Effets des conditions environnementales, de la condition corporelle et du statut hormonal sur la mue de la grande oie des neiges *(Chen caerulescens atlantica)*

Mémoire

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RÉSUMÉ

Les oiseaux en mue font face à des contraintes temporelles et environnementales, surtout chez certains Anatidae parce qu'ils muent toutes leurs plumes de vol simultanément durant le court été arctique. Nous avons examiné comment ces contraintes influencent la phénologie de la mue de la grande oie des neiges ainsi que le rôle des hormones et des facteurs environnementaux dans le contrôle de la mue et de la qualité des plumes. Nous avons utilisé une base de données de plus de 20 ans afin d'examiner l'effet des conditions environnementales et de la reproduction sur la phénologie de la mue, et des hormones thyroïdiennes (T3) et de stress et de la condition physique des individus durant deux ans afin de voir leurs effets sur le déroulement de la mue et la qualité des plumes. Nos résultats mettent en évidence une plasticité phénotypique basée sur un ajustement de la vitesse de croissance des plumes plutôt que sur un avancement de la date de début de la mue lors d'années tardives. Une baisse de la vitesse de croissance des plumes vers la fin de la mue pourrait s'expliquer par une chute de T3 à ce moment. Nous montrons par ailleurs que l'intensité de la mue et la condition corporelle sont réduits par des niveaux élevées d'hormones de stress. Toutefois, la rigidité flexionnelle des plumes, un indice de leur qualité, n'était pas affectée par la condition physique ou le niveau d'hormone de stress des individus. La plasticité phénotypique de la mue permettrait d'achever le renouvellement des plumes de vol avant la fin du court été arctique, indépendamment de la phénologie de la reproduction et des conditions environnementales printanières, tout en maintenant un niveau élevé de qualité des plumes.

ABSTRACT

Molting birds are facing temporal and environmental constraints, especially in some Anatidae because they renew all their flight feathers simultaneously during the short Arctic summer. We examined how these constraints could influence the molt phenology of greater snow geese and we explored the role of hormones and environmental factors in controlling molt and feather quality. We used a 20+ year database to examine the effects of environmental conditions and reproduction on molt phenology and we measured thyroid (T3) and stress hormones and body condition of individuals for two years to examine their effects on molt and feather quality. Our results show phenotypic plasticity based on an adjustment of feather growth speed rather than on advancement of the molt initiation date during late years. A decline in feather growth rate at the end of molt could be explained by a drop in T3 at this time. We also show that high levels of stress hormones could reduce molt intensity and body condition. However, the bending stiffness of feathers, an index of their quality, was not affected by body condition or stress hormone level. The phenotypic plasticity of molt allows a complete renewal of flight feathers before the end of the short arctic summer, regardless of reproductive phenology and spring environmental conditions, while maintaining a high level of quality for feathers.

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REMERCIEMENTS

Cette étude à été financé par le Conseil de Recherche en Sciences Naturelles et en Génie du Canada, Le Plan Conjoint des Oies de l'Arctique (Environnement Canada), le réseau de Centre d'excellence ArcticNet, le Centre d'Études Nordiques et le Programme du Plateau Continental Polaire (ressources Naturelles Canada).

J'aimerais remercier Gilles Gauthier, qui m'a fait confiance pour assurer la continuité de la base de données sur l'oie des neiges à Bylot et qui m'a ainsi permis de continuer mes rêves et mon cheminement polaire. Merci aussi pour sa pédagogie et sa patience face à mes analyses statistiques et mon anglais.

J'aimerais remercier Pierre Legagneux pour son aide précieuse tout au long de ma maîtrise. Au-delà des sciences, merci pour son soutien et ses conseils qui resterons toujours utiles.

Merci à Jacques Larochelle, merci infiniment pour ces moments de partage et pour ces heures de discussion économico-socio-psycho-physico-mécano-éco-physiologique qui m'ont énormément apporté tant sur le plan humain que scientifique.

Merci à l'ensemble des membres du laboratoire qui ont rendu ces trois années particulièrement agréables. Merci DD, Dom, Audrey, Cynthia, Marie-Christine et Marie-Claude pour votre aide et votre bonne humeur.

Merci à tous les Bylotien(nes) avec qui j'ai eu la chance de partager des moments de terrain, de vie et qui ont contribué à rendre ceci encore plus beau. Merci entre autres à Audrey, Caro, Clément, David, Don-Jean, Eric, Etienne, Flo, Fred, Gab, Isabeau, J-Choubinou-F, Jo, Joasie, Joël, Pascal, Steph, Veillette…

Merci à ma copine pour son soutien, sa compréhension et pour le partage de cette passion débordante.

AVANT-PROPOS

Ce mémoire est composé d’une introduction, d’une conclusion générale ainsi que deux chapitres rédigés en anglais pour publications dans des revues scientifiques. Les co-auteurs des articles ont contribué de la manière suivante :

Gilles Gauthier (chapitre 1 et 2) a fourni l’idée originale du projet et a contribué à sa planification, aux analyses et à la rédaction du manuscrit.

Pierre Legagneux (chapitre 1 et 2) a contribué aux analyses et à la rédaction du manuscrit.

Marie Christine Cadieux (Chapitre 1) a contribué au traitement des données et à la logistique de terrain.

Jacques Larochelle (Chapitre 2) a contribué à la conception et la réalisation du dispositif expérimental permettant de mesurer la rigidité des plumes.

Flavie Noreau (Chapitre 2) a contribué aux mesures de la rigidité flexionnelle des plumes.

INTRODUCTION GENERALE

Les contraintes du milieu arctique sur les oiseaux migrateurs

Selon l'IPCC (2013), la température terrestre moyenne a augmenté de 0.85°C au cours du dernier siècle. Cette augmentation est pratiquement deux fois plus rapide dans les régions arctiques que sur le reste de la planète et pourrait atteindre entre 1.8 et 4°C à la fin du XXI siècle. Les projections concernant le réchauffement font apparaître une réduction de la couverture neigeuse et une augmentation d'épaisseur de la couche de dégel dans la plupart des régions à pergélisol (IPCC, 2013). Pourtant, d'autres modèles prévoient également une augmentation des précipitations dans les hautes latitudes (Hassol, 2004) et il est possible que dans les régions arctiques, ces précipitations tombent sous forme de neige au printemps. Quoi qu'il en soit, les changements climatiques constatés et annoncés ont un impact direct sur les conditions de neige, de glace et sur l'épaisseur de la couche active. Ces caractéristiques environnementales contraignent fortement le cycle de vie de nombreuses espèces. Les oiseaux migrateurs qui se reproduisent en Arctique pourraient être considérablement impactés par ces changements.

Les oiseaux migrateurs sont contraints par un été très court pour compléter leur cycle vital dans l'Arctique. Ces oiseaux doivent terminer la totalité du cycle de reproduction avant la fin de la saison estivale pour permettre aux juvéniles d'effectuer leur premier envol lors de la migration vers les sites d'hivernages (Lesage et Gauthier, 1998). En plus de la reproduction, la mue est une autre activité du cycle vital de ces oiseaux qui doit être achevée, généralement, après la reproduction et avant la migration automnale (Fig. 1). La mue est un processus qui intervient annuellement et qui permet le renouvellement des plumes usées (Holmgren et Hedenström, 1995). Chez la plupart des espèces d'oiseaux migrateurs, la mue est initiée peu de temps après l'élevage des jeunes. Cette activité perturbe les fonctions remplies par les plumes soit le vol et l'isolation thermique des oiseaux (Jenni et Winkler, 1994). Le contrôle de la mue est complexe et fait intervenir de nombreux facteurs endogènes et environnementaux. La période de mue est en effet contrainte par la longueur des saisons (Earnst, 1992) et par la latitude des sites de nidification et d'élevage de la progéniture (Van Der Jeugd *et al*. 2009).

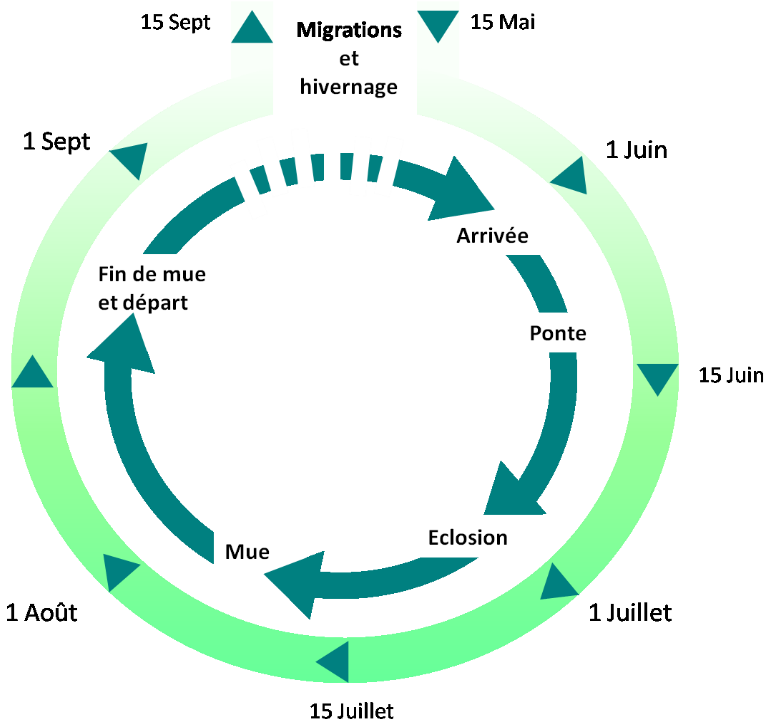

***Figure 1** : Phénologie des principales activités estivales d'un oiseau migrateur Arctique. Les dates correspondent à l'oie des neiges sur l'île Bylot (Nunavut ,Canada)*

L'impact des conditions environnementales et climatiques sur la reproduction a été beaucoup étudié et représente une contrainte importante pour des oiseaux dont le cycle vital est long. La date de ponte de ces oiseaux est en effet fortement reliée à la couverture de neige et aux températures printanières sur les sites de nidification (Bêty *et al.* 2003; Gauthier *et al.* 2003; Dickey *et al.* 2008). Bien que l'effet des conditions environnementales sur la reproduction des oiseaux qui nichent en arctique soit bien documenté, très peu d'études se sont intéressées à l'impact que cela pourrait avoir sur la mue.

Cette étude s'intéresse au cas de l'oie des neiges (*Chen caerulescens)*, une espèce qui niche dans l'Arctique et qui fait face à des contraintes environnementales sévères durant la reproduction et la mue. Le projet permettra d'appréhender l'effet des conditions environnementales et des facteurs endogènes comme la condition corporelle ou le statut hormonal des individus sur la phénologie d'une activité essentielle du cycle annuel des oiseaux telle que la mue et sur la qualité des plumes produites chez l'oie des neiges.

Phénologie et phénomènes de synchronie/asynchronie

La phénologie correspond au calendrier d'initiation des activités essentielles du cycle vital d'un organisme selon les saisons (Berteaux *et al.* 2004). Il apparaît clairement que dans un contexte arctique où les changements climatiques sont accélérés, la phénologie des différentes espèces locales peut être rapidement bouleversée. D'après Both et Visser (2001), les organismes vivants devraient répondre à l'augmentation des températures printanières par un avancement de la période de reproduction. Pourtant, cette adaptation aux changements climatiques est souvent contrainte par des facteurs qui interviennent durant la période de migration, notamment chez les espèces migratrices parcourant de longues distances (Both et Visser, 2001). La photopériode, qui n'est aucunement affectée par les changements climatiques, influence fortement le rythme circannuel propre à chaque espèce et détermine par exemple la date de migration (Gwinner, 1996; Both et Visser, 2001). Ainsi, la réponse au réchauffement climatique à travers les changements phénologiques peut s'avérer bien différente entre les espèces sédentaires et les espèces migratrices. Selon Durant *et al.* (2007), quand tous les organismes ne répondent pas à la même vitesse aux changements climatiques, cela peut conduire à une asynchronie trophique (*match/mismatch hypothesis* en anglais).

En allongeant la durée de la saison estivale, un printemps précoce pourrait avoir des effets bénéfiques pour les oiseaux nichant en Arctique (Møller *et al.* 2009). Pourtant, des effets négatifs dus à une asynchronie avec la disponibilité en nourriture sont également possibles (Visser et Both, 2005; Doiron, 2014). Par exemple, des études réalisées sur la mésange charbonnière (*Parus major*) ou le gobemouche noir (*Fidecula hypoleuca*) ont montré que l'avancement du pic d'abondance de chenilles due aux changements climatiques n'est plus synchronisé avec la demande énergétique maximale de la progéniture de ces oiseaux (Both et Visser, 2001; Visser *et al.* 2004). Chez les espèces herbivores, une accélération de la croissance des plantes suite au réchauffement pourrait induire une asynchronie entre le pic de production végétale et le pic de demande en énergie et en nutriments pour la croissance des jeunes (Dickey *et al.* 2008, Doiron *et al.* 2014). Si la demande énergétique des consommateurs est synchronisée avec le pic de disponibilité de nourriture, alors le recrutement sera maximal. Dans le cas contraire, la disponibilité de nourriture ne concorderait pas avec les exigences énergétiques des consommateurs (i.e. asynchronie) et se traduirait par une baisse de recrutement (Both *et al.* 2006). Il est aussi possible que la discordance entre les besoins énergétiques d'un consommateur et la disponibilité des ressources puissent affecter d'autres activités du cycle vital comme la mue.

Physiologie et coût énergétique de la mue

Coût énergétique de la mue

La mue est un processus physiologique qui intervient annuellement et qui est énergétiquement coûteux, surtout chez les oies et les canards (Dean, 1978; Raveling, 1979; Guillemette, 2007). En effet, chez ces espèces toutes les plumes de vol sont remplacées simultanément plutôt que séquentiellement comme chez la plupart des autres espèces d'oiseaux, ce qui empêche les individus de voler pendant 3 à 4 semaines chaque été. De plus, chez les oies, la mue chevauche la reproduction car elle survient pendant l'élevage des jeunes en été, ce qui est exceptionnel chez les oiseaux. Bien que ceci ait été rendu possible par le mode de reproduction nidifuge de ces oiseaux où les parents ne nourrissent pas leurs jeunes, les adultes fournissent néanmoins des soins parentaux durant l'élevage, ce qui représente un coût (e.g. vigilance accrue, temps d'alimentation réduit, défense face aux prédateurs, Schindler et Lamprecht, 1987).

