are coded in the transition matrix, as advocated in section 9.5.3 of Kéry and Schaub (2012).

Bibliography

Gauthier, G., Lebreton, J.-D., 2008. Analysis of band-recovery data in a multistate capture-recapture framework. Can. J. Stat. 36, 59–73. https://doi.org/10.1002/cjs.5550360107

Kéry, M., Schaub, M., 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective, 1st ed. ed. Academic Press, Boston.

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

Pradel, R., 2005. Multievent: An extension of multistate capture-recapture models to uncertain states. Biometrics 61, 442–447. https://doi.org/10.1111/j.1541-0420.2005.00318.x

Annexe S5.2 **– Encounter and emigration probabilities**

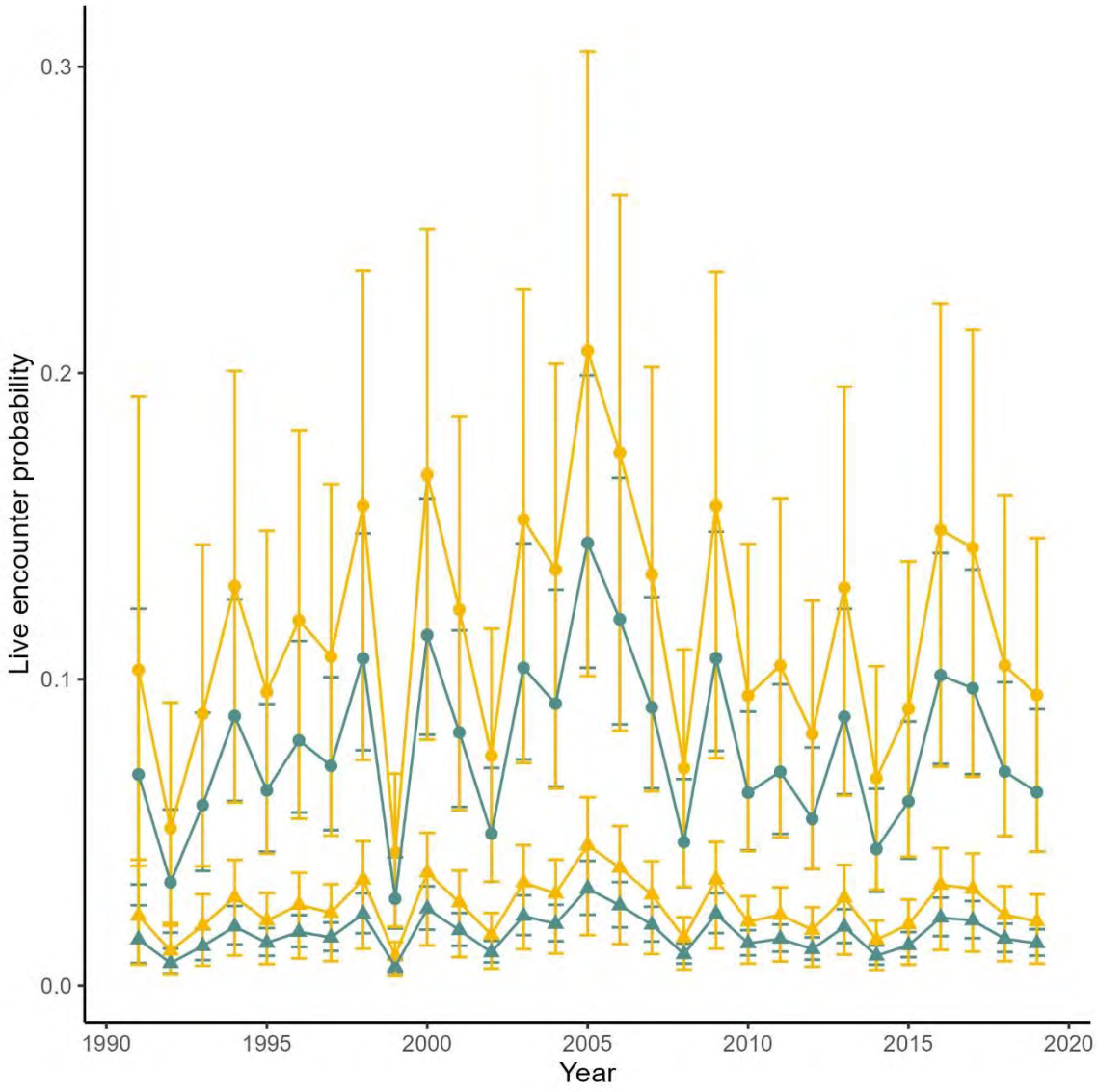

Figure S5.1 Annual live encounter probability estimates for highly capturable (circles) and weakly capturable (triangles) male (green) and female (yellow) adult greater snow geese captured in banding drives at the end of the breeding season on Bylot Island between 1991 and 2019. Error bars are 95% credible intervals.

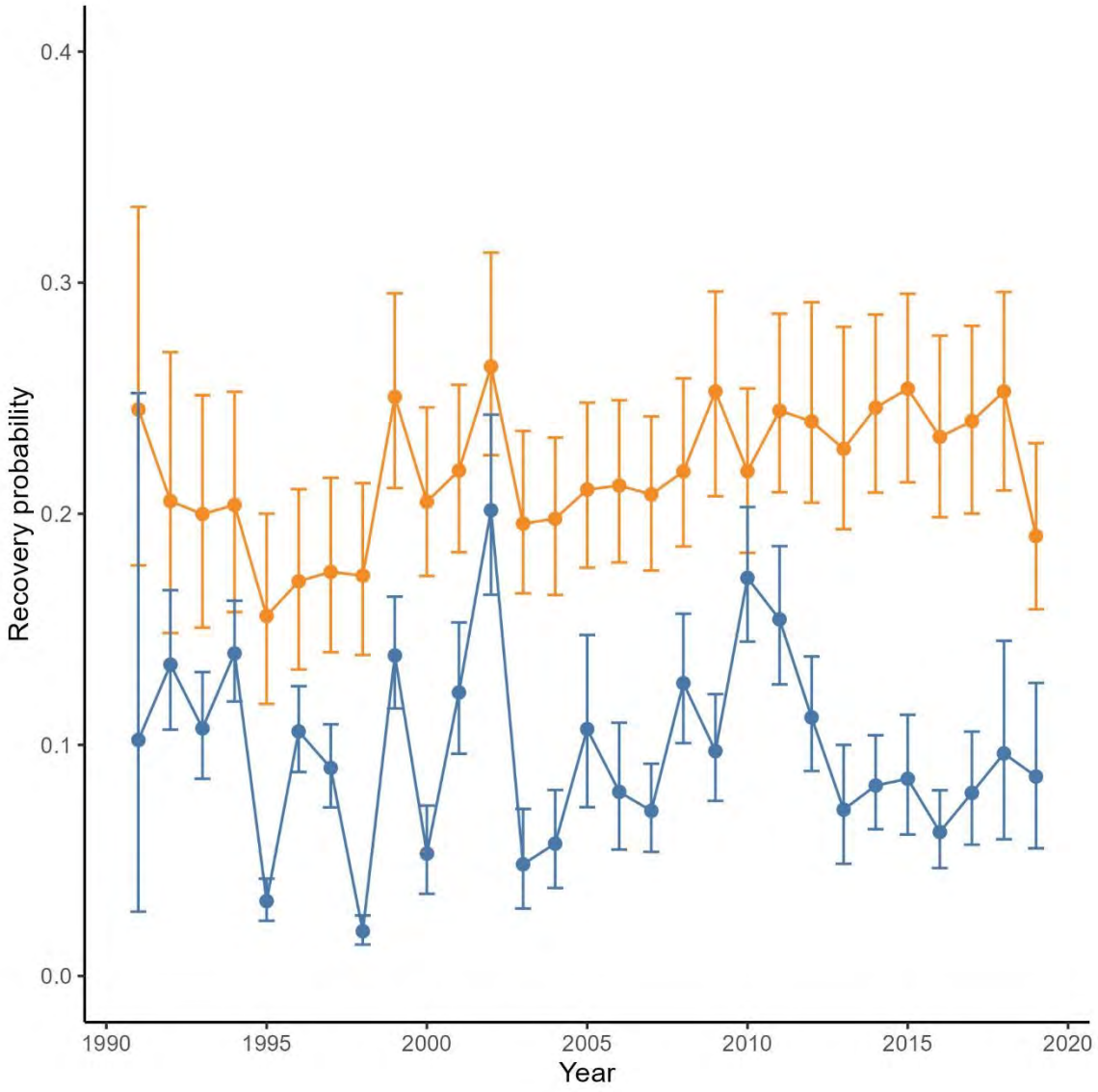

Figure S5.2 Annual recovery probability estimates of adult (orange) and juvenile (blue) greater snow geese marked on Bylot Island between 1990 and 2018.