La durée de la mue varie d'une espèce à l'autre et dépend entre autre de la distance de migration et de la latitude des sites de mue (Payne, 1972). D'après Murphy et King (1992), la dépense énergétique de la mue est corrélée à la durée de celle-ci. Des études menées sur la bernache nonette (*Branta leucopsis*) en captivité rapportent que ces oiseaux perdent environ 25% de leur masse entre le début et la fin de la mue (Portugal *et al.* 2007). Les même tendances de réduction de la masse des individus en mue ont été mis en évidence sur des bernaches en milieu naturel sur l'archipel du Svalbard (Tombre et Erikstad, 1996; Phillips *et al.* 2003). Cette perte de poids serait liée à une augmentation importante du métabolisme et une dépense énergétique élevée. L'augmentation du métabolisme durant la mue, mesurée à partir de la consommation d'oxygène, à été mise en évidence chez différentes espèces d'oiseaux (Payne, 1972; Green *et al.* 2004). Dans leurs travaux, Portugal *et al.* (2007) concluent que la perte de poids est principalement causée par le fait que la forte demande énergétique de la mue pour la synthèse de nouvelles plumes est assurée principalement par les réserves endogènes. Les travaux réalisés par Owen et Ogilvie (1979) sur la bernache du canada (*Branta canadensis*) ont permis d'estimer qu'environ 10% des dépenses énergétiques de l'oiseau sont allouées à l'activité de mue durant l'été.

La plume est composée à 95% de kératine, une protéine riche en acides aminées sulfurées (cystéine et méthionine; Murphy et King, 1992). La synthèse protéique est un processus énergétiquement coûteux mais la dépense énergétique totale des oiseaux en mue est largement supérieure au seul coût de la synthèse de kératine. Les travaux de Murphy et Taruscio (1995) rapportent que le coût total de synthèse de nouveaux tissus par un individu en mue peut être trois fois supérieur au coût de synthèse de la kératine seule. Le maintien des tissus nécessaires à la production de la kératine pourrait représenter en effet la majorité des dépenses énergétiques lors de la mue (Lindström *et al.* 1993; Dawson, 2003). Des changements physiologiques énergétiquement coûteux comme l'augmentation de la volémie ou de la vascularisation sont également observés lors du processus de la mue (Chilgren et DeGraw, 1977; Murphy *et al.* 1992). Enfin, le renouvellement des plumes entraine une déperdition de chaleur due notamment à l'augmentation de la conductance et de l'évaporation, ce qui provoque des coûts supplémentaires pour la thermorégulation des oiseaux lors de l'activité de mue (Chilgren et DeGraw, 1977)

Contrôle physiologique de la mue

La mue chez les oiseaux est sous contrôle hormonal et serait notamment influencée par les hormones thyroïdiennes (Davis et Davis 1954; Wilson et Farner 1960). La thyroxine (T4) et la triiodothyroïne (T3) sont deux hormones circulantes secrétées par la glande thyroïde. L'activité de cette glande endocrine est contrôlée notamment par les hormones hypophysaires et par la photopériode. Les hormones thyroïdiennes sont impliquées dans de nombreux processus physiologiques complexes comme la prolifération cellulaire, le développement, la croissance et la thermogénèse (Hulbert, 2000). Du fait que ces hormones aient différentes fonctions (hormones pléiotropiques), il est parfois difficile de conclure à une relation de cause à effet en présence d’une corrélation entre une activité physiologique précise et l’augmentation des hormones thyroidiennes (Jenni-Eiermann *et al.* 2002). Néanmoins, de nombreuses études mettent en évidences les variations saisonnières de l’activité de la thyroïde grâce aux mesures des niveaux circulatoires de T3/T4 (Scanes, 1979; Campbell et Leatherland, 1980; Groscolas et Leloup 1986; Lien et Siopes, 1993). Plusieurs travaux ont montré une relation entre l’augmentation des hormones thyroïdiennes, notamment de la thyroxine circulante, et l’activité de mue (Smith *et al.* 1982; Groscolas et Leloup, 1986 ; Groscolas et Cherel, 1992; Jenni-Eiermann *et al.* 2002). D’après Newcomer (1957), les hormones thyroïdiennes stimulent la croissance et la prolifération cellulaire dans la papille dermique de la plume et selon Stokkan *et al.* (1985) les niveaux élevés de thyroxine circulant coïncident avec le renouvellement des plumes chez le lagopède alpin (*Lagopus muta hyperborea*). Enfin, Vézina *et al.* (2009) rapportent que l’augmentation des niveaux de thyroxine est reliée à une augmentation du métabolisme basal d’environ 10% lors de la mue chez le bécasseau maubèche (*Calidris canutus islandica*).

Facteurs environnementaux et endogènes pouvant influencer la phénologie de la mue

L’effet des conditions environnementales sur la phénologie de la mue a été peu étudié comparativement aux autres activités du cycle vital comme la reproduction, notamment à cause de la difficulté logistique de suivre plusieurs espèces en milieu naturel au moment de la mue. De nombreux travaux ont permis d’évaluer l’impact des conditions climatiques sur la phénologie de la reproduction (Both et Visser, 2001; Durant *et al.* 2007; Post et Forchammer, 2008). Ces impacts sont particulièrement importants chez les espèces nichant dans l’Arctique. Par exemple, des travaux ont mis en évidence la corrélation entre la couverture neigeuse au printemps et l’initiation de la reproduction chez différentes espèces d’oies (voir Bêty *et al.* 2003 ; Dickey *et al.* 2008 chez la grande oie des neiges *Chen caerulescens atlantica* ou Madsen *et al.* 2007 chez l’oie à bec court *Anser brachyrhynchus*). Le début de la nidification est en effet retardé et la taille des couvées réduite lors des années où la couverture de neige est importante au printemps. Lorsque les oies échouent leur nidification, la mue intervient généralement plus tôt que chez les oiseaux qui nichent avec succès et qui doivent élever des jeunes. La date de mue apparaît donc comme un compromis entre les coûts d'une initiation tardive de la mue (e.g. lorsque les oies se reproduisent) et les bénéfices associés au commencement de la mue tôt dans la saison (e.g. lorsqu'il n'y a pas la contrainte de reproduction).

Les oies sont un modèle biologique très pertinent pour étudier les compromis possibles entre mue et reproduction car les individus reproducteurs demeurent sur les sites de reproduction pour effectuer leur mue, ce qui facilite le suivi (Reed *et al.* 2003). Les oies dépendent à la fois des réserves endogènes accumulées lors des haltes migratoires et de la disponibilité de nourriture sur les sites de nidification pour investir dans la reproduction et notamment dans la formation des œufs (Choinière et Gauthier, 1995; Gauthier *et al.* 2003). Lors d'un printemps tardif, non seulement le début de la nidification sera retardé mais la condition corporelle des individus risque aussi d'être réduite à cause d'un manque de ressources en pré-ponte. Ceci pourrait avoir des répercussions importantes sur la mue, notamment en retardant le début de cette activité ou en forçant les individus à l'entreprendre avec une condition corporelle réduite. Si le début de la mue est retardé, les oies pourraient manquer de temps pour compléter cette activité importante avant la fin du court été arctique. D'autre part, si la phénologie de la mue n'est pas retardée lors de printemps tardifs, les oies pourraient ne pas avoir assez de temps pour reconstituer leurs réserves endogènes après la fin de l'incubation, ce qui pourrait affecter le déroulement de la mue, notamment en diminuant la qualité des nouvelles plumes (voir plus bas). Des études menées sur différentes populations de bernache nonette (*Branta leucopsis*) suggèrent que la phénologie de la mue apparaît moins flexible que la phénologie de la reproduction (Van der jeudg, 2009), peut-être à cause de facteurs de régulations endogènes (e.g. hormones) qui seraient peu sensibles aux facteurs environnementaux.

Stress durant la mue et qualité des plumes

Des conditions environnementales difficiles ou une condition physique réduite des individus peuvent être des sources importantes de stress chez les animaux et avoir des répercussions sur certaines fonctions physiologiques. La réponse au stress chez les oiseaux est accompagnée d'une libération d'hormone stéroïde telle que la corticostérone (Romero, 2004) qui permet notamment de maintenir en alerte un individu en situation de stress et de mieux y répondre (Sapolsky *et al.* 2000). Les oiseaux migrateurs nichant en Arctique sont souvent exposés à des conditions climatiques très rudes comparativement aux espèces qui nichent dans les milieux plus tempérés, ce qui peut induire une source de stress supplémentaire (Wingfield et Hunt, 2002; Bokony *et al.* 2009). Toutefois, des niveaux prolongés de corticostérone peuvent avoir un effet négatif sur certaines fonctions physiologiques comme le système immunitaire (Khansari *et al.* 1990; O'Neal et Ketterson 2012) ou le renouvellement des plumes en ralentissant ou en provoquant des interruptions de croissance comme chez l'étourneau sansonnet (*Sturnus vulgaris*; Strochlic et Romero, 2008). D'autres expérimentations réalisées sur la même espèce ont montré qu'un stress chronique comme la restriction en nourriture pouvait aussi influencer la qualité des nouvelles plumes formées lors de la mue (Desrocher *et al.* 2009). En effet, dans des conditions de stress chronique, la distance inter-barbule augmente, le nombre de barbules sur les primaires diminue et les plumes deviennent plus cassantes lorsqu'elles sont soumises à des contraintes de tension.

La régulation de la corticostérone pourrait apparaître comme un compromis entre des niveaux élevés permettant une bonne réponse à un stress aigu et des niveaux relativement bas qui assurent par exemple une bonne croissance des plumes lors de la mue (Romero *et al.* 2005; Strochlic et Romero, 2008). Il faut toutefois rester prudent car les expérimentations induisant une diminution de la qualité des plumes ont été réalisées à des taux de corticostérone supérieurs à ce qu'on retrouve en milieu naturel. Néanmoins, plusieurs travaux rapportent que la contraction de la durée de la mue altère aussi la qualité des plumes (Dawson *et al.* 2000; Hall, 2000; Serra, 2001) et pourrait se répercuter sur les capacités de vols, la survie et la reproduction des oiseaux (Dawson *et al.* 2000).

La mesure du stress d'un individu est particulièrement difficile puisque la capture et la manipulation lors du prélèvement d'échantillons provoquent une élévation des niveaux de corticostéroïde, ce qui peut biaiser les résultats si la prise de sang n'est pas réalisée immédiatement après capture (Romero et Reed, 2005). De plus, il n'existe pas de relation entre le niveau basal de corticostérone plasmatique d'un individu et l'élévation des niveaux hormonaux suite à la capture chez l'oie des neiges (Legagneux *et al.* 2011). Par contre, d'après Bortolotti *et al.* (2008), la corticostérone mesurée dans les plumes de perdrix rouge

(*Alectoris rufa*) reflète bien les niveaux plasmatiques de l'hormone durant la croissance des plumes et pourrait donc être un bon indice pour la mesure du stress aviaire pendant la mue.

Objectifs de l'étude

Ce projet vise à évaluer l'impact des conditions environnementales, de la condition corporelle et du statut hormonal des individus sur la mue de l'oie des neiges en combinant des données à long terme (> 20 ans) et une approche éco-physiologique. La grande oie des neiges est une espèce migratrice qui se reproduit dans le haut arctique canadien et qui peut être ainsi confrontée à de sévères conditions environnementales. La date de ponte (médiane = 12 juin) suit de près la disparition du couvert neigeux. Peu de temps après l'éclosion (début du mois de juillet), les oies initient leur mue et renouvellent la totalité des plumes de vol, ce qui entraine une incapacité de voler durant 3 à 4 semaines. Le recouvrement des capacités de vol intervient au mois d'août et précède la migration automnale vers les sites d'hivernage.

Le premier chapitre de ce mémoire vise à examiner, à l'échelle populationnelle, l'effet de la phénologie annuelle de la reproduction et des conditions environnementales sur la phénologie de la mue et la condition corporelle des oies adultes femelles en mue. Face aux contraintes temporelles auxquelles sont confrontées les oies nichant en arctique, nous nous attendons à de possibles ajustements de la date d'initiation de la mue et nous émettons l'hypothèse que la phénologie de la mue est moins flexible que la phénologie de la reproduction.

L'objectif principal du deuxième chapitre vise à examiner, à l'échelle individuelle, l'effet de la phénologie de la mue, des hormones thyroïdiennes (T3), du stress (corticostérone) et de la condition corporelle sur le déroulement de la mue de l'oie des neiges et la qualité des plumes nouvellement synthétisées. Nous émettons l'hypothèse que la date d'initiation de la mue se répercute sur l'activité métabolique et sur les niveaux de corticostérone mesurés durant la mue. De plus, nous émettons l'hypothèse que la condition corporelle et les niveaux de corticostérone pourraient affecter la qualité des nouvelles plumes.

CHAPITRE 1

PLASTICITY IN MOLT SPEED AND TIMING IN AN ARCTIC-NESTING GOOSE SPECIES

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RESUMÉ

Les contraintes environnementales sont particulièrement fortes chez les espèces migratrices qui se reproduisent dans l'Arctique. En plus de la reproduction, les Anatidae doivent renouveler simultanément l'ensemble de leurs plumes de vol durant la courte période estivale. Nous examinons ici comment les contraintes temporelles et climatiques affectent la phénologie de la mue des plumes de vol chez une espèce qui niche dans le Haut Arctique, la grande oie des neiges (*Chen caerulescens atlantica*). Nous utilisons une base de données comprenant 1412 femelles adultes en mue mesurées pendant 15 ans à l'île Bylot, Nunavut. La longueur de la 9^{e} primaire a été utilisée pour déterminer le stade et la vitesse de mue. Nous avons trouvé une relation positive entre les dates annuelles médianes d'éclosion et d'initiation de la mue, et la pente ne différait pas de 1 (b1 = 1.3, 95% CI : 0.9-1.7). Ceci suggère que l'intervalle entre l'éclosion et la mue est fixe et que les oies ne devancent pas la mue lorsque la phénologie de la reproduction est tardive. Il n'y avait par contre aucune relation entre les dates annuelles médianes d'éclosion et de recouvrement des capacités de vol en fin de mue. Ceci suggère que la date de fin de la mue est indépendante de la phénologie de la reproduction. La vitesse de croissance des plumes semblait augmenter dans les années où l'éclosion était tardive et ceci pourrait être le principal mécanisme par lequel les oies ajustent la phénologie de la mue. Finalement, une relation positive entre la longueur de la 9^{e} primaire (corrigée pour les variations interannuelles) et la condition corporelle a été trouvée, suggérant un retard dans la mue chez les individus en mauvaise condition. Ces résultats mettent en évidence une plasticité de la mue de l'oie des neiges caractérisée par un ajustement de la vitesse de croissance des plumes. Cette plasticité phénotypique permettrait d'achever le renouvellement des plumes de vol avant la fin du court été Arctique, indépendamment de la phénologie de la reproduction et des conditions environnementales printanières. Ces résultats sont particulièrement novateurs car jusqu'ici, il était admis que la vitesse de mue était très peu flexible chez les oies.

ABSTRACT

Environmental constraints are particularly strong in migratory species that breed in the Arctic. In addition to breeding, Anatidae have to renew simultaneously all their flight feathers during the short Arctic summer. We examine how temporal constraints and climate affect the phenology of flight feather molt in the greater snow goose (*Chen caerulescens atlantica*), a High Arctic nesting species. We used a database of 1412 molting adult females measured over 15 years on Bylot Island, Nunavut. Ninth primary length was used to determine the molt stage and speed of feather growth. We found a positive relationship between median annual hatching and molt initiation dates and the slope did not differ from 1 (b1 = 1.3, 95% CI: 0.9-1.7). This suggests that, contrary to our expectation, the interval between hatching and molt initiation is rather fixed and geese do not advance the start of molt when the reproductive phenology is late. Nonetheless, there was no relationship between median hatching date and the date at which birds regained flight capacity at the end of molt. This suggests that date of end of molt is relatively fixed and independent of the reproductive phenology. There was a trend for an increase in the speed of flight feather growth in years when hatching date was delayed and this could be the main mechanism that could explain adjustment in molt phenology in this species. Finally, we found a positive relationship between ninth primary length (corrected for inter-annual variations) and body condition, suggesting a delay in molting for individuals in poor condition. These results suggest that molt plasticity is primarily achieved by variations in feather growth speed in snow geese. This phenotypic plasticity could be necessary to complete flight feather renewal before the end of the short summer in the High Arctic, independently of reproductive phenology and spring environmental conditions. These results are particularly novel because until now, molt speed had be found to be rather in flexible in geese.

INTRODUCTION

Timing of breeding is a key determinant of reproductive success in many species. (Perrins, 1970; Lepage *et al.* 2000; Dickerson *et al.* 2005). In migratory species, reproduction is conditioned by arrival date on the breeding ground, which is thus crucial for the chain of events leading to a successful reproduction (Both and Visser, 2001; Bêty *et al.* 2003, 2004). Environmental conditions encountered during the migration and upon arrival on the breeding ground are both susceptible to affect the timing of breeding, either directly or indirectly by affecting arrival date or body condition (Both *et al.* 2005, Eichhorn *et al.* 2009; Van der Jeudg *et al.* 2009; Legagneux *et al.* 2012). In addition to the reproduction, molting is another important activity of the life cycle of birds that often needs to be completed during the summer. In many migratory species, the annual molt follows shortly after the completion of breeding. Thus, delays in breeding may lead to a delay in molting, or an overlap between molt and reproduction or migration, potentially increasing stress and energetic costs for individuals (Hemborg and Lundberg, 1998).

Molting is a complex process that requires large amounts of nutrients and energy. Protein requirement increases to build new feathers, which are composed at 95% of keratin (Murphy and King 1984). In addition, several other metabolic and physiologic changes are required for integument regeneration such as increases in vascularisation, blood volume and erythrocytes (Meister, 1951; Chilgren and DeGraw, 1977; DeGraw and Kern, 1985; Murphy *et al.* 1992). Moreover, feather renewal potentially increases the energetic cost of thermoregulation due to a decrease in plumage insulation. Loss of wing feathers also disrupts flight efficiency or totally eliminates flight capabilities as in some waterbirds that shed all flight feathers simultaneously (Slagsvold and Dale, 1996; Swaddle and Witter, 1997; Portugal, 2010). Depending on species and duration of feathers renewal, energetic cost of molt may represent up to 20% of daily energy expenditure, such as in the white-crowned sparrow (*Zonotrichia leucophrys*), and result in a body mass loss of up to 25 %, as in barnacle geese (*Branta leucopsis*) (Murphy and King, 1992; Portugal *et al.* 2007).

Several authors have suggested that the timing of molt has evolved to avoid overlap with other energetically-demanding processes such as breeding or migration (Foster, 1974;

Heitmeyer, 1987; Svensson and Nilsson, 1997; Yuri and Rohwer, 1997, Singer *et al.* 2012). However, for some species that molt flight feathers all at once rather than sequentially, such overlap is difficult to avoid. This is the case in many Anatidae species, and especially swans and geese, which have a lengthy breeding season due to their large body size. In order to complete their flight feather molt before the onset of the fall migration, it must occurs during the brood-rearing season, when adult are caring for their young (Dean, 1978; Raveling, 1979; Ankney 1984). This may create a conflict between brood-rearing and molting, especially in females which must replenish their body reserves depleted during incubation before initiating their remigial molt.

Temporal constraints faced by molting birds have been recently studied in the black brant (*Branta bernicla nigricans*) in Alaska. Timing of molt initiation was found to be partially dependent upon nesting phenology (Singer *et al.* 2012). A minimum of 16 days was required between hatching and molt initiation, leading to a delay in molt initiation during late nesting years. However, in early nesting years, the interval between hatching and molt initiation lengthened to 19 days in average. This suggests an advantage for females to delay their molt in order to restore more fully their body reserves when temporal constraints are relaxed (Singer *et al.* 2012).

Depending of the local climatic conditions where species breed in the Arctic, environmental and temporal constraints vary. For species breeding further north, the snow-free period is shorter and climatic conditions are harsher and more variable (Lesage and Gauthier, 1997). This is the case of the greater snow goose (*Chen caerulescens atlantica*), a species that breeds in the High Arctic and where the phenology of reproduction is highly dependent upon the timing of snow melt and temperature near laying time (Bêty *et al.* 2003; Dickey *et al.* 2008). Here, we examined how both temporal and climatic constraints affect the timing of remigial molt in this species.

Considering that previous studies in brants found little variation in the speed of feather growth (Taylor, 1995; Singer *et al.* 2012), we expected that possible adjustments in molt phenology in response to environmental conditions should be primarily governed by change in the timing of molt initiation. We hypothesized that the timing of molt should be less flexible than the timing of breeding due to the constraint of regaining flight capabilities before the onset of the fall migration. We predicted (1) greater inter-annual variability in the egg-laying and hatching dates compared to date of molt initiation; (2) In late-nesting years, the interval between hatching and molt initiation should be reduced; (3) molt initiation should be less strongly related to snow-melt date than egg-laying; and (4) female body condition of molting females should be reduced in late-nesting years, due to a reduced interval between hatching and the onset of molt. However, an alternative hypothesis could be that birds adjust their molt phenology by modulating molt speed rather than by change in molt initiation date. Under this hypothesis, we predicted that (1) the interval between hatching date and molt initiation should be constant and (2) molt speed should increase in late-nesting year to ensure that molt completion is not delayed in those years. We examined these predictions using a 15-year dataset.

MATERIALS AND METHODS

Study area

This study was carried out on Bylot Island, Nunavut, Canada (73°08N, 80°08W; Fig. 1.1) from 1992 to 2013. The south plain of the island (ca 1600 km^2) supports a colony of greater snow geese estimated at 20,000 pairs (Reed *et al.* 2002). Geese typically arrive in late May/early June and initiate nesting around 12 June. Most geese nest in a large colony located in the central part of the south plain. Hatching occurs around 10 July and most goose families disperse across much of the island for brood-rearing, though mostly in a northward direction (Mainguy and Gauthier, 2006). They select freshwater wetlands such as tundra polygons for foraging. By the end of August, shortly before the onset of the fall migration in early September, both adults and young are able to fly (Menu *et al.* 2005).

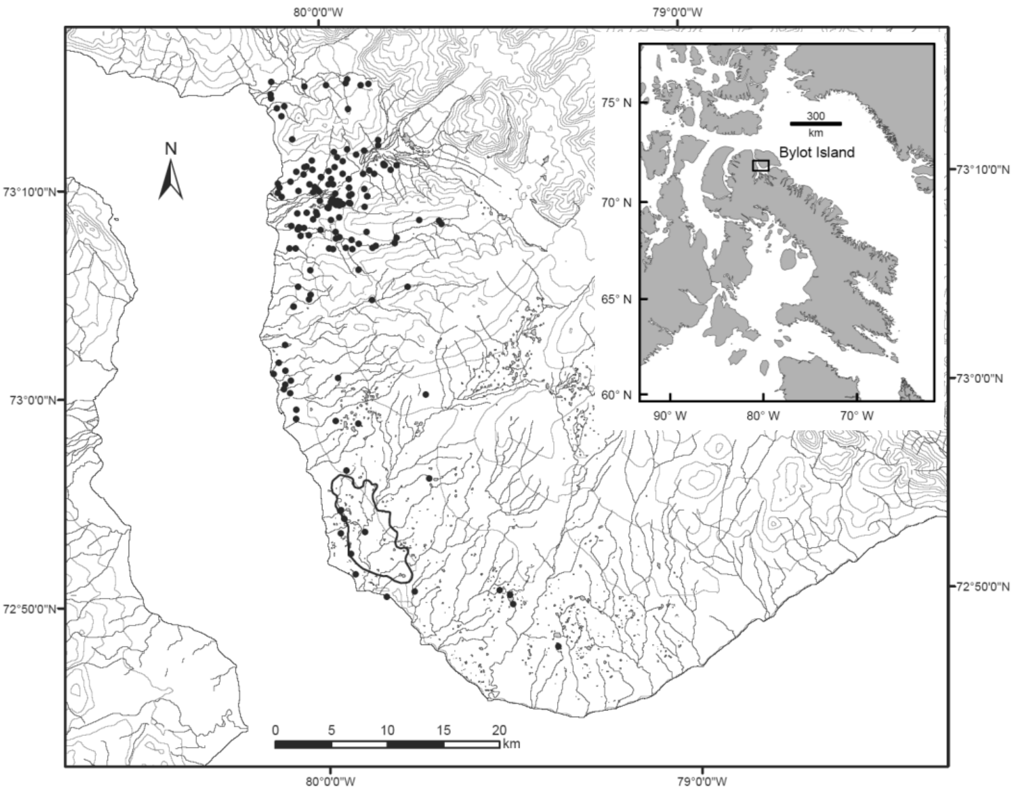

Figure 1.1*: Map showing the study area on the south plain of Bylot Island and its localisation in Nunavut, Canada. Black dots represent capture sites during the 15 years of data used in the analysis and the thick line represents the limit of the nesting colony.*

Goose reproductive data

Since 1992, we monitored the nesting biology of greater snow geese. In the core of the colony, we systematically searched the same area (~ 50 ha) and monitored ca. 200 nests each year. A second sample of ca 200 nests was also monitored in a variable number of 100x100 or 200x200 m plots (≥ 10 plots/year) randomly located throughout the colony. We determined the date at which the first egg was laid (i.e. laying date) by different methods depending of the nest stage. When a nest was found during egg-laying, we back calculated from the date of discovery assuming a laying interval of 33h between each egg. For nests found during incubation with a known hatching date, laying date was estimated by back-calculating from hatching date based on the recorded clutch size and the incubation length (23 days). Finally, laying date of nests found during incubation with unknown hatching date was estimated by using a relationship between egg density when first found (calculated from measure of egg length, width and mass) and incubation stage (see Lepage *et al.* 1999 for details). Hatching date was defined as the date at which at least half of the brood was hatched and clutch size as the maximum number of eggs recorded in a nest after the start of incubation. Laying date differed between nests located in the core and in the rest of the colony ($F_{[1;\,2992]} = 93.2$, $p < 0.001$) with a significant interaction between location and year ($F_{[3;\,2990]} = 57.3$, $p < 0.001$). However, the magnitude of the difference between the two locations was small (i.e. 0.6 d; Core = 163.9 (day of the year), rest of the colony = 164.5) and we decided to pool all nests monitored to calculate median laying date each year.

Capture and measure of molting geese

Goose families composed of flightless molting adults and their young were captured, with the help of a helicopter, in mass banding drives between 5 and 17 August each year, toward the end of the molting period (Menu *et al.* 2005). Only successful breeding adults were susceptible to be captured because most of the non-breeders or failed breeders (those that failed to hatch a brood) leave the island to molt (Reed *et al.* 2003). Moreover, the few non-/failed breeders that remain on the island start molting earlier and have regained flight ability by the beginning of August. Most banding drives occurred north of the colony and where concentrated in a valley located ~25 km from the colony (Fig. 1.1), which had the highest concentration of wetlands on the island and was heavily used by geese (Hughes *et al.* 1994, Reed *et al.* 2002). Thus, 95% of the captures were made within an area of approximately 350km² (Fig. 1.1).

Each year, captures were spread over 4 to 9 days and included from 1 to 4 captures (capture groups) per day (mean = 1.2). We moved > 2 km between each capture in a systematic fashion to avoid recapturing the same individuals. Capture groups averaged 395 geese including both young and adults (min = 13, max = 1185). We took morphometric measurements (culmen, tarsus and head length with an electronic calliper to the nearest 0.1 mm), body mass (to the nearest g with an electronic balance) and the length of the 9th primary feather (to the nearest mm with a ruler) to estimate the molt stage on a sample of adult females. We measured on average 15 females per catch (min = 1, max = 49) and 89 females per year (min = 32, max = 189) for a total of 1967 females during the 22 years of data collection (Appendix 1).

Environmental covariates

We monitored snow-melt at the study site by visually estimating snow cover from a vantage point every 2 days from 1 June until snow disappearance. We used the date at which snow had melted over 50% of the study area as an index of snow-melt phenology (SNOW). An automated weather station located at the study site recorded hourly air temperature, ground temperature (2 and 10cm) and snow depth since 1994 (CEN 2013). For the period before 1994 and some months with missing data, we extended the times series using weather data recorded at the Environment Canada weather station located at the Pond Inlet airport, 80 km away. Data from the two stations were highly correlated and we used the same approach as Dickey *et al.* (2008) to correct the Pond Inlet data. The mean of monthly July and August temperature (TEMP in °C) as well as the sum of mean daily temperature above 0°C from June to 15 August (cumulative thawing degree-days, TDD) were used as two temperature metrics in the analyses. Moreover, we used monthly North Atlantic Oscillation (NAO) indices as a global climatic index of atmospheric circulation in the Artic (data obtained from www.cpc.ncep.noaa.gov/products/precip/)

To estimate food availability for geese, which may influence body condition, annual plant production in wetlands was monitored. Each year, twelve exclosures were installed in mid-June to prevent goose grazing. In early August, when plant growth is completed, the vegetation was sampled by removing a piece of turf (20 x 20 cm) from inside the exclosures. Live (i.e. green) aboveground biomass was extracted, sorted out by taxa (grasses, *Eriophorum* and *Carex*; graminoids accounted for >95% of the biomass), dried and weighed. Annual standing crop is a good measure of annual plant production in this habitat (for details see Gauthier *et al.* 1995). Plant biomass (PLANT) was based on lived parts of *Eriophorum*, *Dupontia* and *Carex* combined (dry matter, g/m^2).

Analysis

A preliminary check of the 9th primary length measurements of the 1967 individuals revealed the presence of 9 measurements that were clearly outliers (Grubbs test, $p < 0.05$), likely due to measurement errors; these were deleted from the dataset. We used measurements of the 9th primary feather taken on different days during the banding period to obtain an estimate of average speed of feather growth (hereafter referred to as molt speed). We used linear mixed models (nlme package of R) with 9th primary length as dependant variable, capture date as explicative variable and the capture group as a random factor. This assumes that random samples of the local population are captured every day (this assumption will be addressed in the discussion). The slope of the relationship between the 9th primary length and capture date was used as an index of annual, population-level molt speed. We tested if molt speed differed among years by including year and the year x capture date interaction in the model selection. We used AICc to rank our models and determine if molt speed was constant among years.