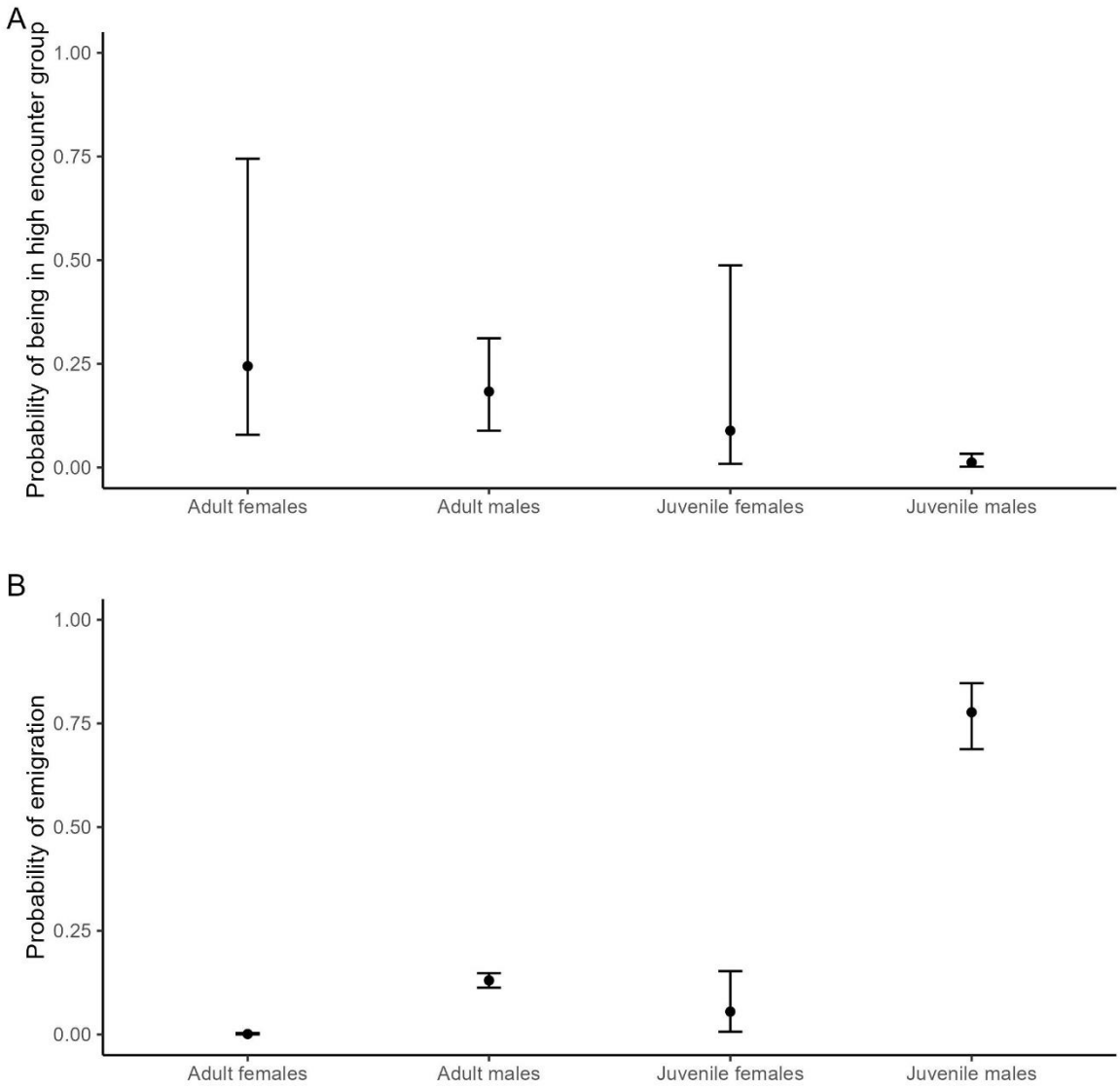

Figure S5.3 Probability estimates of adult and juvenile male and female greater snow geese marked on Bylot Island between 1990 and 2018 to belong to different states. Points are mean model estimates and error bars are 95% credible intervals. A: Probability of belonging to the state Adult Alive and highly-capturable. Details in Appendix S5.1. B: Probability of transition to the state 'Adult Alive Emigrated' from other alive states (i.e., permanent emigration).

Annexe S5.3 **– Relationships between phenology and hatching**

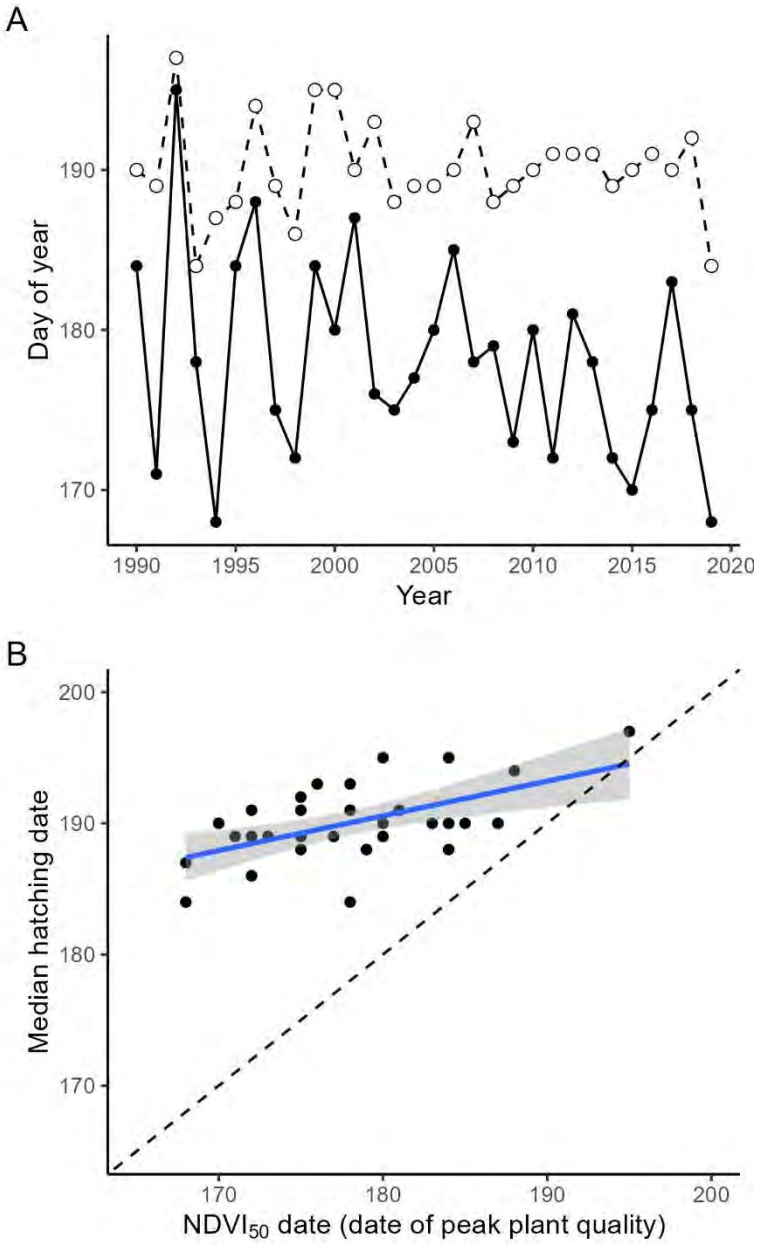

Figure S5.4 Relationship between hatching date of greater snow geese and plant phenology on Bylot Island between 1990 and 2019. Figure updated from Doiron et al. (2015). A: Time series of median hatching date (open dots) and date of peak plant quality derived from NDVI data ($NDVI_{50}$ date, see text; closed dots). B: Relationship between annual median hatching date and date of peak plant quality (blue line, relationship: predicted hatching date = 143 + 0.26*$NDVI_{50}$ date, R^2 = 0.29) and its 95% C.I. (shading). The dotted line represents a 1:1 relationship.

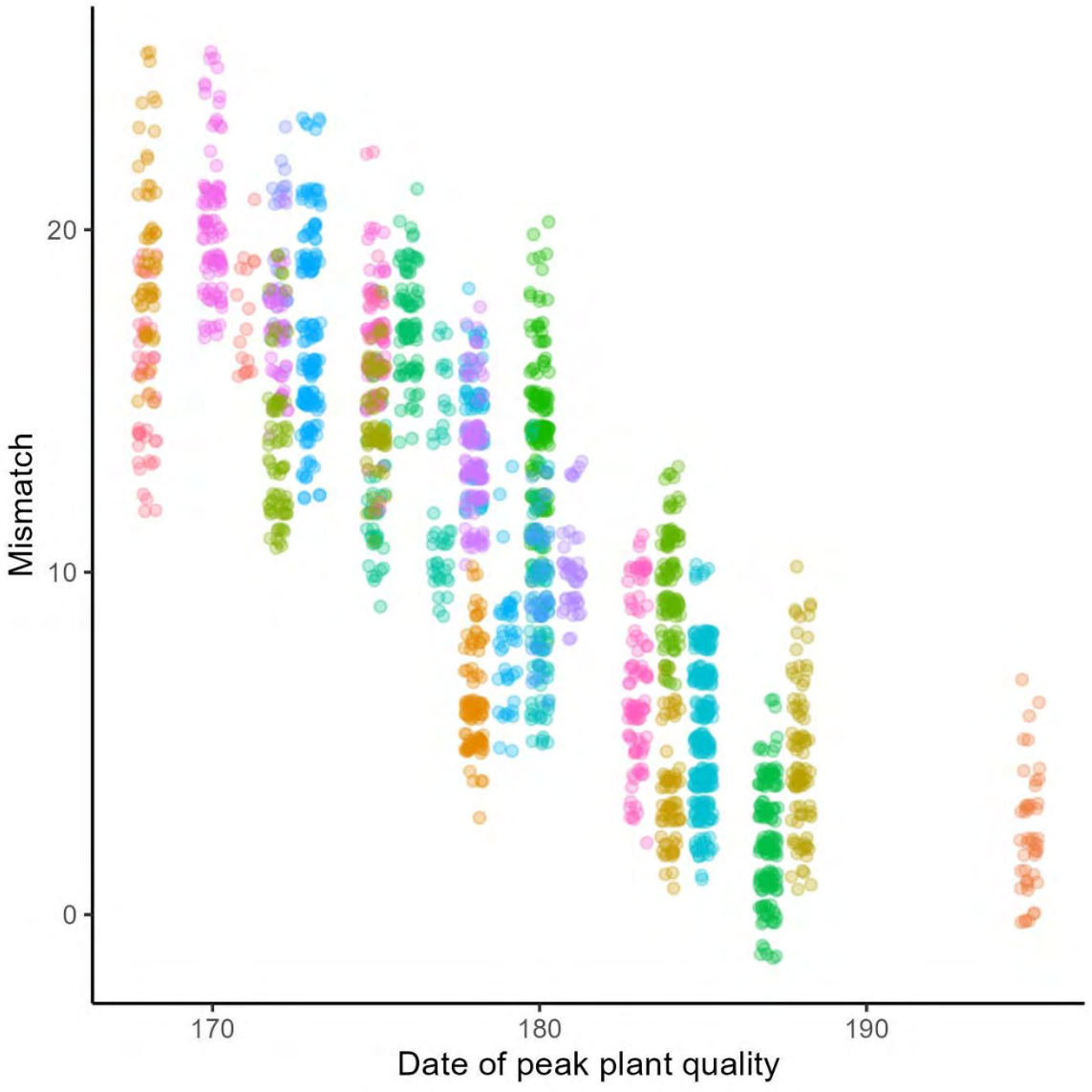

Figure S5.5 Relationship between individual mismatch values (difference between individual hatching date and annual date of peak plant quality) and annual date of peak plant quality for known-age, juvenile greater snow geese recaptured at the end of brood rearing on Bylot Island (Nunavut) between 1991 and 2019. Colors are used to differentiate years. A small jitter was used to better appreciate the distribution of mismatch values for every date of spring phenology.

Bibliography

Doiron, M., Gauthier, G., Lévesque, E., 2015. Trophic mismatch and its effects on the growth of young in an Arctic herbivore. Glob. Chang. Biol. 21, 4364–4376. https://doi.org/10.1111/gcb.13057

Annexe S5.4 **– Model validation: analysis of simulated data**

We ran simulations to validate the performance of our multievent model in estimating the effect of a trophic mismatch on juvenile survival. We simulated 45 000 individuals over 27 occasions (1000 juveniles and 667 adults marked per occasion). Input parameter values were chosen to reflect either results of a previous analyses of a subset of our dataset (LeTourneux et al., 2022) or our a-priori knowledge of the system for parameters that were not previously estimated. The dataset was simulated with a random effect of year on adult and juvenile survival and on live and dead encounter probabilities. We included a negative effect of hunting regulation changes for occasions 14 to 26 that was strong for adults (β_{hunt_ad} = -0.62) and weak for juveniles (β_{hunt_juv} = -0.30), and a moderate mismatch effect on juvenile survival ($\beta_{mismatch}$ = -0.12). We simulated probabilities that birds belonged to a high or low encounter group, and these differed between age classes (adults: 0.15 in high encounter group) and between sexes for juveniles (0.01 and 0.1 in high encounter group for males and females, respectively). Finally, we also simulated a probability of permanent emigration which also differed between sexes and age classes. This probability was 0 for adult females and was set equal to the adult mortality probability (i.e., 1-survival) at each occasion for adult males. For juveniles, permanent emigration probability was 0.9 and 0.1 for males and females, respectively.

Estimation of parameters linked to heterogeneity in live encounter probability was unstable, as evidenced by the traceplots and posterior distributions of estimates for probabilities of belonging to either encounter group for adults and to a lesser extent for juveniles (Fig. S5.6). Despite this instability, annual survival estimations for both adults and juveniles as well as the effect of the mismatch on juvenile survival were close to simulated values and were all included in the 95% credible intervals of parameter estimates (Figs S5.7 and S5.8).

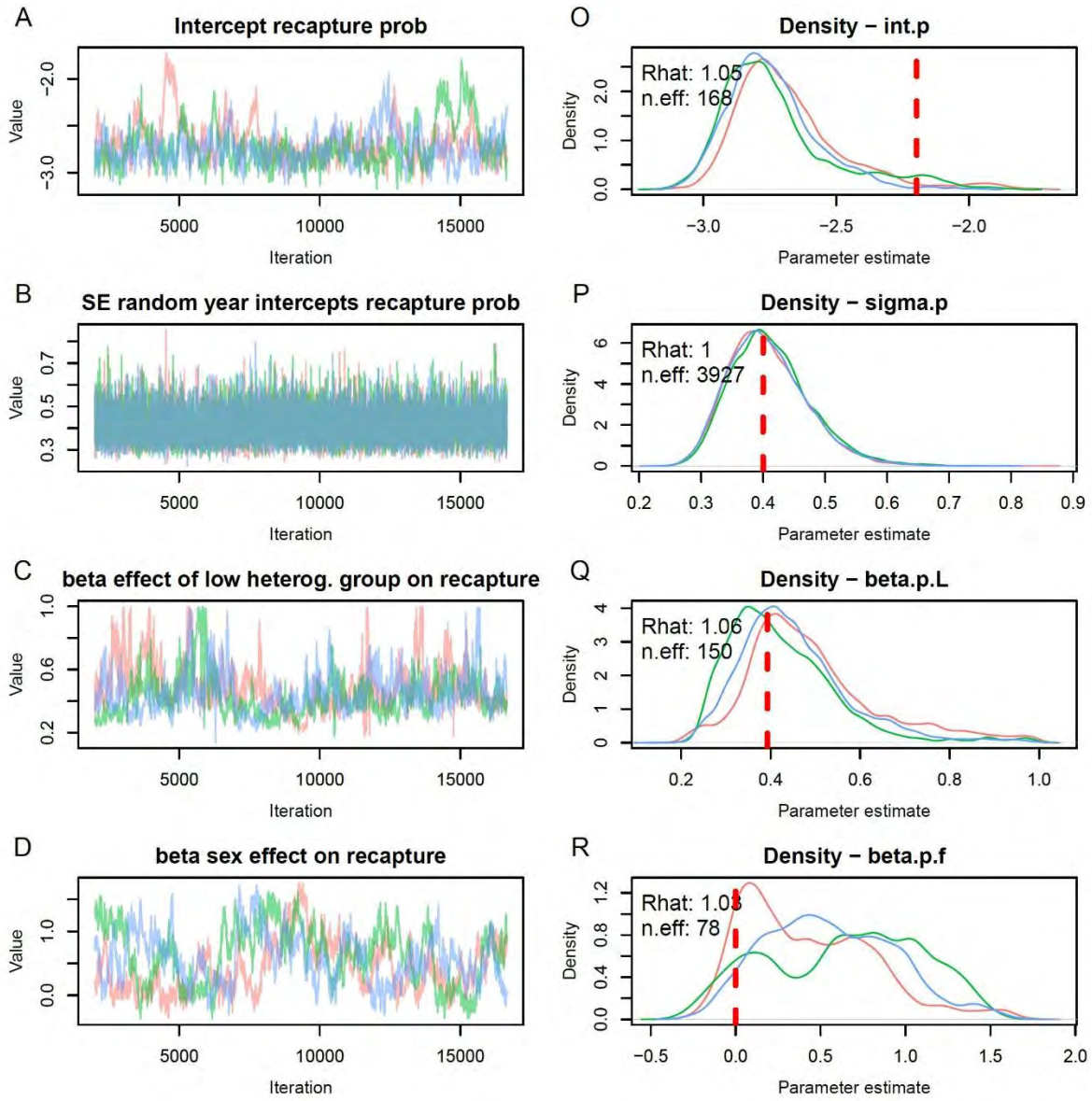

Figure S5.6 Trace plots (left, A to N) and density plots (right, O to AB) of parameters linked to heterogeneity in live encounter probability from the analysis of the simulated dataset (see text). The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot. The red dashed lines represent input parameter values.

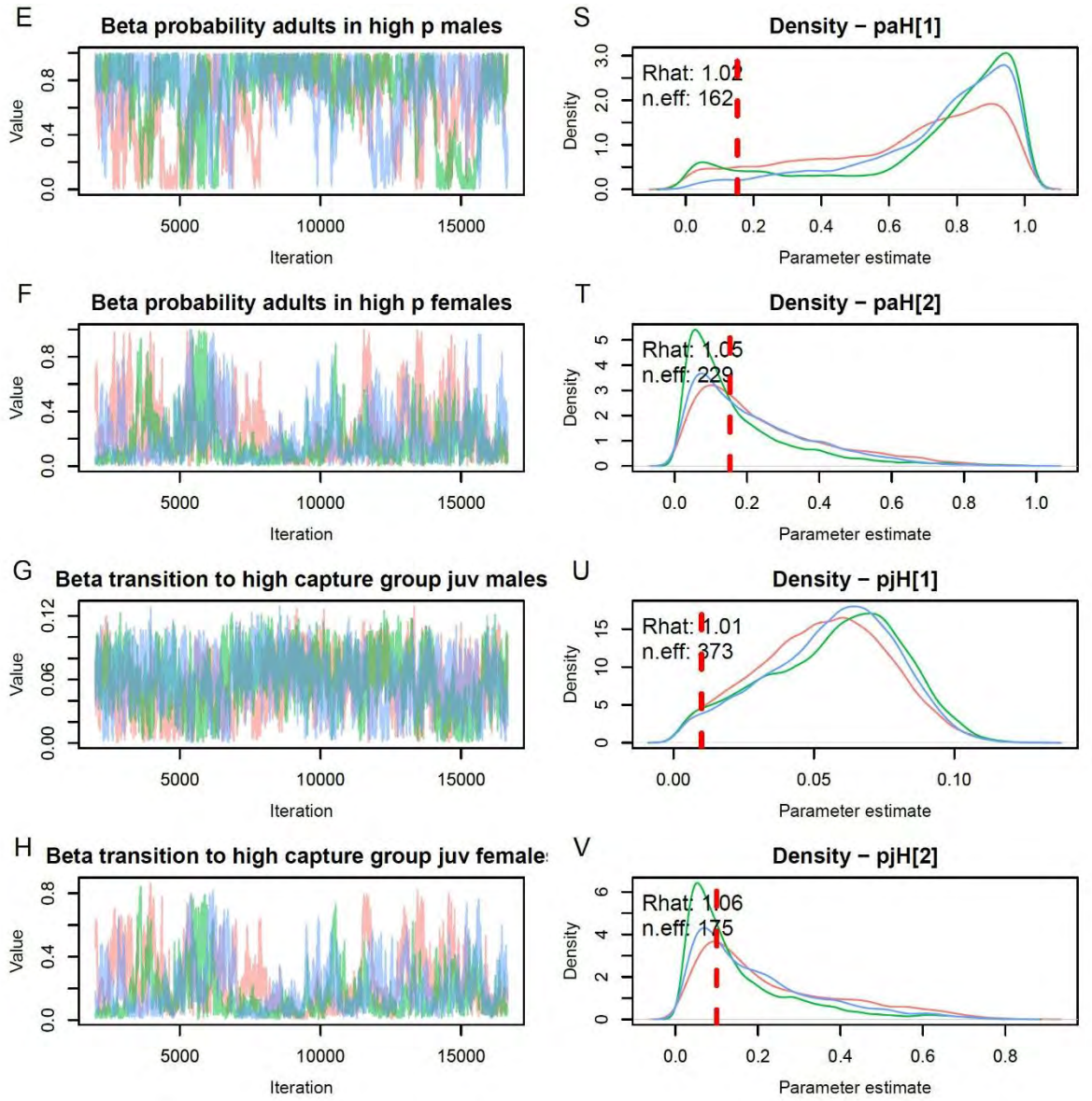

Figure S5.6 Trace plots (left, A to N) and density plots (right, O to AB) of parameters linked to heterogeneity in live encounter probability from the analysis of the simulated dataset (see text). The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot. The red dashed lines represent input parameter values.