Using molt speed determined in the previous analysis, we could, in theory, calculate the annual median molt initiation date (MI; day of the year) by subtracting the 9th primary length (L; in mm) divided by yearly specific molt speed (MS; in mm/day) to the date of capture (DC; day of the year) of each individual: $MI = DC - L/MS$. However, due to annual differences in phenology, measurements of geese did not occur exactly at the same stage of molt each year (mean annual 9th primary length ranged from 124 to 189 mm; appendix 1). We found that annual MS was inversely related to mean L at the time of measurement (see results), suggesting that molt speed decreased near the end of molt. We corrected for that as follows. We first determined MS predicted by the previous relationship for the average L at capture, plus the residual from that relationship to account for the annual variation in molt speed ($MS_{pred+resid}$). We used this value to determine L the day (d) before ($L_{d-1} = L_d - MS_{pred+resid}$). We then obtained a new MS_{pred} value from the relationship for the value L_{d-1}, to which we added again the residual and calculated L on d-2 using the same process (i.e. $L_{d-2} = L_{d-1} - MS_{pred+resid}$). We continued this procedure iteratively until reaching a L value of 121 mm. Because we had no information < 121 mm (i.e. the minimum value in our relationship between MS and L), we considered that molt speed was constant and similar below that value in all year and we used the same MS_{pred} value to continue calculation until L = 0. Molt initiation date was the date when L = 0 was reached. The same approach was used in the opposite direction to estimate the date when the 9th primary reached 75% of its final length i.e when birds regain their flight capabilities (Mathiasson, 1973; Brown and Saunders, 1998; Guillemette, 2007; we will hereafter refer to this date as molt completion). Final length of 9th primary was 271mm (calculated from the mean of 138 adult females measured in October from 1993 to 1997) at the fall migratory stopover site of this population in southern Quebec (Gauthier unpublished data). We also applied a constant value of molt speed in our calculations beyond the largest value of L in our relationship between MS and L (192 mm).

We determined if intrinsic (e.i. body condition) and environmental (e.i. temperature, plant biomass, snow cover) covariates could affect molt initiation and molt speed. Body condition was based on body mass corrected for body size. As an index of body size, we used the individual scores from the first axis (PC1) of a principal component analysis (PCA) based on the morphometric measurements (head, culmen and tarsus length, for details see appendix 2). We used the scale mass index (SMI) as an index of condition as recommended by Peig and Green (2009). We first calculated the slope (b) of the relationship between body mass (M) and (PC1) on a log-log scale using a standardized major axis (SMA) regression ($r^2 = 0.32$, $n = 1391$, $p < 0.001$). Condition of each individual was then obtained by $M_i \times (PC1_{mean}/PC1_i)^{b_{SMA}}$. Because SMI differed according to year, capture date and 2 way interaction (delta AIC vs null model: 223.3), we used residuals from this analysis as an index of condition (SMIr) to control for year and capture date variation.

The effect of SMIr, PLANT, TEMP, NAO and TDD on 9th primary length corrected for date of capture and year effects (see results) was assessed using a mixed linear model with catch size as the random factor. Model selection was based on AICc. We also tested for possible non-linear relationships using square terms.

RESULTS

Molt speed

Typically, the 9th primary length showed a linear relationship with capture date in a given year (see example in Fig. 1.2). Such linear relationships were significant ($p < 0.05$) in 13 years, marginally so in 2 others ($p = 0.07$ and 0.075) and not significant ($p > 0.1$) in 7 other years (Appendix 3). The absence of a relationship in the latter years was presumably due to some sampling biases (see discussion). For subsequent analyses, we thus excluded the 7 years for which molt speed could not be estimated (i.e. $p > 0.1$). Molt speed still varied among the 15 remaining years (Appendix 4), ranging from 4.27 mm/day, SE = 1.59, in 1998 to 11.28 mm/day, SE = 1.35, in 1992 (overall mean = 7.13 mm/day, SE = 0.34).

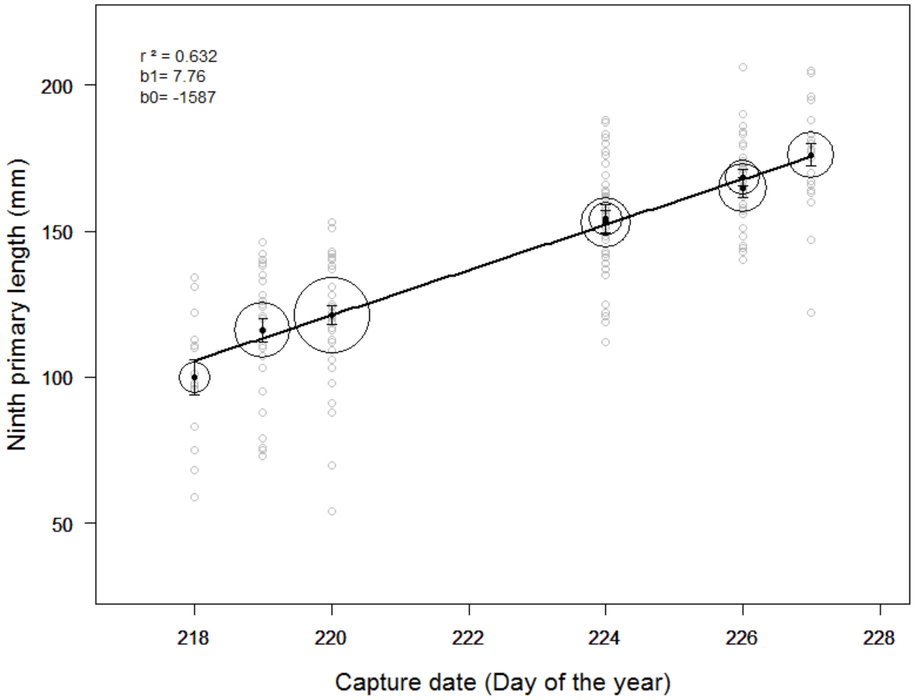

***Figure 1.2**: Relationship between ninth primary length of adult female greater snow geese and capture date on Bylot Island, Nunavut, in 2012. Open grey circles represent individuals. Black dots represent the mean ninth primary length per capture date while the size of the surrounding black circle is proportional to the numbers of individuals per*

groups of capture. The vertical lines represent standard error per capture date. Also shown are the slope (b1) and intercept (b0) of the linear mixed model (regression line) with individual catch as the random factor (n = 185, p < 0.001).

Annual molt speed and mean ninth primary length were negatively related (b1 = -0.06, 95CI [-0.01;-0.11], $r^2 = 0.29$, p = 0.02, Fig. 1.3), suggesting a reduction of molt speed toward the end of molt. In subsequent analyses, molt speed was corrected for annual variation in the timing of measurement by using the residuals of the latter relationship. Although the relationship with median hatching date was not significant, annual molt speed tended to increase in years of late hatching (b1 = 0.27, SE = 0.14, $r^2 = 0.22$, p = 0.07, Fig. 1.4).

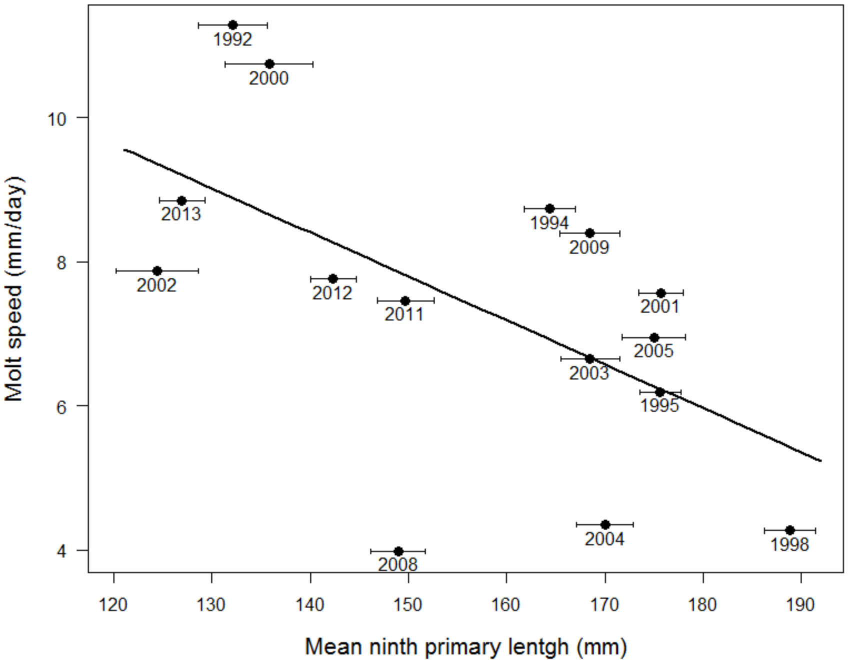

***Figure 1.3**: Relationship between annual molt speed and mean 9^{th} primary length of adult greater snow geese on Bylot Island, NU with standard error bars. The line represents the regression (y = -0.06x + 16.94). The year associated with each data point is shown.*

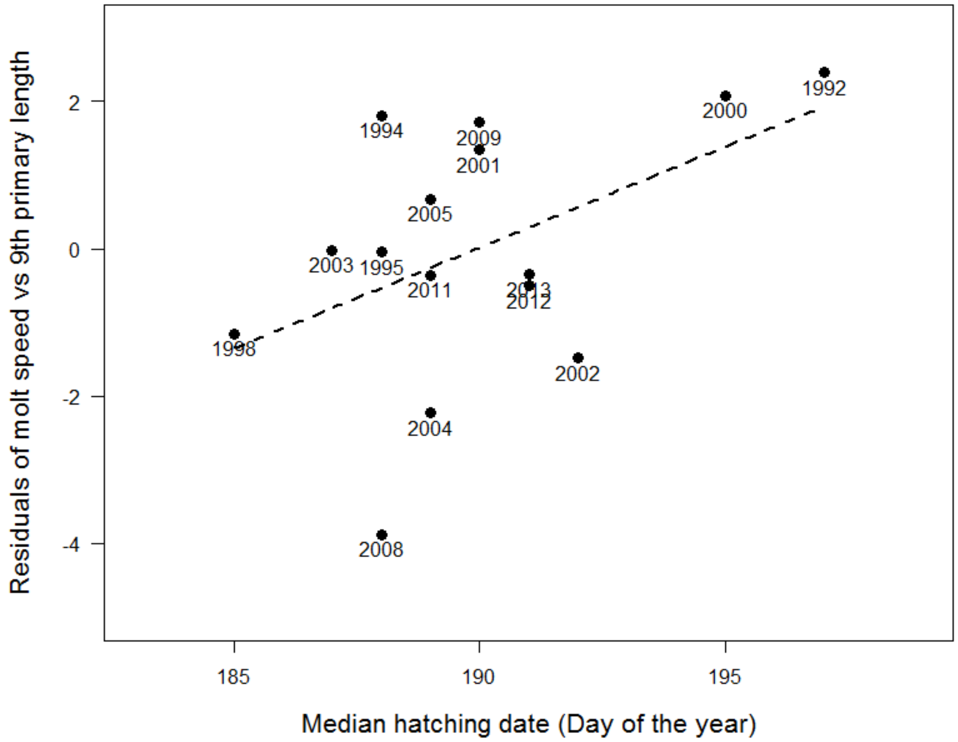

Figure 1.4: *Relationship between the residuals of the relationship between annual molt speed and* 9^{th} *primary length (from Fig. 1.3) and annual median hatching date of adult female greater snow geese on Bylot Island, Nunavut. The line represents the regression (p = 0.07). The year associated with each data point is shown.*

Molt phenology

Overall, molt was initiated on 25 July (day 206 of the year) with large annual variation (from 14 July in 2008 to 2 August in 1992). Molt was initiated on average 16 days after the median hatching date (8 July; range: 8 to 18 days). Inter-annual variability in date of molt initiation (coefficient of variation (CV) = 2.5%) was higher than in laying or hatching dates (CV = 2.1 and 1.6%, respectively) but equal to date of 75% molt completion (CV = 2.5%). We found a strong positive linear relationship between molt initiation dates and median hatching dates ($r^2 = 0.73$, $p < 0.001$; Fig. 1.5A) with a slope not significantly different from 1 (b1 = 1.31, 95% confidence interval = 0.88 – 1.74). For each day of delay in hatching, molt initiation was delayed by 1.3 days and thus showed no evidence for a shorter interval between hatching and molt initiation during years of late hatching. Interestingly, we found no relationship between the estimated date of 75% molt completion and median hatching date (b1 = 0.38, SE = 0.53, r^2 = 0.04, p = 0.49; Fig. 1.5B).

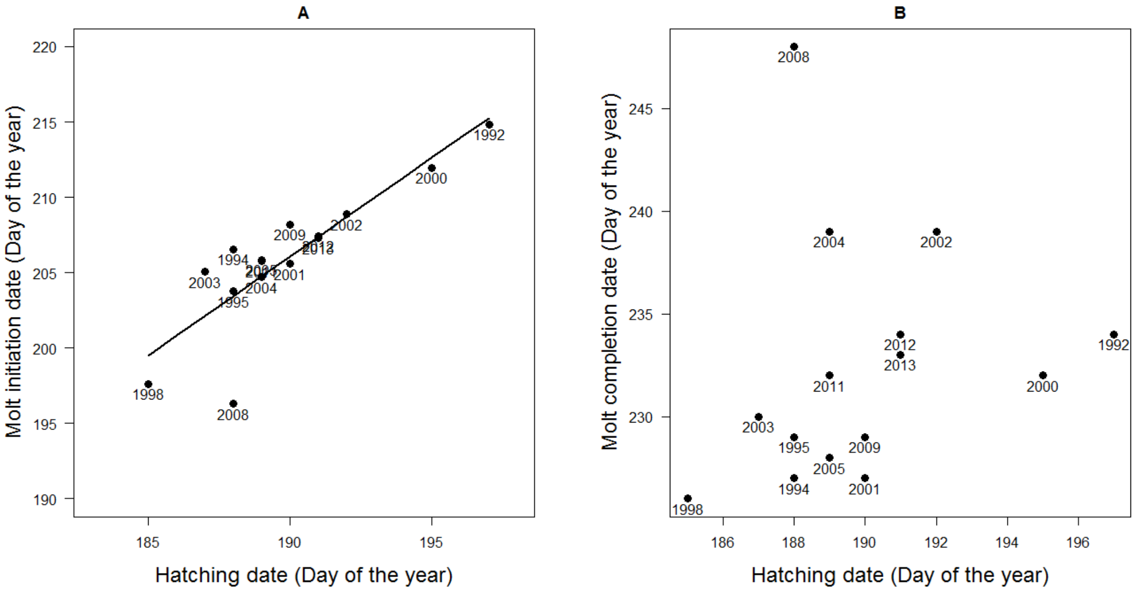

Figure 1.5: *Relationships between estimated molt initiation date (A) or molt completion date (B) and hatching date of adult female greater snow geese on Bylot Island, Nunavut. When significant, the regression line is shown. The year associated with each data point is shown.*

As expected, annual variation in reproductive phenology was related to date of 50% snow cover (laying date: r^2 = 0.42, p = 0.01, b1 = 0.43, SE = 0.14; hatching date: r^2 = 0.48, p = 0.006, b1 = 0.40, SE = 0.12). Median annual molt initiation date was also related to the date of 50% snow cover with a slope of similar magnitude (r^2 = 0.34 p = 0.03, b1 = 0.53, SE = 0.21; Fig. 1.6). Finally, annual date of molt completion was not related to date of 50% snow cover (r^2 = 0.05, p = 0.46, b1 = -0.24, SE = 0.31).