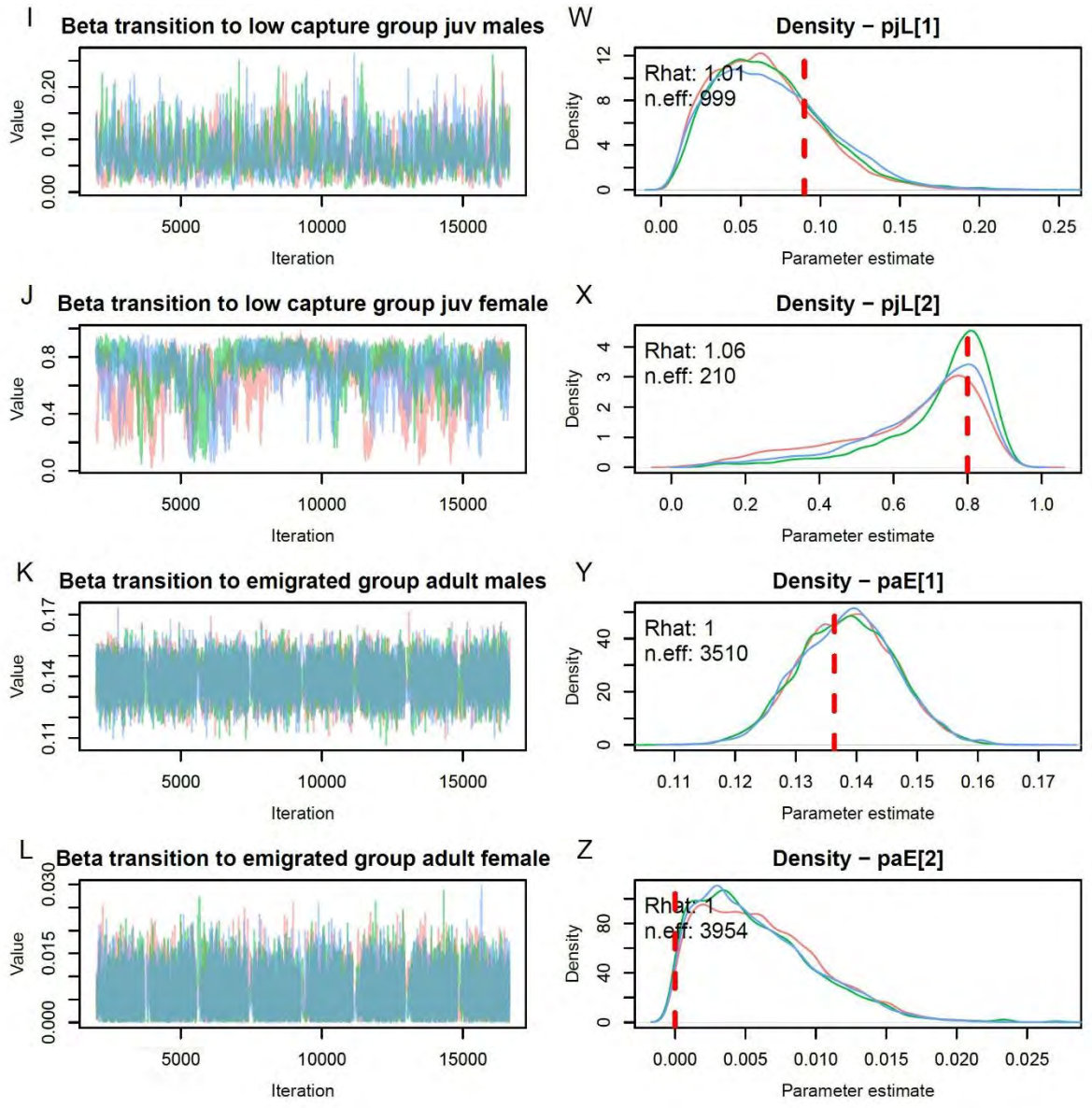

Figure S5.6 Trace plots (left, A to N) and density plots (right, O to AB) of parameters linked to heterogeneity in live encounter probability from the analysis of the simulated dataset (see text). The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot. The red dashed lines represent input parameter values.

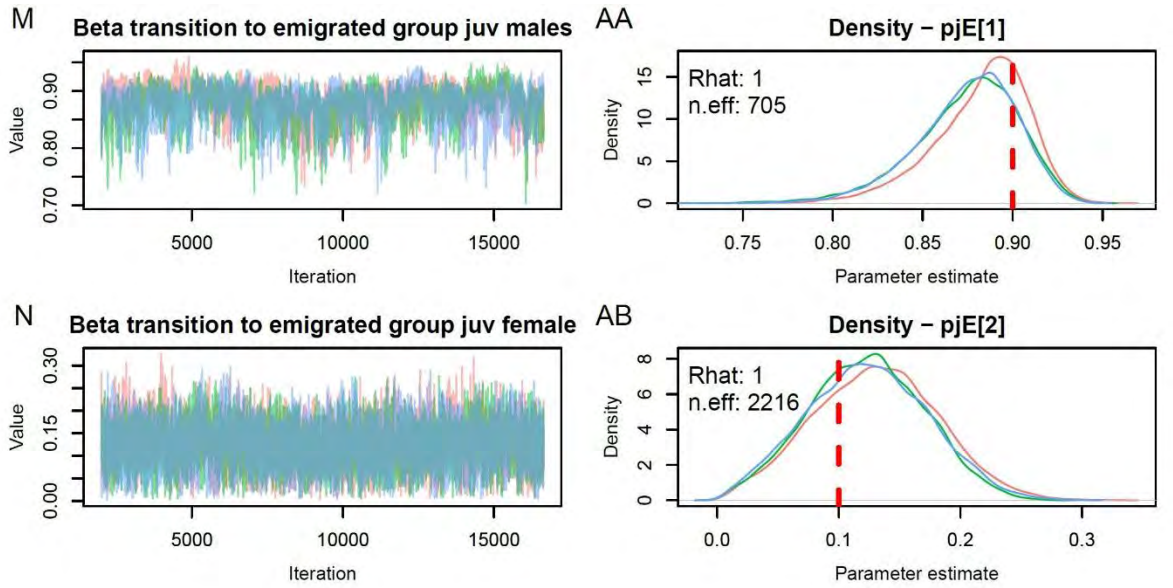

Figure S5.6 Trace plots (left, A to N) and density plots (right, O to AB) of parameters linked to heterogeneity in live encounter probability from the analysis of the simulated dataset (see text). The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot. The red dashed lines represent input parameter values.

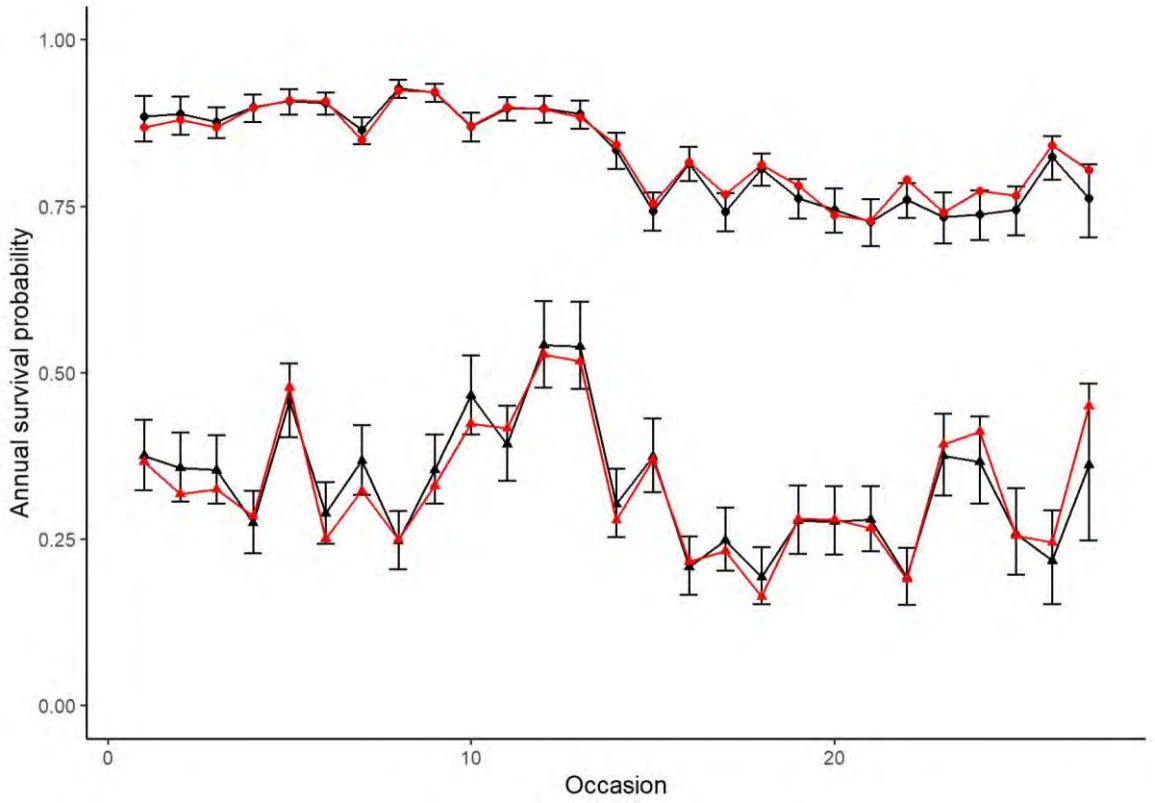

Figure S5.7 Simulated (red) and estimated (black) values of annual survival for adults (circles) and juvenile (triangles) from the analysis of the simulated dataset (see text). Error bars are the 95% credible intervals.

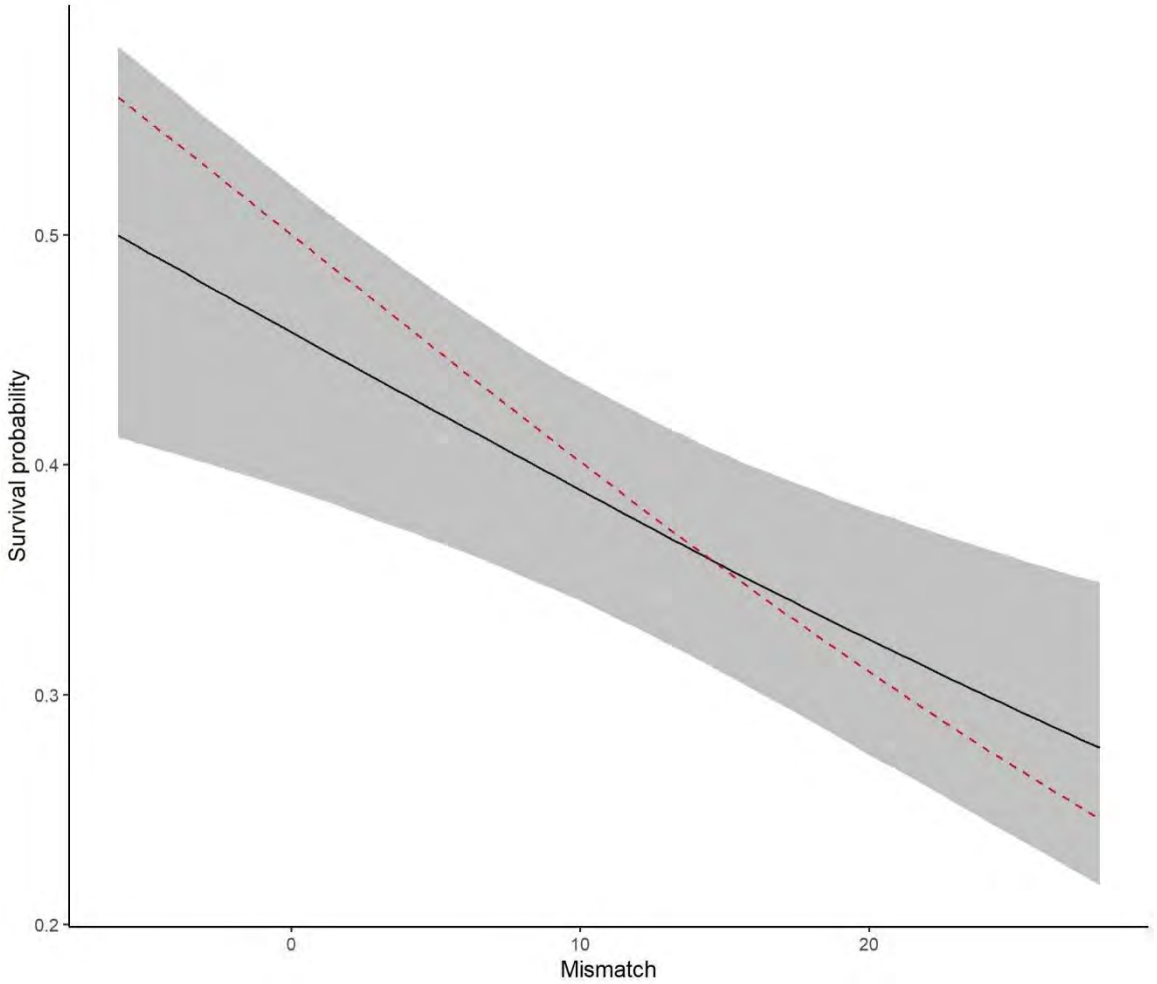

Figure S5.8 Relationship between annual survival probability and the mismatch (differences between hatching date and date of peak plant quality) from the analysis of the simulated dataset (see text). The black line represents mean model predictions along with its 95% credible interval (gray shading). The red dotted line represents the simulated relationship between annual survival and the trophic mismatch.

Bibliography

LeTourneux, F., Gauthier, G., Pradel, R., Lefebvre, J., Legagneux, P., 2022. Evidence for synergistic cumulative impacts of marking and hunting in a wildlife species. J. Appl. Ecol. 1365-2664.14268. https://doi.org/10.1111/1365-2664.14268

Annexe S5.5 – Trace plots and density plots from the analysis of the real dataset

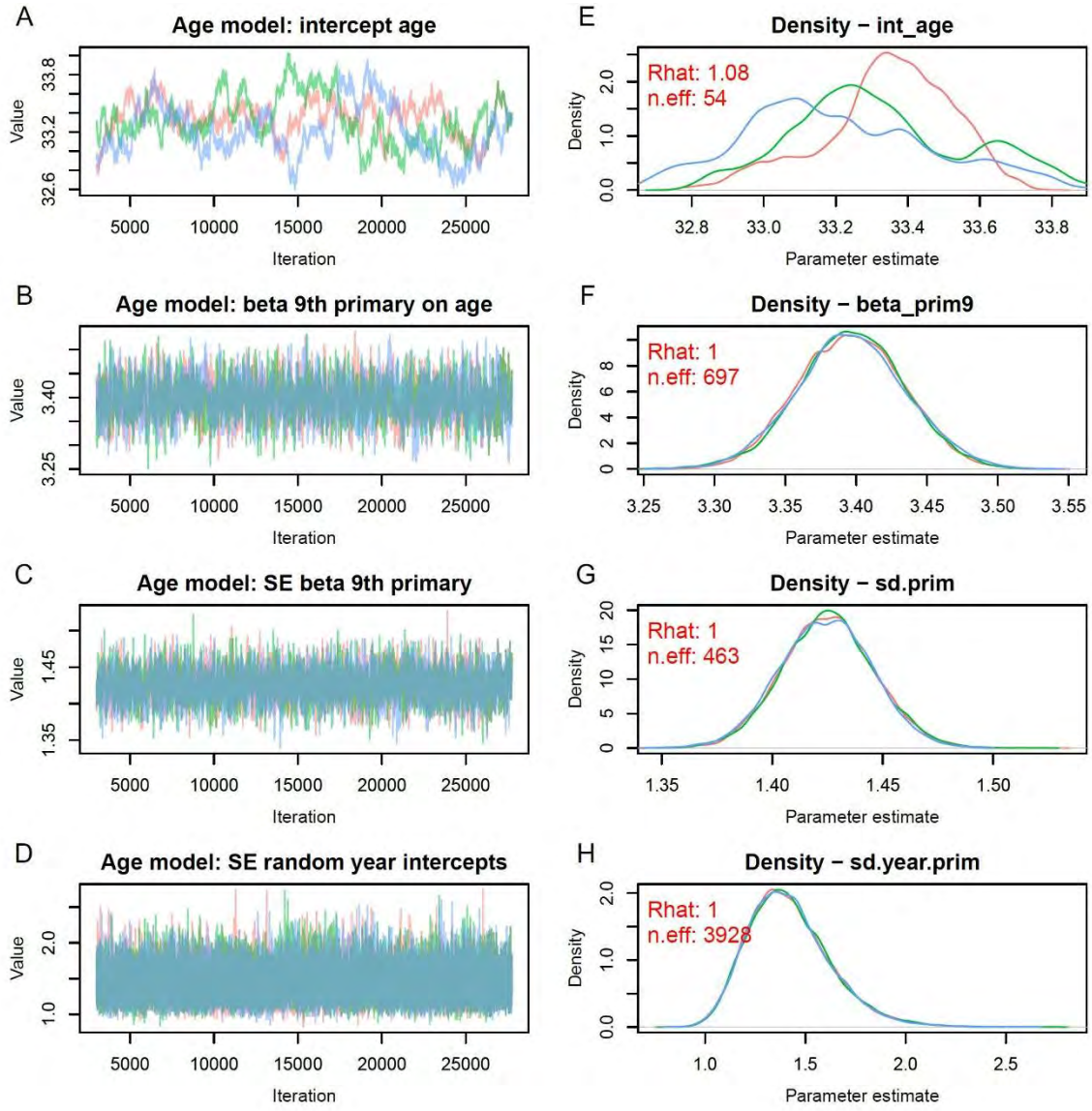

Figure S5.9 Trace plots (left, A to D) and density plots (right, E to H) of model parameters for the age estimation model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