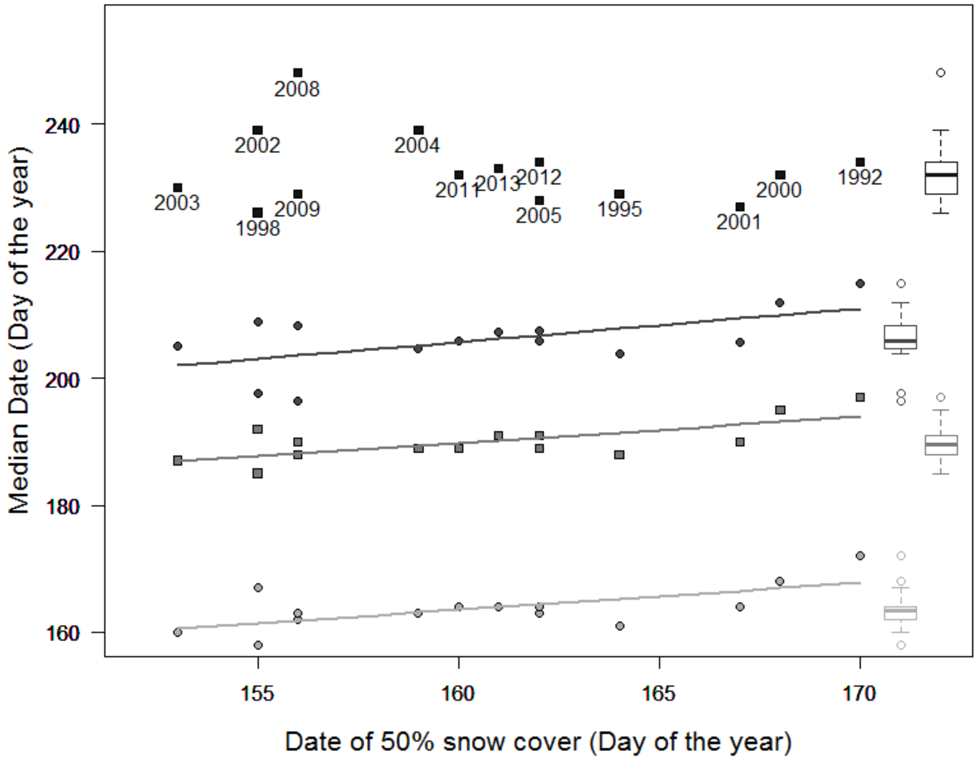

Figure 1.6: *Relationships between annual median dates of laying (light grey circles), hatching (dark grey squares), molt initiation (dark grey circles) and 75% molt completion (black squares) of female greater snow geese in relation date of 50% snow cover in spring on Bylot Island. Box plots show the median date (bold line), the 25/75 percentiles (box) and 1.5 interquartile range (error bars). Year 1994 was deleted from the analysis because snow had disappeared before our arrival in the field due to an almost complete absence of snow during that winter. The year associated with each data point is shown.*

Factors affecting molt

Because 9th primary length varied significantly among years and with capture date (Appendix 4), we used the residuals of this model (9th primary length vs Date + Year + Date × Year with catch size as random factor) to examine the potential effects of covariates on molt. The only variable retained in the model was body condition (Table 1.1). Ninth primary length was positively related to body condition (linear term: $b1 = 1.29 \times 10^{-2}$, SE =

4.28×10^{-3}, $p = 0.003$; square term: $b2 = - 3.68 \times 10^{-5}$, $SE = 1.81 \times 10^{-5}$, $p = 0.043$; $r^2 = 0.01$; Fig. 1.7). The square term suggested a reduction in ninth primary length at the highest body condition but this trend was driven by a single year (i.e. 2000). Indeed, when we excluded 2000, the reduction in 9th primary length at high body condition disappeared (linear term: $b1 = 1.22 \times 10^{-2}$, $SE = 4.28 \times 10^{-3}$, $p = 0.004$; square term: $b2 = - 3.45 \times 10^{-5}$, $SE = 1.80 \times 10^{-5}$, $p = 0.056$; $r^2 = 0.01$). Finally, we found no relationship between body condition and median hatching date ($b1 = 4.68 \times 10^{-8}$, $SE = 1.49$, $p = 1$, $n = 1383$).

Table 1.1: *Model selection for the effect body condition index (SMIr, corrected for capture date and year effects; see methods), temperature (TEMP) and 2 way interaction on 9th primary length (also corrected for capture date and year effects). Other variables tested (PLANT, TDD and NAO) performed more poorly than the null model*

Variables	**K**	**Log-Likehood**	**Δ_AICc**
SMIr + (SMIr)²	4	-6258.7	0
SMI	3	-6260.8	2.10
TEMP + SMIr	4	-6260.8	4.11
TEMP + SMIr + TEMP*SMIr	5	-6260.6	5.74
Null	2	-6263.9	6.48

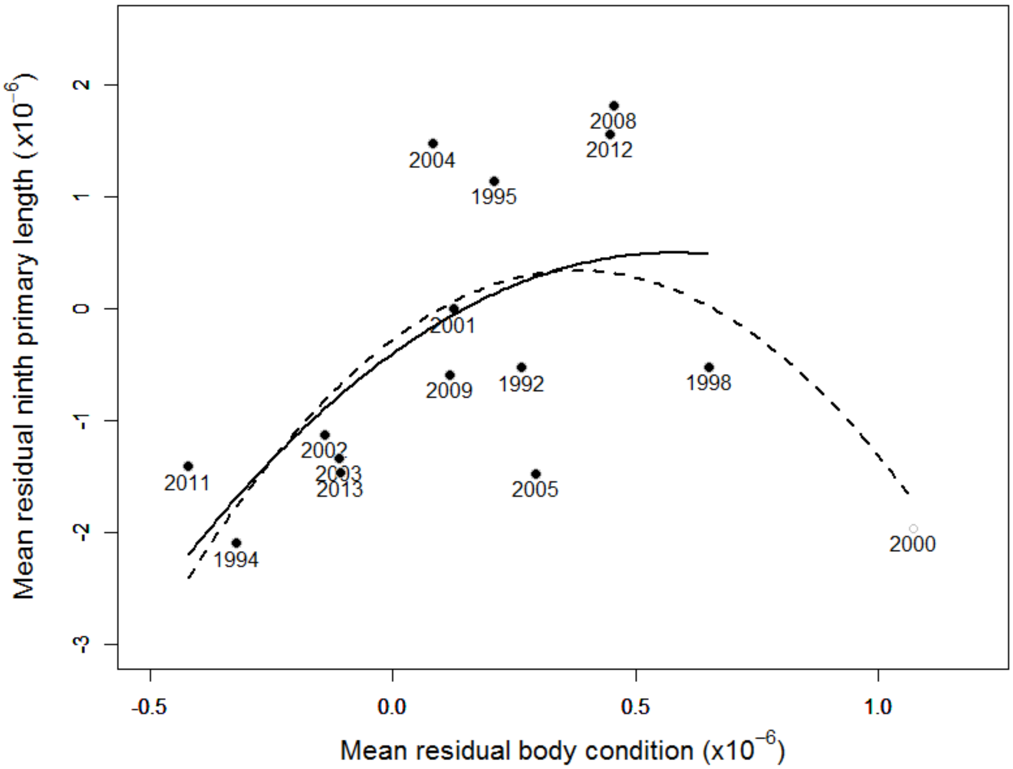

Figure 1.7: *Relationship between the residual 9th primary length and the residual body condition (i.e. accounting for the effects of year and date of capture on those two variables; see metho*ds*) in molting greater snow geese females on Bylot Island, NU. The dashed and full lines represent the regression for the best model including all years (n = 1383) and excluding year 2000 (n = 1312), a highly influential point.*

DISCUSSION

Our study provides new insights on molt ecology in a high Arctic migratory species. In Anatidae, molt is the final step in the reproductive “cascade”. Our results suggest that change in molt phenology through a modification in the timing of molt is not an option when breeding at high latitude. Indeed, we found no support for the hypothesis that greater snow geese could adjust the timing of molt by reducing or increasing the interval between hatching and molting, as previously found in brant geese in Alaska (Singer *et al.* 2012). We showed that molt initiation date was directly related to previous reproductive events and to the timing of snow-melt, a dominant factor governing nest initiation date in greater snow geese (Dickey *et al.* 2008). Interestingly, molt completion date was not related to those previous events. This adjustment was likely caused by a modulation in the speed of feather growth, which was highly variable among years and with a tendency to increase in late-nesting years.

Among the 22 years of data, we were unable to detect an increase in 9th primary length during the banding period in 7 of them. Several factors may have contributed to that. First, the numbers of capture dates and the numbers of day between the first and the last day of capture varied among years. The absence of a significant relationship between 9th primary length and date often occurred in years where the time span of banding was fairly short (e.g. 4 days), usually a consequence of field constraints due to poor weather, or when the measurements of birds were concentrated on few days (e.g. 1996, 1997, 1999 and 2010; Appendix 1). Second, our calculations assume that random samples of the local population are captured every day. However, geese are captured in flocks and the distribution of birds with respect to their hatching date may not always be random among those flocks. For instance, geese captured closer to the colony may have a higher proportion of late-hatching birds than those captured further away, and in years of low brood density, some catches were conducted closer to the goose colony (Fig. 1.1). Nonetheless, we noted that among the 15 years for which a significant relationship was found between 9th primary length and date, the average growth rate was 7.13 mm/d, which is very similar to values found by Lindholm *et al.* (1994) in captive greater snow goose goslings (values ranging from 6.8 to 7.8 mm/days). This suggests that biases in the estimation of molt speed linked to our method were slight in most years.

A small reduction in the speed of feather growth as molt progresses had been shown in mallards (*Anas platyrhynchos*) by Pehrsson (1987) and in black brant by Taylor (1995). However, the magnitude of this effect was about ten times larger in our study (b1 = -0.06 mm/d per mm of feather) than in black brants (b1 = -0.007). Thus, this was not negligible and, contrary to Singer *et al.* (2012), we had to correct for it to infer molt initiation dates considering that geese were not measured exactly at the same stage of molt every year. We could correct for the decrease in growth speed of the ninth primary over the range of annual measurements, i.e. between 121 and 192 mm. However, we had no information before or after this range of values (i.e. from 0 to 121 mm and from 192 to 203 mm, when 75% of feather growth is completed) and we had to use a constant value during these periods. Although this may have introduced some biases, these were constant across years and should therefore not affect our inter-annual analysis. We also note that Lindohlm *et al.* (1994) found a constant growth speed of the 9th primary in captive greater snow goose goslings for at least the first half of the growth period. Interestingly, once we corrected for the variability in molt speed due to the molt stage, the average delay of 16 days between hatching and molt initiation estimated in greater snow geese was identical to the value reported by Singer *et al.* (2012) in black brants molting in Alaska. Therefore, this makes us confident that molt initiation dates were correctly estimated in our study.

Globally, our results did not support the hypothesis that molt phenology should be less flexible than reproductive phenology, as found by Van der Jeudg *et al*. (2009) when they compared temperate and arctic-nesting populations of barnacle geese. Despite the high temporal constraints associated with breeding and molting in the High Arctic, molt initiation date was delayed in the same proportion than nest initiation date in late years. Late nesting in geese is usually associated with poor environmental conditions such as cold temperature and late snow-melt, which interferes with feeding and resource acquisition during the pre-nesting and nesting periods (Prop and deVries, 1993; Bêty *et al.* 2003; Reed *et al.* 2004; Madsen *et al.* 2007; Dickey *et al.* 2008). The trend for an increased delay in molt initiation during late nesting year may be due to an overall lower body condition of females after hatching. In those years, the time to recover a minimum condition to initiate the energy-demanding process of molt could be extended compared to early nesting years. However, we did not find a relationship between molt completion date and the timing of snow-melt, which indicate that contrary to molt initiation, molt completion was independent of conditions prevailing earlier during the breeding season and that affected reproductive phenology. Therefore, some compensation must occur during molt to allow geese to complete it more or less at the same time even in years when molt initiation was delayed due to environmental conditions. This adjustment is most likely through an increase in molt speed in those years, as we found some evidence for that. This illustrates the important constraint of regaining flight capabilities before the end of the summer, in time for the onset of fall migration.

If geese are able to speed up molt in late years, this begs the question of why they do not molt at the maximum possible speed in all years, as regaining flight rapidly has obvious advantages, such as reduced predation risk. The only logical response is that increasing the speed of feather growth must entail some cost, such as a reduced body condition or reduced feather quality. Some studies have shown that variations in feather growth can affect rate of keratin deposition and thus feather mass, rachis width, asymmetry and feather mechanical properties (Dawson, 2000; 2004). Poor feather quality could have a lasting impact on individuals, for instance by reducing flight efficiency and increasing the energetic cost of flight (Swaddle *et al.* 1996; Tubaro, 2003). This may be especially damaging for long distance migrants and may ultimately affect their survival and future reproduction (Nilsson and Svensson, 1996; Dawson, 2004). Intense feather growth could also affect other vital functions as an experimental study in house sparrow (*Passer domesticus*) provided evidence for a trade-off between the immune response and molt speed (Moreno-Rueda, 2010). It is therefore interesting to see that the primary mode of adjustment of high-arctic molting geese to a delayed reproduction seems to be through a speeding up of flight feather growth rather than in a change in the timing of molt initiation. As found by Singer *et al.* (2012) in black brants and in our study, there seems to be an incompressible delay of about 2 weeks between hatching and molt initiation in geese. This could be partly due to endocrinological control of molting activity. Studies have shown a concomitant decrease of prolactin and increase in thyroid hormones associated with molt activity in some avian species (Groscolas and Leloup, 1986; Lien and Siopes, 1993) and could partially explain the incompressible delay between hatching and molt initiation. The time required for internal physiological adjustments in preparation for molt before the apparition of visible changes (e.g. feather loss) could also contribute to this delay.

The positive relationship between 9th primary length and body condition suggest a reduced molt speed for birds in low body condition. Poor body condition and subsequent energetic limitation can affect the molt process. Pehrson (1987) showed that molt is preceded by an increase in stored nutrient level, which can be used during the flightless period (Portugal *et al.* 2007). These results and those of Singer *et al.* (2012) suggest that, after hatching, females need a minimum time to recover a sufficient body condition to initiate their flight feather molt. Low body condition may also be a source of stress, which could have repercussions on feathers quality (Desrochers *et al.* 2009; Hera *et al.* 2009). Nonetheless, we recognize that body condition explained only a small proportion of variation in 9^{th} primary length and thus other factors should also affect molt process. None of the environmental covariates that we examined such as plant biomass and July temperature was related to 9^{th} primary length. Presumably, other, non-identified environmental factors could explain some of the variability in feather growth.

Our study conducted revealed at the population level, plasticity in molt including in feather growth speed, a little studied mechanism. Nonetheless, fine tuning of molt should occur at the individual level. Combining physiological information (i.e. stress, metabolism, feather quality) with feather growth rate at the individual level would help to fully understand the molt process.

CHAPITRE 2

PHYSIOLOGICAL DETERMINANTS OF MOLT AND FEATHER QUALITY IN ARCTIC GEESE: THE ROLE OF THYROID AND STRESS HORMONES

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RESUMÉ

Chez les oiseaux, les plumes jouent un rôle essentiel dans l'isolation thermique et le vol et le renouvellement périodique des plumes usées est primordial pour conserver un plumage de qualité. Le rôle des hormones, en particulier des hormones thyroïdiennes (T3) et de stress (corticostérone), et des facteurs environnementaux dans le contrôle de la mue demeurent toutefois peu connus. Nous avons étudié ces questions chez l'oie des neiges, une espèce qui niche dans l'Arctique où les contraintes environnementales et temporelles sont sévères et qui doit renouveler toutes ses plumes de vol simultanément, perdant ainsi momentanément la capacité de vol. Nous avons examiné comment le stade de mue, déterminé par la longueur de la 9^e primaire, influençait les niveaux sanguins de T3 et vérifié l'hypothèse que la condition physique et le niveau de corticostérone pouvait affecter la rigidité flexionnelle des plumes, un indice de leur qualité. L'étude a été réalisée à partir d'un échantillon de 361 femelles adultes en mue capturées et mesurées en 2012 et 2013 à l'Île Bylot, Nunavut, Canada. Le niveau de T3 a diminué par un facteur de 6 durant la période où les plumes ont passé de 30% à 70% de leur longueur finale, ce qui suggère un déclin de l'activité métabolique durant la deuxième moitié de la mue et pourrait expliquer le déclin dans la vitesse de croissance des plumes observé à ce moment. Il n'y avait pas de relation entre la date d'initiation de mue et les niveaux de T3 ou de corticostérone. La T3 était positivement reliée à la condition physique des individus mais négativement à la corticostérone, ce qui suggère que l'intensité de la mue augmente chez les individus en bonne condition et diminue lorsque les niveaux de stress sont élevés. Nos résultats montrent également une relation inverse entre le niveau de corticostérone et la condition physique des individus. Néanmoins, la condition corporelle et le niveau de corticostérone n'ont pas influencés la rigidité flexionnelle des plumes. Ceci suggère qu'en conditions naturelles, les individus ne font pas de compromis sur la qualité de leurs plumes, du moins en absence de conditions extrêmes.

ABSTRACT

In birds, feathers play an essential role in thermoregulation and flight and periodic renewal of old feathers is necessary to maintain a high quality plumage. The role of hormones, particularly thyroid (T3) and stress (corticosterone) hormones, and environmental factors in controlling molt is however poorly understood. We studied these questions in greater snow geese, a species that nests in the Arctic where environmental and time constraints are severe. Geese must renew all their flight feathers simultaneously, leading to a flightless period during the summer. We examined how the molting stage, determined by 9th primary length, influenced levels of T3 in blood and we tested the hypothesis that body condition and corticosterone levels could affect bending stiffness of feathers, an index of their quality. The study was based on a sample of 361 molting adult females captured and measured in 2012 and 2013 on Bylot Island, Nunavut, Canada. T3 levels decreased by a factor 6 during the period when feathers grew from 30% to 70% of their final length, suggesting a decline of metabolic activity during the second half of molt, which could explain the reduction in feather growth rate observed at that time. There was no relationship between the molt initiation date and T3 or corticosterone levels. T3 was positively related to the individual body condition but negatively related with corticosterone levels, suggesting that molt intensity increases for individuals in good condition and decreases with high levels of stress. Our results also show an inverse relationship between corticosterone level and body condition. However, body condition and corticosterone level did not influence the feather bending stiffness. This suggests that, under natural conditions, individuals do not compromise their feather quality, at least in the absence of extreme conditions.

INTRODUCTION

The timing and progress of important events in the life cycle of animals such as migration, reproduction, or molting are under hormonal control. However, environmental conditions can affect the endocrine system and thus physiological activities or behaviors mediated by hormone levels. The most predictable environmental variation is the seasonal change in photoperiod away from the Equator. Physiological responses to changes in photoperiod have been well documented (Wingfield and Farner, 1980; Hahn *et al.* 1995) with vernal migration apparently regulated by androgens in fishes and birds (Dickhoff, 1989; Wingfield *et al.* 1990). Reproduction is another highly seasonal activity under hormonal control, with testosterone playing a key role in male parental care and territory defense (Hunt *et al.* 1999; Ramenofsky and Wingfield 2007; Wingfield, 2012).

The physiological and environmental determinants of molt, a key process in the life cycle of birds, are still not well understood. Studies of molt endocrinology in the wild turkey (*Melleagris gallopavo*) and european starling (*Sturnus vulgaris*) showed that molt initiation occurred after a peak in prolactin (Lien and Siopes, 1993; Dawson, 2006), although causal relationship between decreasing prolactin and molt initiation have not been shown conclusively. In addition, circulating level of thyroid hormones, and in particular thyroxine (T4), have been found to increase with molt initiation (Pati and Pathak 1986; Cherel *et al.* 1988). In some species like the emperor penguin (*Aptenodytes forsteri*), triiodothyronine (T3) levels also increase during the later stage of feather renewal (Groscolas and Leloup, 1986). However, other studies showed that T3 circulating level do not play an active role in molting although high level of circulating T3 was correlated with an increase in basal metabolism and in the rate of body molt (Chastel *et al.* 2003). It is difficult to establish causal relationships between molting, metabolism and thyroid hormones because these hormones are implied in several physiological processes such as growth, cell proliferation and thermogenesis (Hulbert, 2000; Jenni-Eirmann *et al.* 2002).

Glucocorticoids are of particular interest when examining how individuals respond to environmental conditions. Glucocorticoids are the main mediators of allostasis in vertebrates and allow individuals to cope with both predictable and unpredictable environmental conditions, including stressful events (Sapolsky *et al.* 2000; McEwen *et al.* 2003; Landys *et al.* 2006). Corticosterone (CORT), the primary glucocorticoid in birds, has been investigated in numerous studies attempting to identify physiological mechanisms linking individual state to environmental parameters and fitness (Bonier *et al.* 2009). Elevated levels of CORT can compromise immune functions (e.g., Barton, 2002; Loiseau *et al.* 2008), metabolism (e.g., Buttemer *et al.* 1991; Barton 2002; Miles *et al.* 2007) or reproduction (Silverin, 1998; Salvante and Williams, 2003; Meylan and Clobert, 2005; Goutte *et al.* 2010). During pre-basic molt, CORT is down-regulated because elevated levels of CORT can inhibit feather growth (Romero *et al.* 2002; 2005). Unpredictable stressful events known to drastically increase CORT levels (i.e., severe climatic conditions, food restriction or high predator abundance) can potentially affect feather quality by altering their mechanical properties and resistance due to an interruption of their growth, a decreased mass or changes in their structure or geometry (Strochlic and Romero, 2008; Desrochers *et al.* 2009). CORT deposited in feathers incorporate CORT secreted during the period of feather growth and thus represents an integrated measure of both baseline and stress-induced CORT secretion during the molt period (Bortolotti *et al.* 2008; 2009; Legagneux *et al.* 2013).

Polar areas are characterised by low temperature, relatively dry conditions, and a short snow-free summer season. Most arctic-nesting birds must wait for snow free areas to initiate reproduction in spring and thus late snow melt could impact all subsequent activities such as breeding (Bêty *et al.* 2003), pre-basic molt (Singer *et al.* 2012), and fall migration. Anatidae face unique constraints in that respect because they shed and renew all their flight feathers simultaneously during the summer, which implies a flightless period of a few weeks before the onset of the fall migration. In large-bodied species such as the greater snow goose (*Chen caerulescens altlantica*), this flight feather renewal strategy occurs during the brood rearing period, causing an overlap between two energetically demanding activities and thus potentially affecting their body condition. In this species, speed of feather growth tends to increase in years when molt initiation is delayed and this could be the main mechanism used to adjust molt phenology (Chapter 1).

Here, we examine variations in thyroid and stress hormones during molt in adult female greater snow geese exposed to the severe constraints of the arctic environment. Assuming that thyroid hormones reflect metabolic activity (Hulbert, 2000; Chastel *et al.* 2003; Vézina *et al.* 2009) and thus molt intensity, we predicted that circulating T3 level (1) vary over the duration of molt and (2) should be higher in individuals that initiate their molt later in the season. Secondly, we hypothesised that a late molt phenology could be a source of stress and thus expected a positive relationship between CORTf and molt initiation date. Finally, we hypothesised that both body condition and CORTf could affect feather quality. We predicted that (1) body condition should be negatively related to CORTf and (2) feather quality should be reduced in weaker or (3) more stressed individuals. We examined these predictions by sampling molting greater snow geese during two consecutive summers in the High Arctic.

MATERIALS AND METHODS

Study area and species

This study was carried out on Bylot Island, Nunavut, Canada (73°08N, 80°08W; Fig. 1.1) in 2012 and 2013. The south plain of the island (ca 1600 km^2) supports a greater snow goose colony estimated at 20,000 pairs (Reed *et al.* 2002). Geese typically arrive in late May/early June and initiate nesting around 12 June on average. Most geese nest in a large colony located in the central part of the south plain. Hatching occurs around 10 July and most goose families disperse across much of the island for brood-rearing (Mainguy and Gauthier, 2006). Adults with young starts their molt in late July during the brood-rearing period and by late August, shortly before the onset of the fall migration in early September, both adults and young are able to fly (Menu *et al.* 2005). An automated weather station located at the study site records hourly air temperature year-round (CEN 2013). In 2012 and 2013 the minimum and maximum daily temperatures recorded during the 10-day period of capture were 3.2°C and 9.9°C. In 2012, temperature recorded during this period showed a slight increasing trend of 0.6°C but a decreasing trend of 1.0°C in 2013 .

Field methods

Goose families composed of flightless molting adults and their young were captured in mass banding drives between 5 and 14 August each year. This corresponds roughly to the second half of the flightless period of molting geese as individuals were captured when their feather had reached approximately 30 to 70% of their final length. Only successful breeding adults were susceptible to be captured because most of the non- or failed breeders (i.e. those that failed to hatch a brood) leave the island to molt (Reed *et al.* 2003). Moreover, the few non-/failed breeders that remain on the island start to molt earlier and have regained flight ability by the beginning of August.

Each year, captures were spread over 6 to 9 days and included 1 or 2 captures per day. Capture locations were separated by ~2 km or more to limit recaptures of same individuals. Capture groups averaged 446 geese including both young and adults (min = 214, max = 1113). We took morphometric measurements (culmen, tarsus and head length with an electronic caliper to the nearest 0.1 mm), body mass (to the nearest g with an electronic balance) and length of the 9th primary feather (to the nearest mm with a ruler). We measured on average 22 females per catch (min = 14, max = 40) for a total of 374 females (2012: 185, 2013: 189). We collected two growing secondary feathers on all measured females; feather were placed in dark paper envelopes and stored in dry conditions until laboratory analysis. We aimed to collect secondary feathers # 2 and #6 though in 2012 the sampling was less systematic than in 2013. We also took a blood sample (±1 ml) from the calamus of growing feathers when they were pulled out from the bird. Blood samples were centrifuged in eppendorf tubes with heparin within 6 hours after collection to extract plasma and stored at -15°C.

Corticosterone (CORT) measurements

We weighed and measured the length of secondary feather #6 before cutting and crushing at room temperature both the rachis and vanes during approximativly 1 min using an ultra turrax (Heidolph Instruments, DIAX 100) in order to obtain a powedered sample. We determined CORT level of entire feathers (in 2012 only) following the protocol of Bortolloti *et al.* (2008, 2009). CORT assays were performed at the Centre d’etude

Biologique de Chizé. Extractions were done by placing powdered samples in capped test tubes with 10 ml of methanol at 50°C overnight. The solution was then spearated from the feather material by filtration and the methanol was evaporated in a water bath at 50°C. Radioimmunoassay (RIA) was performed on reconstituted methanol extract with phosphate buffered saline (0.05M, pH 7.6). Data values are expressed as pg CORT per mm of feather as suggested by Bortolloti *et al.* (2008, 2009) (for methodological details, see Legagneux *et al.* 2013). Inter-individual coefficient of variation (CV) of CORT concentration was 30.5% (n = 166; 19 samples were damaged during sample preparation or analysis and thus excluded). The lowest detectable concentration was 11.4 pg CORT/assay tube and the lowest measurement was 16.8 pg CORT/assay tube.

Triiodothyronine (T3) measurements

We performed plasma T3 measurements (2012, n = 136 and 2013, n = 83) using a Siemens Immulite 1000 immunoassay system. Sample size was reduced due to insufficient amount of material or malfunction of the apparatus in some cases and, in 2013, the necessity to randomly select a reduced set of samples due to lack of time to analyse them all. This method is based on a reaction between assay-specific antibody or antigen-coated plastic beads as solid substrate, an alkaline phosphate-labeled reagent and a chemoluminescent enzyme substrate (Soldin *et al.* 2005). A photomultiplier tube measured the light emission from the reaction. We used a diagnostic kit to measure total T3 (kit Siemens LK T31) and followed then sample dilution protocol to obtain a final volume of 100µl. Duplicata measurements were done on 13 individuals to measure repeatability. We found that inter-individual CV was 39.0% while inter assay percentage of difference on the same individuals averaged 5.3% (range: 1.1 to 9.1%) indicating a good detectability of T3 variations among individuals.

Stiffness measurements

We adapted the protocol of Wang *et al.* (2012) and Bachmann *et al.* (2012) to design an experimental device that could measure feather stiffness using a two point bending test. This measurement (bending stiffness) was used as an index of feather quality. We note that during flight, the bending rigidity is a major contribution of lift (Worcester, 1996) and this is why we consider that high bending stiffness is an index of a high quality feather. Because we collected growing feather that had variable length, we standardized the test by measuring stiffness on a distal portion of fixed length. We cut the last 4.5 cm of secondary feather #2 from each individual and removed all the barbs by cutting them with scissors.