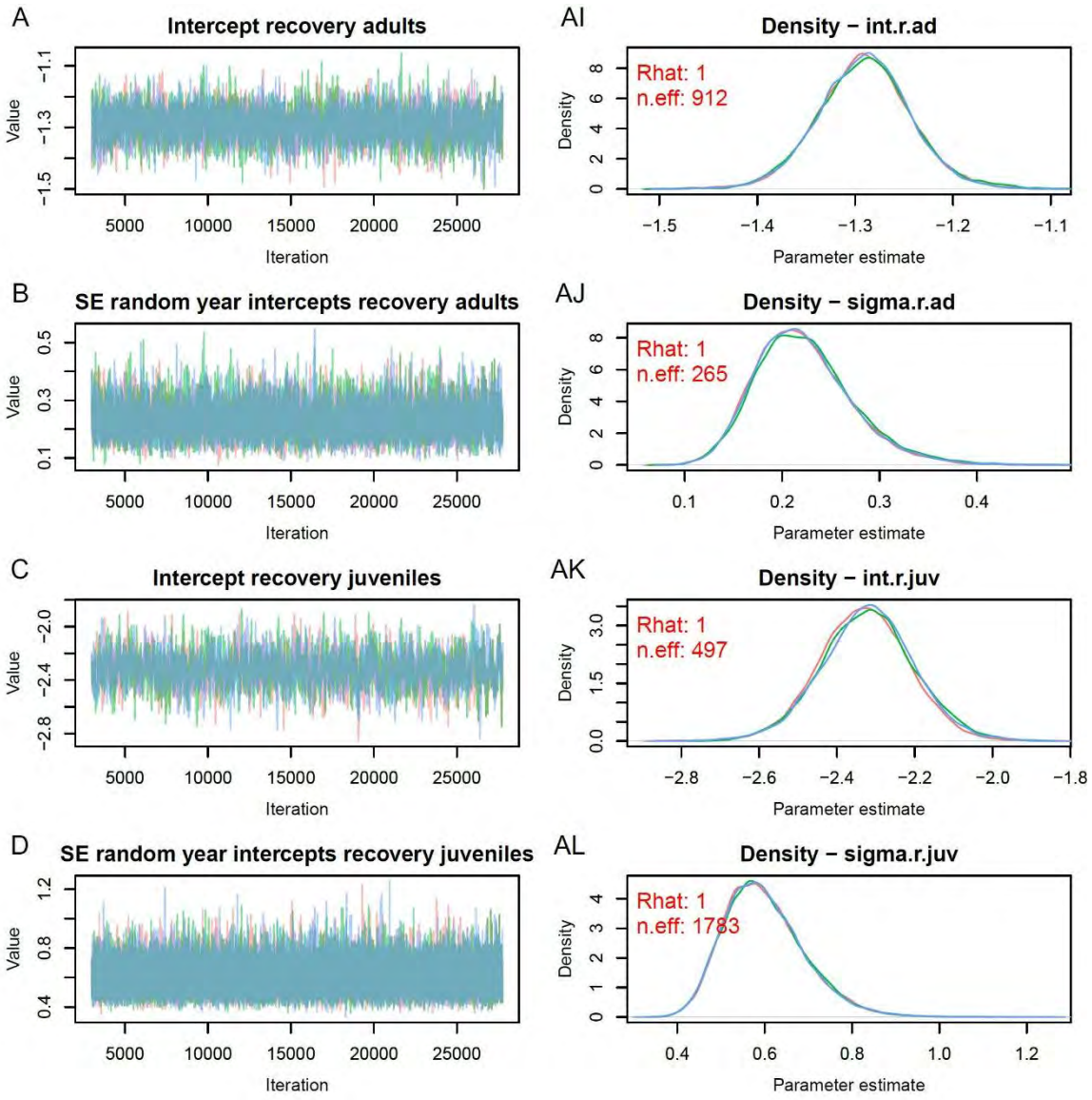

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

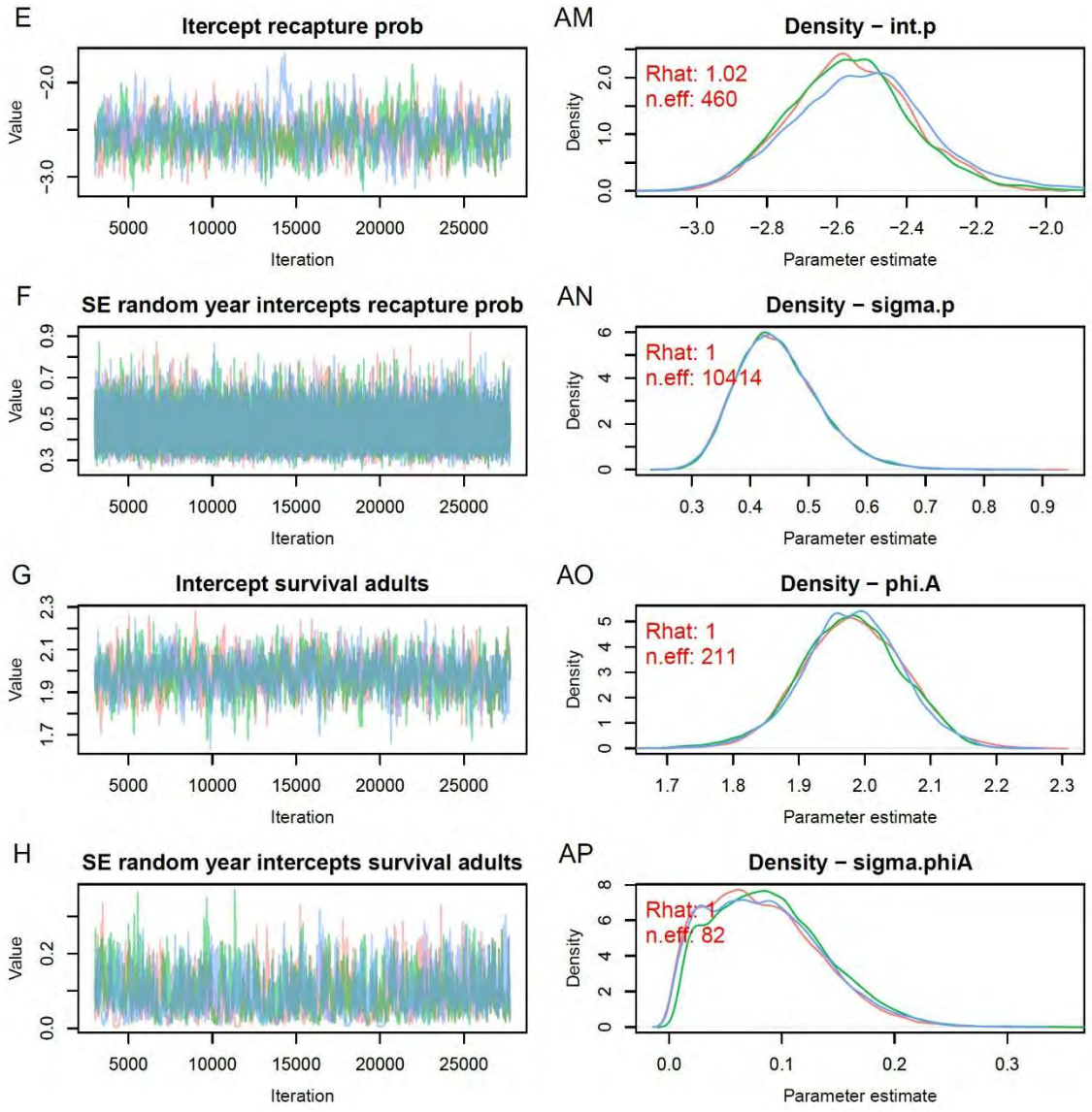

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

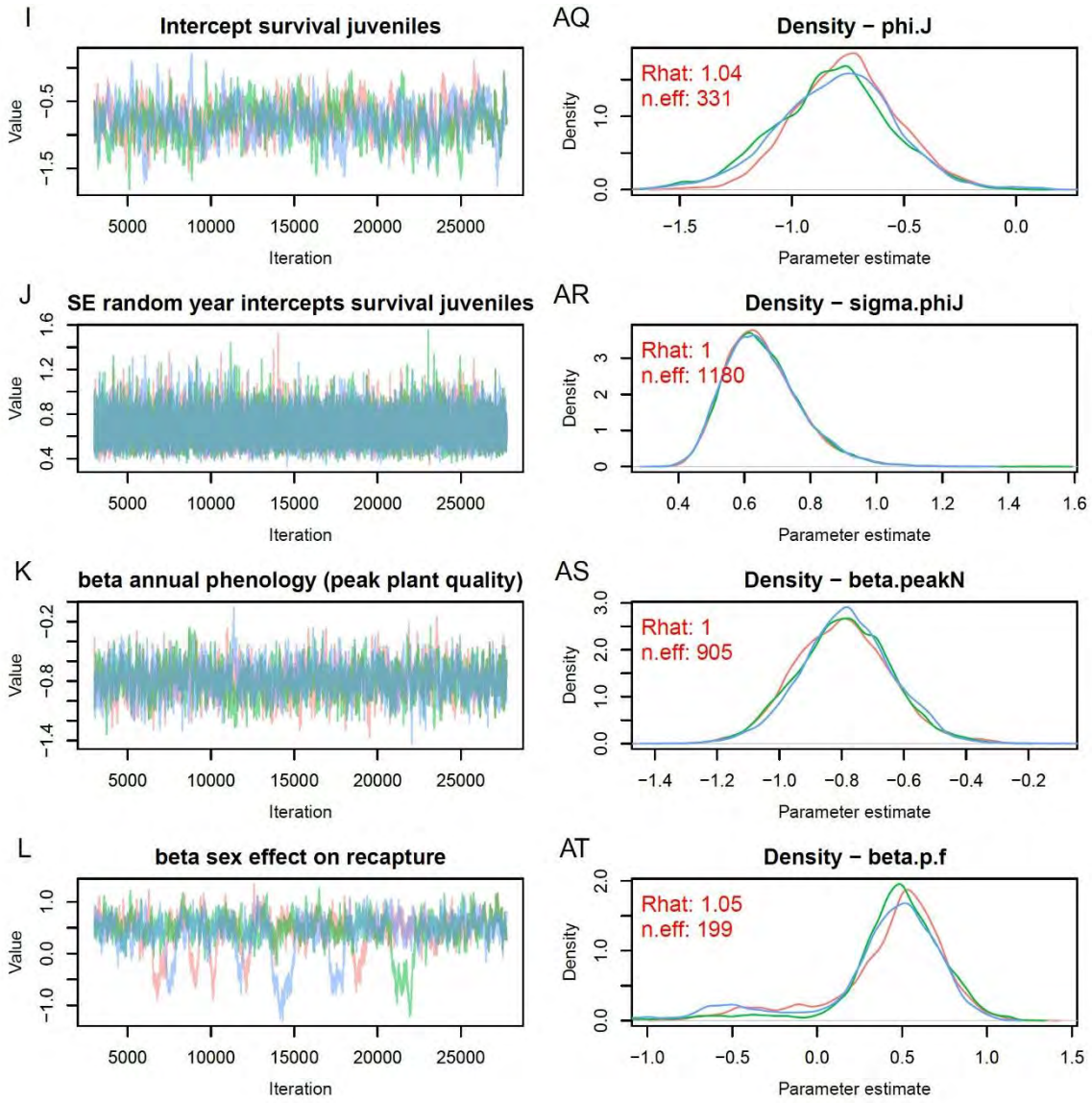

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

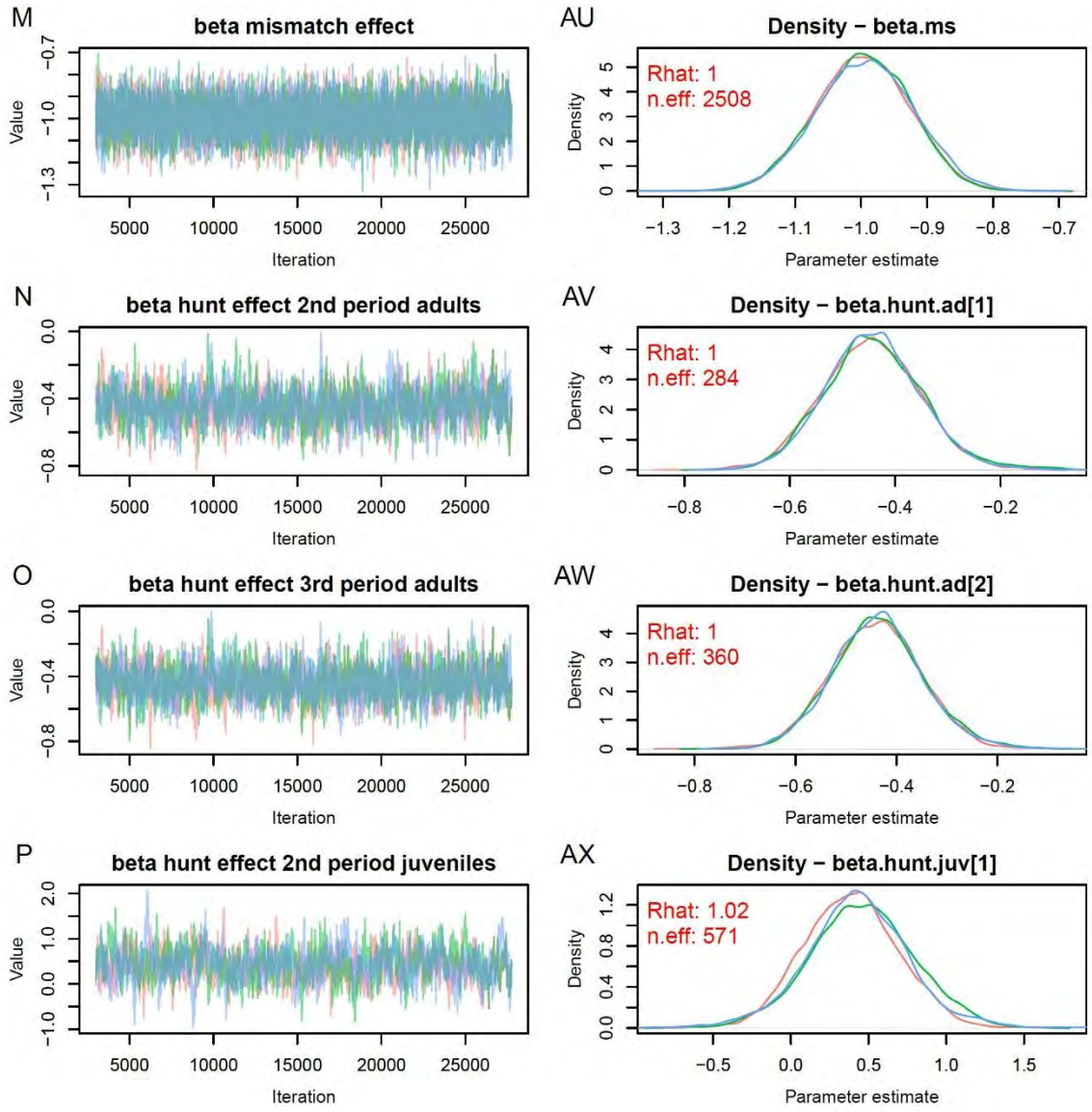

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

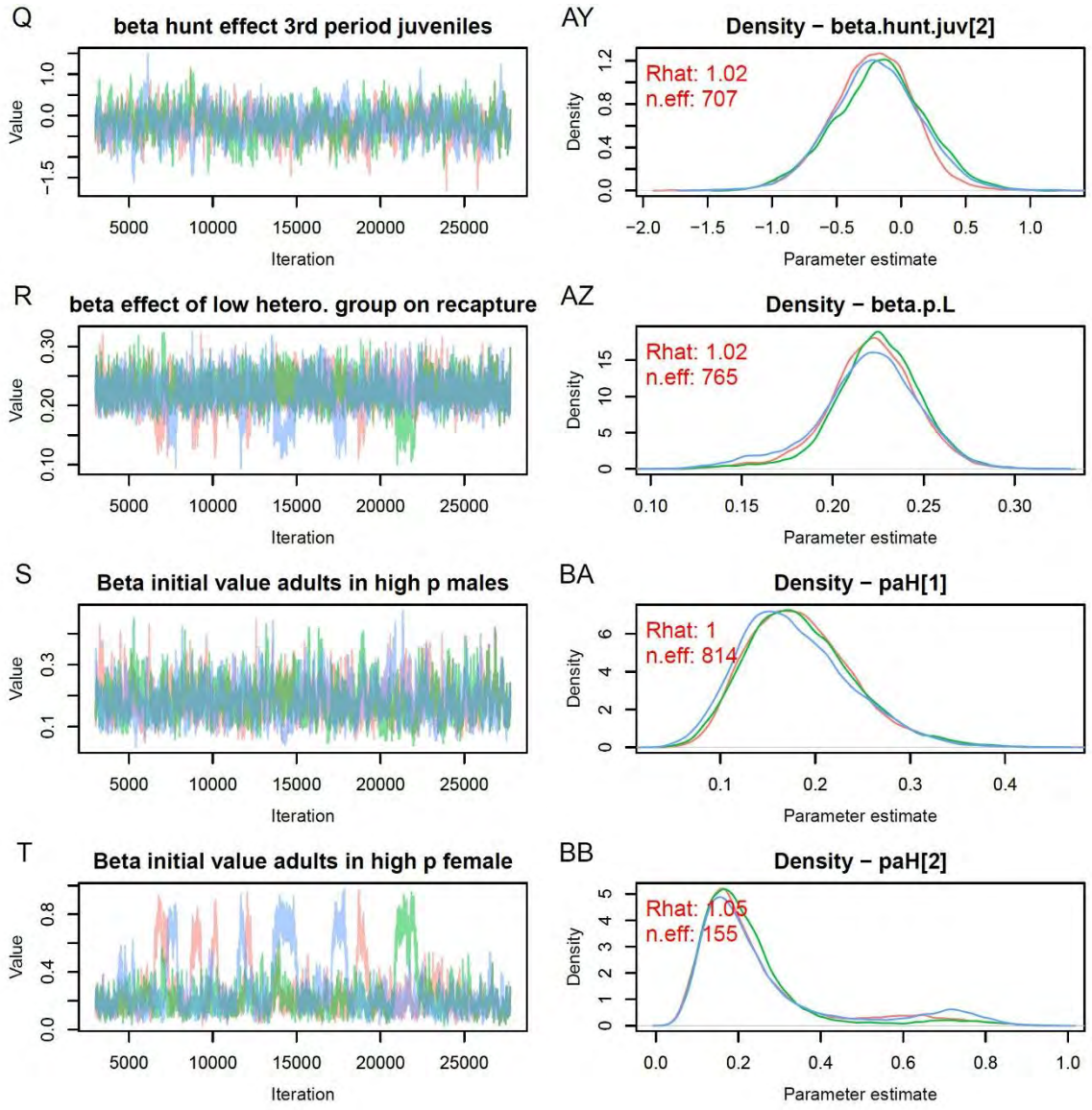

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

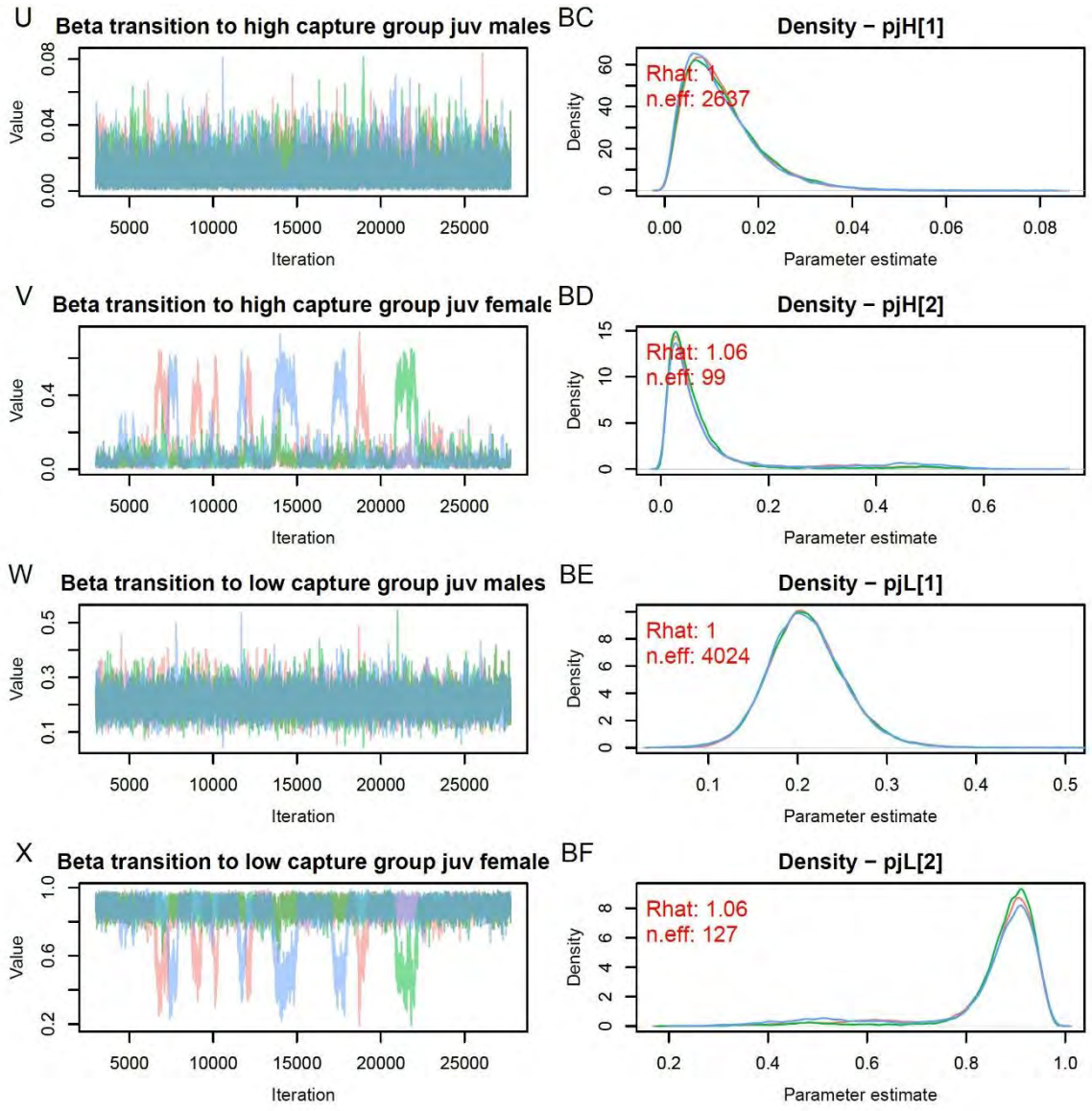

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

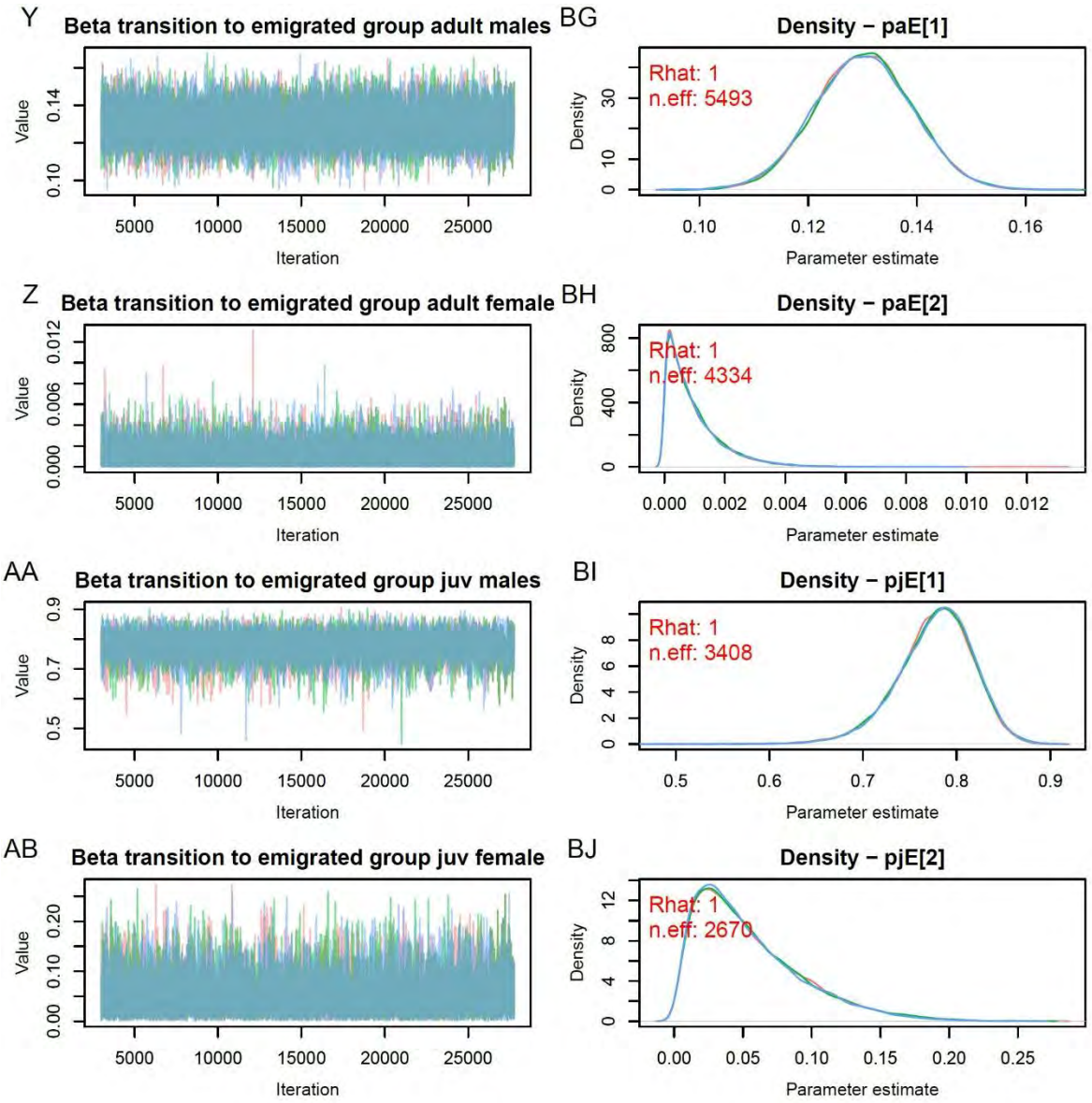

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

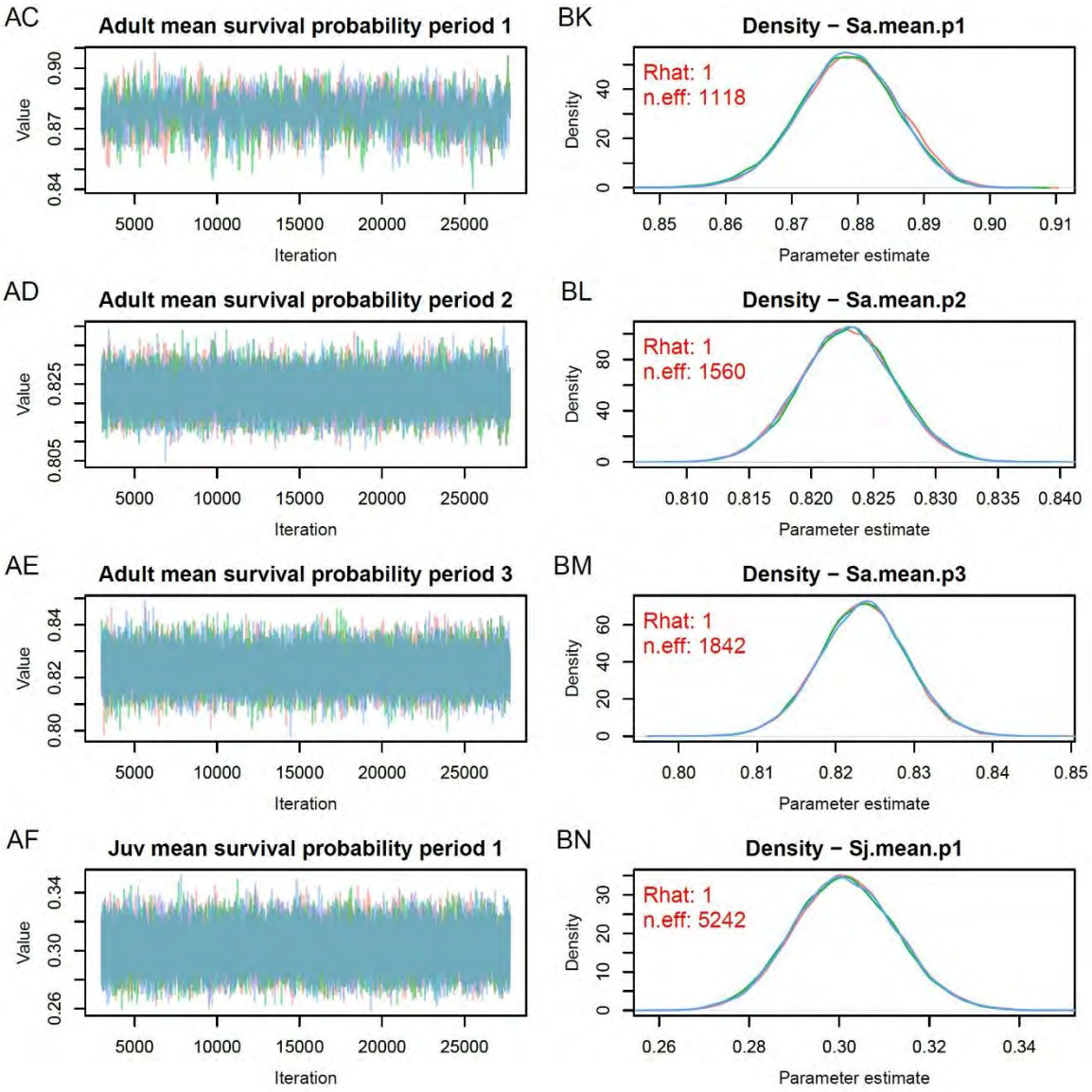