We inserted the proximal part of the rachis in an aluminium tube, leaving a portion of standard length (3 cm) extending outward, and fastened it to the tube with a nylon screw to prevent rachis deformation. When rachis was long enough (i.e. > 4cm; length of 11 feathers was below that value), we estimated bending stiffness by applying a deflection load at a distance corresponding to 75% of the length of the 3-cm rachis fragment as suggested by Bonser and Purslow, 1995; Worcester, 1996; and Wang *et al.* 2012 (see appendix 5). We repeated the same measurements in 2013 for individuals with T3 measurements. The vertical deflection distance was set at 6% of the fragment length and measured by using an electronic caliper placed on a vertical cast iron support. The deflection load was applied to the rachis by a thin metal membrane (blunt razor blade; as suggested by Wang *et al.* 2012) placed vertically on an electronic balance. Any deformation to the razor blade caused by the load was measured with a laser and corrected by horizontal displacement of the feather support to restore the 90° angle between the blade and the rachis. The load induced by the vertical deflection was measured on the electronic balance (to the nearest 0.01g) each second for the first 10 seconds after the load was applied, each 10 seconds for the following 2 minutes and each 30 seconds for the following 5 minutes. Measurements taken after 10 seconds were the most repeatable and were chosen to assess stiffness. On some feathers, we took two measurements (before and after removing the barbs) and we found a strong positive relationship indicating a good repeatability of our experimental device ($b1 = 0.79$, $SE = 0.06$, $r^2 = 0.92$ $p < 0.001$, $n = 15$).

Data analysis

Length of the 9th primary was used as an index of molting stage. We first used general linear models (GLM) to analyse 9th primary length in relation to date and year to check if molt phenology differed between the two years of data. Secondly, we used GLM to examine whether T3, feather CORT and body condition varied with molting stage (i.e. 9th primary length) and year (when relevant). Thirdly we examined relationships between T3, molt initiation date, feather CORT, bending stiffness and body condition according to our initial predictions. Because T3 is involved in thermoregulation (Silva, 1995; Hulbert, 2000), we also examined the relationship between T3 levels and mean temperature from 1 to 3 days before capture.

Body condition was based on body mass corrected for body size. As an index of body size, we used the individual scores from the first axis (PC1) of a principal component analysis (PCA) based on the morphometric measurements of head, culmen and tarsus length (for details see appendix 2). We used the scale mass index (SMI) as an index of condition as recommended by Peig and Green (2009). We first calculated the slope (b) of the relationship between body mass (M) and (PC1) on a log-log scale using a standardized major axis (SMA) regression ($r^2 = 0.42$, $n = 361$, $p < 0.001$). Condition of each individual was then obtained by $M_i \times (PC1_{mean}/PC1_i)^{b_{SMA}}$. We did not find any effect of Year, Capture date and their interactions on SMI (in top model year was not significant, $p = 0.07$; Δ AICc vs null model = 1.31).

We estimated the individual date of molt initiation by combining information on 9th primary length, date of measurement and speed of feather growth. Speed of feather growth (or molt speed), however, could only be determined at the population level each year, and thus the same value was applied to all individuals for a given year. Molt speed was assessed from measurements of the 9th primary feather (a single value per individual) taken on different days during the banding period. The slope of the relationship between 9th primary length and date provided an estimate of feather growth speed (see chapter 1 for details). We could calculate individual molt initiation date (MI) as MI = DC – L/MS where L = 9th primary length (mm), MS = molt speed (mm/day) and DC = date of capture. However, because molt speed decreases near the end of molt and birds were not all measured at the same stage of molt, we corrected MI as follow. Marmillot *et al.* (chapter 1) provided a relationship between annual molt speed and mean 9th primary length for the latter part of molt using data collected over a 15-year period. The average molt speeds measured in 2012 and 2013 were very close to the ones predicted by this relationship, with residuals of only -0.5 and -0.35 mm/d, respectively (in comparison, residuals in other years could be as large as -3.88). We first determined MS predicted (mm/d) by the previous relationship based on L (mm) at capture and used this value to determine L the day (d) before ($L_{d-1} = L_d - MS_{pred}$). We then obtained a new MS_{pred} value from the relationship between 9th primary length and MS for the value L_{d-1} and calculated L on d-2 using the same process (i.e. $L_{d-2} = L_{d-1} - MS_{pred}$). We continued this procedure iteratively until L reached a value of 121 mm (the minimum L measured in our dataset). Below this value, molt speed was considered constant and similar in the two years and thus the same MS_{pred} value was used until L = 0 (for details see chapter 1). This process was repeated for each individual. We acknowledge that this approach ignores individual variability in molt speed (i.e. individuals with a given 9th primary length were all considered to have the same molt speed). Although failure to account for this individual variation likely affected our estimate of molt initiation date, we have no reason to believe that it introduced a systematic bias.

RESULTS

The 9th primary length was strongly affected by the date of measurement (Appendix 6) but was very similar in the 2 years of the study (Table 2.1; in the top model, year was not significant, $p = 0.10$) indicating that individuals were measured at a similar stage of molt in the two years. Overall molt speed was estimated at 8.37 (SE = 0.35) mm/day ($r^2 = 0.61$, $p < 0.001$, $n = 375$). Body condition (SMI) was not related to 9th primary length ($b1 = 0.11$, SE = 0.23, $p = 0.65$; $n = 361$)

Table 2.1 *: Model selection for the effect of capture date (Date), year and their interaction on 9th primary lentgh of adult female greater snow geese (linear model; n = 375).*

Variables	**K**	**Log-Likehood**	**Δ_AICc**
Date + Year	4	-1661.3	0
Date + Year + Date × Year	5	-1660.5	0.53
Date	3	-1662.6	0.71
Year	3	-1827.8	330.92
Null	2	-1837.9	349.24

We found a strong negative relationship between T3 and 9th primary length (b1 = -0.02, SE = 9.32×10^{-4}, $r^2 = 0.66$, $p < 0.001$; Fig. 2.1) indicating that T3 levels decreased with molt advancement.

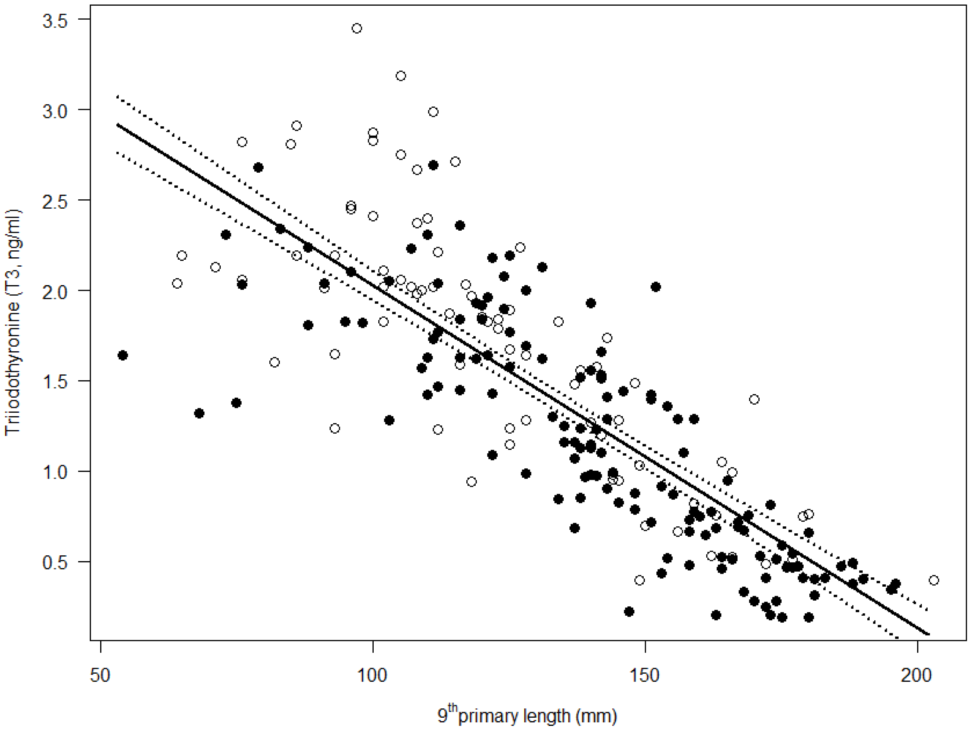

Figure 2.1: *Relationship between plasma T3 level and 9th primary length of molting adult female greater snow geese. Black dots represent 2012 and white dots 2013. The solid line represents the linear regression and dotted lines the 95% confidence interval. Fully grown feathers average 270 mm and flight capabilities is regained around 205 mm.*

T3 level also differed between years (Table 2.2; in the best model, $p < 0.001$ for year) as T3 levels were slightly higher in 2013 compared to 2012 (mean annual values were 1.73 and 1.18 ng/ml respectively). When we corrected 9th primary length for capture date (i.e. residuals of 9th primary length vs date), there was also a weak negative relationship with T3 (Appendix 7).

Table 2.2 *: Model selection for the effect 9th primary lentgh (Prim9), year and their interaction on T3 levels of adult female greater snow goose (linear model ; n = 219).*

Variables	**K**	**Log-Likehood**	**Δ_AICc**
Prim9 + Year	4	-113.3	0
Prim9 + Year + Prim9 × Year	5	-113.2	1.77
Prim9	3	-119.3	9.88
Year	3	-222.6	216.47
Null	2	-238.7	246.58

We found a weak but significant negative relationship between T3 and mean temperature during 2 or 3 days before capture (e.g., 3-day before: b1 = -0.36, SE = 0.07, r2 = 0.11, $p < 0.0016$), but not when we considered only the day of capture or the day before ($p > 0.05$). When we compared the influence of temperature and 9th primary length on T3, the model with 9th primary was clearly preferred (Δ AICc between these two models = 211.7). We added a temperature covariate in subsequent analyses with other variables of interest but trends were always similar with or without it. For sake of simplicity, we report subsequent results without any temperature covariate.

In order to examine if date of molt initiation affected T3 level of individuals, we corrected T3 for the molt stage (i.e. we used residuals from the relationship on Fig. 2.1) because (1) individuals were measured at various stage of molt (i.e. different 9th primary length) and (2) T3 was related to 9th primary length. We found a weak negative relationship between T3 corrected for molting stage and molt initiation date (b1 = -0.04, SE = 0.01, r^2 = 0.04, p = 0.003; Fig. 2.2). We also found a weak positive relationship between T3 corrected for molting stage and body condition (b1 = 4.95×10^{-4}, SE = 1.99×10^{-4}, r^2 = 0.02, p = 0.014; Fig. 2.3) but we did not find significant relationship between T3 and body mass (b1 = 4.67×10^{-4}, SE = 2.67×10^{-4}, r^2 = 0.01, p = 0.082).

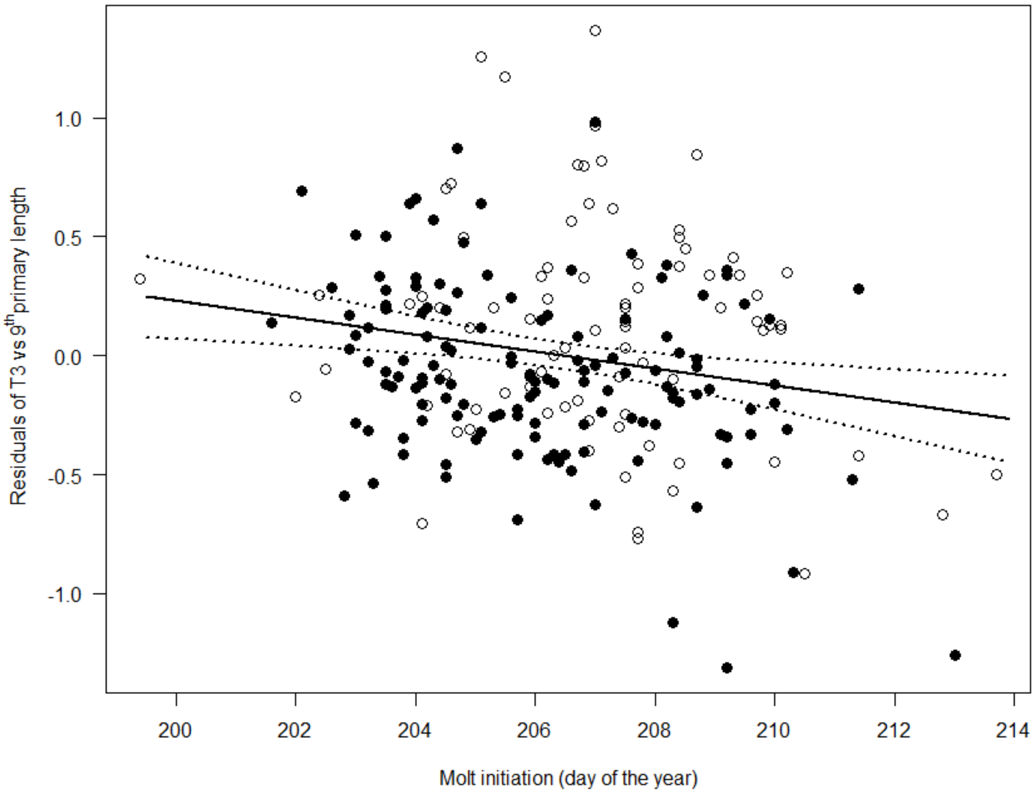

Figure 2.2: *Relationship between plasma T3 level corrected for molting stage (i.e. residuals of the relationship between T3 and 9th primary length) and molt initiation date of molting adult female greater snow geese. Black dots represent 2012 and white dots 2013. The solid line represents the linear regression and dotted lines the 95% confidence interval.*