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.

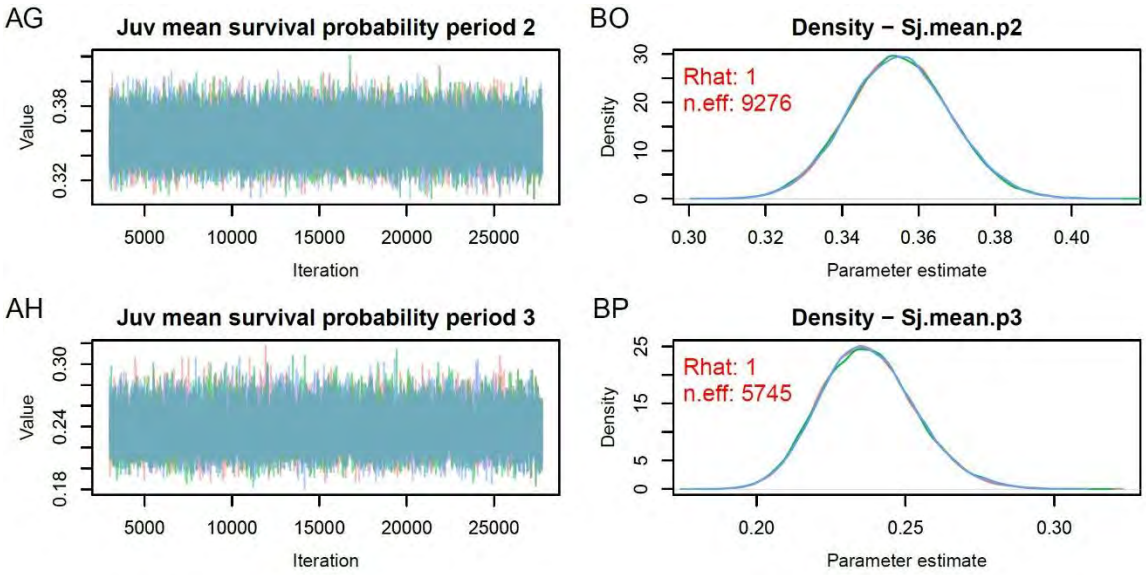

Figure S5.10 Trace plots (left, A to AH) and density plots (right, AI to BO) of model parameters for the survival model. The R-hat statistic and the number of effective samples (n.eff) are provided in the top left corner of each density plot.