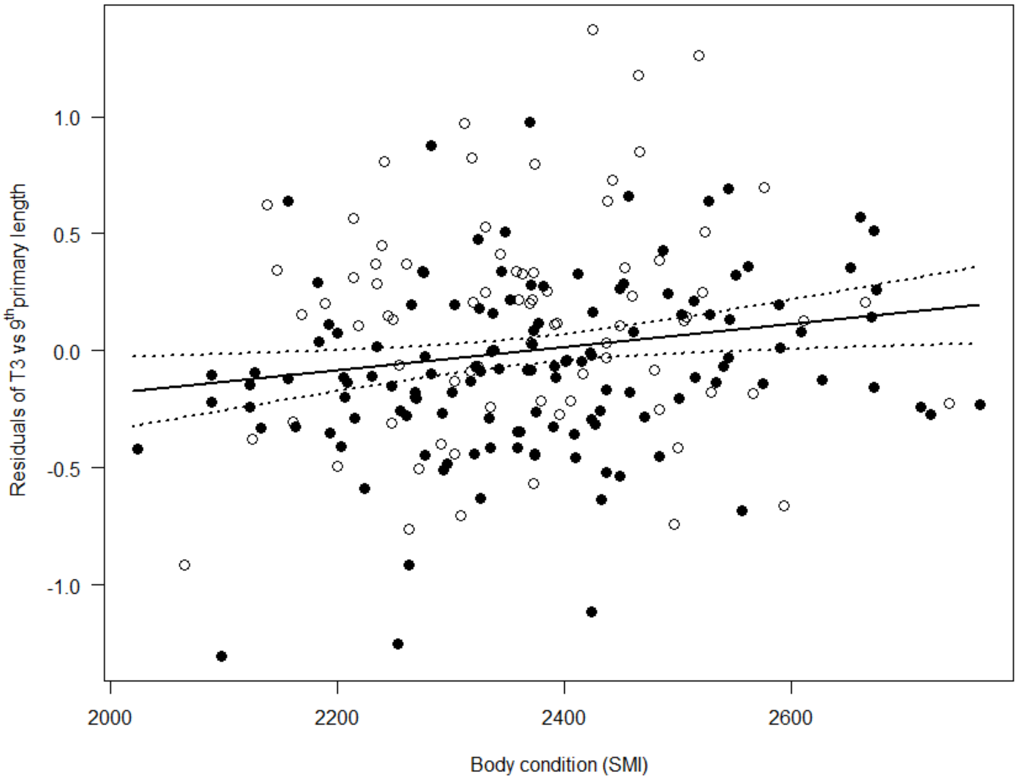

Figure 2.3*: Relationship between plasma T3 levels corrected for molting stage (i.e. residuals of the relationship between T3 and 9th primary length) and body condition (Scale Mass Index; see methods for a description of this index) of molting adult female greater snow geese. Black dots represent 2012 and white dots 2013. The solid line represents the linear regression and dotted lines the 95% confidence interval.*

There was no relationship between feather CORT and 9th primary length (b1 = -0.33, SE = 1.41, p = 0.81; n = 165) or between feather CORT and molt initiation date (b1 = 6.66×10^{-3}, SE = 5.69×10^{-2}, p = 0.91, n = 165, Appendix 8). However, there was a negative relationship between T3 corrected for molting stage and feather CORT (b1 = -0.06, SE = 0.02, r^2 = 0.05, p = 0.007; Fig. 2.4) indicating that high CORT level was associated with a reduced relative T3 level. We also found a negative relationship between body condition and feather CORT (b1 = -22.22, SE = 6.48, r^2 = 0.06, $p < 0.001$; Fig. 2.5) indicating that individuals in better condition had reduced levels of CORT. Finally, there was no relationship between bending stiffness and feather CORT or between bending stiffness and body condition ($P > 0.05$; Appendix 9 and 10).

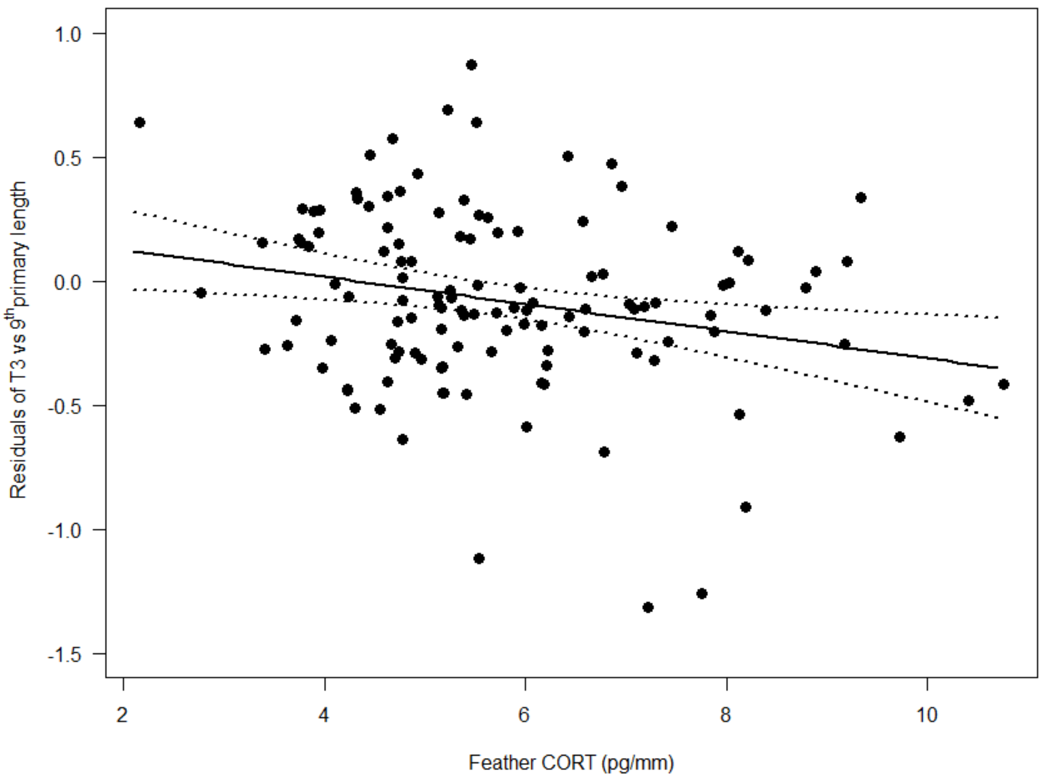

Figure 2.4: *Relationship between plasma T3 level corrected for molting stage (i.e. residuals of the relationship between T3 and 9th primary length) and corticosterone (CORT) measured in growing feathers of molting adult female greater snow geese in 2012. The solid line represents the linear regression and dotted lines the 95% confidence interval.*

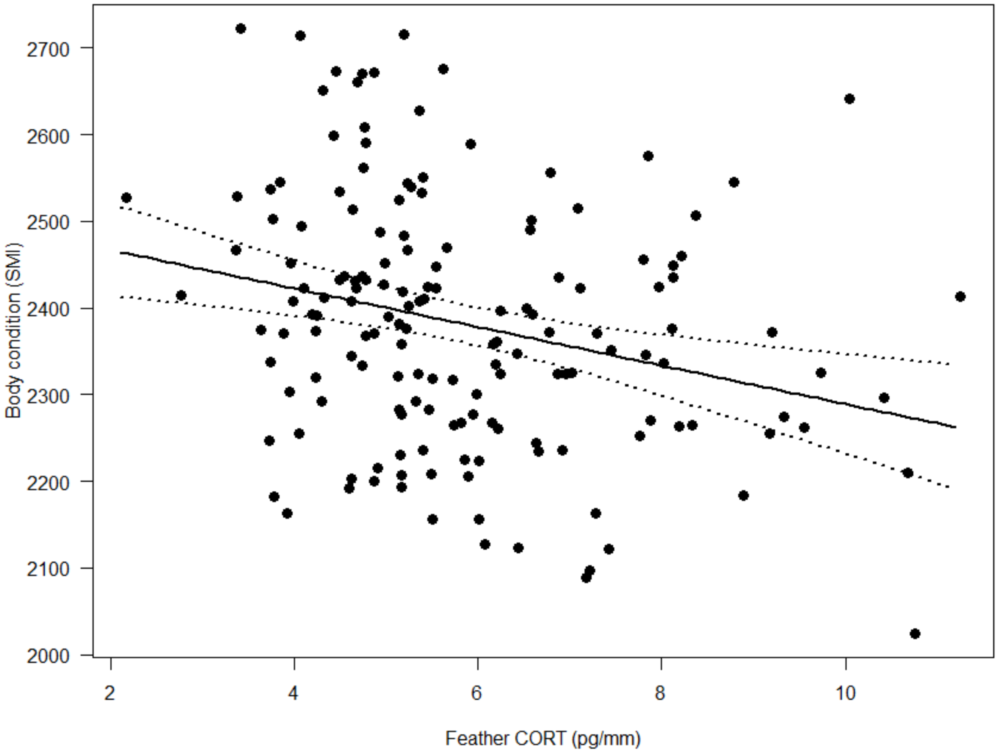

***Figure 2.5**: Relationship between body condition (Scale Mass Index; see methods for a description of this index) and corticosterone (CORT) measured in growing feathers of molting adult female greater snow geese in 2012. The solid line represents the linear regression and dotted lines the 95% confidence interval.*

DISCUSSION

We examined physiological factors associated with the molt of flight feathers in the greater snow goose, a species exposed to severe environmental constraints in the High Arctic. Our study revealed higher levels of plasmatic T3 half-way through the molt period, though these values were comparable to those measured in non-molting females during spring staging in southern Québec (mean = 2.42, SD = 0.92, n = 149; P. Legagneux unpubl. data), a period of rapid fat accumulation (Gauthier *et al.* 1992). T3 levels of molting females decreased considerably (at least 6-fold) between the time that 9th primary increased from 30 to 70% of its final length to reach very low values (≤ 0.5 ng/ml). T3 level has been shown to be related to basal metabolic rate in several studies and is considered to be closely associated with metabolic activity (Assenmacher, 1973; Vézina *et al.* 2009). Our results thus suggest that metabolism was elevated during molt but that this activity decreased rapidly during the second half of molt, well before the completion of flight feather growth. This reduction in metabolic activity could explain why the speed of feather growth decreased during this period, as shown in chapter 1.

Large increases in T3 during molt has been previously reported in other species like penguins and domestic turkeys but, surprisingly, the return of T3 to low levels typically occurs at the very end of molt or after its completion rather than during the latter part of it as we found (Groscolas and Leloup, 1986; Lien and Siopes, 1993). Reasons for these differences are unclear but could be related to different molt patterns among species. Penguins renew their entire body feather over a very short period of time while ashore whereas anatideae molt their body feather gradually, over a much longer period of time than their flight feathers (Pyle, 2005; Craik *et al.* 2009). A decrease in insulation due to the simultaneous molt of body feathers in penguins could explain why T3 levels remained high until molt completion (Schieltz and Murphy, 1997; Vézina *et al.* 2009). Indeed, high thyroid hormone levels have been related to increased thermoregulatory cost and low ambient temperature in other studies (Hulbert, 2000; Collin *et al.* 2005). Although temperature also influenced T3 level in our study, its effect was quite small compared to the effect of molting stage (i.e., 9th primary length). Moreover, even though temperature followed opposite temporal trends in 2012 and 2013, it had no effect on the relationship between T3 levels and 9th primary length, confirming the overriding effect of the latter variable. The weak influence of temperature on T3 in our study could be due to the relatively small variation in daily temperature over the course of the study and the fact that geese were primarily molting flight feathers rather than body feathers.

We had previously shown that birds initiating molt later in the season tended to increase the speed of feather growth (Chapter 1). If T3 is related to molt intensity, we expect that T3 should be elevated in individuals that initiate their molt late. However, we found a weak trend in the opposite direction. Also contrary to our prediction, corticosterone levels were not elevated in individuals that initiated their molt later in the season. We recognize, however, that we had to apply population-level estimates of molt speed at the individual level to back-calculate molt initiation dates, which could have introduced unknown biases and weakened our ability to correctly estimate the relationship between T3 or corticosterone levels and molt initiation date. Alternatively, other factors may have been more important in affecting levels of these hormones (see below).

Individuals in good body condition had higher T3 levels than those in poor condition, which could reflect higher molt intensity in the former group. This is consistent with results in Chapter 1 where we showed that, across years, individuals in good body condition had longer 9th primary feather (adjusted for date the of measurement). Stressed individuals, as measured by feather corticosterone, also had a lower body condition as expected, and reduced T3 levels. This suggests that chronic stress could reduce metabolic activity and possibly molt intensity, and could provide the link between body condition and feather growth. This is consistent with a study showing that individual passerines with experimentally elevated corticosterone levels had a 19% reduction in feather growth rate 5 days after receiving CORT implants (Romero *et al.* 2005).

Contrary to our predictions, feather quality, as measured by bending stiffness, was not affected by either feather corticosterone levels or body condition. Previous studies have shown that high CORT levels could affect feather quality in molting common starling (*Sturnus vulgaris*) can interrupt feather growth and disrupt their mechanical properties, resulting in increased risks of breakage during tensile constraints (Strochlic and Romero, 2008; Desrochers, 2009). However, these studies artificially increased CORT levels by using implants or psychological stressors and thus the stress levels experienced by these individuals could have been much higher than under natural conditions, such as in our study. Our results suggest that long distance migrants such as the greater snow goose do not make compromise on feather quality when stressed, possibly because it is essential to maintain their mechanical properties. It is also possible that the range of environmental conditions encountered by individuals in our study was not large enough to elicit a response. CORT levels were only measured in 2012 when phenology and timing of molt was near the average at our study site (see Chapter 1) and thus the absence of extreme environmental conditions could have induced a low inter-individual CORT variation. Legagneux *et al.* (2013) showed that feather corticosterone in common eiders (*Somateria* *mollissima*) mainly reflect yearly environmental conditions and that inter-annual differences could potentially be more important than intra-annual ones. We also recognize that bending stiffness is only one measure of feather quality and it is possible that other feather properties such as Young Modulus or keratin deposition could be more sensitive to stress (Bonser, 1996; Cameron *et al.* 2003).

Molt is a plastic activity in birds that can be affected by multiple constraints. However, how physiological and environmental factors interact with each other to shape molt strategies and ultimately feather quality and fitness remain poorly known. As suggested by Viain *et al.* (2014), molt strategy in Anatideae could be a compromise between a low rate of feather growth to ensure feather quality and a high rate to reduce the flightless period and predation risk. Experimentally-induced high rate of flight feather growth in starlings has indeed been shown to reduce feather quality, which compromised survival (Dawson *et al.* 2000). Therefore, under natural conditions, individuals should adopt strategies that will maintain feather quality, as suggested by our study.

CONCLUSION GÉNÉRALE

A travers une approche écophysiologique et l'utilisation de différentes échelles (i.e. populationnelle et individuelle), dans un contexte arctique où les contraintes temporelles et environnementales sont particulièrement sévères, cette étude a permis d'examiner l'effet des conditions environnementales, de la reproduction, de la condition corporelle et du statut hormonal sur la phénologie de la mue de la grande oie des neiges et sur la qualité des plumes produites. Les résultats de notre étude ont permis de démontrer des capacités d'ajustement dans le timing d'une activité essentielle du cycle vital des oiseaux telle que la mue. Nous montrons en effet que les variations phénologiques de la reproduction de la grande oie des neiges, fortement reliées aux conditions climatiques printanières (Bêty *et al.* 2003, Dickey *et al.* 2008), peuvent être amoindries par une certaine plasticité phénotypique de la mue. L'ajustement principal se ferait par une modulation de la vitesse de croissance des plumes, cette vitesse s'accélérant dans les années où la reproduction et le début de la mue sont retardés à cause des conditions environnementales. Ce mécanisme permettrait d'achever le renouvellement des plumes de vol avant la fin du court été arctique et le début de la migration automnale, indépendamment des conditions environnementales printanières. À notre connaissance, ces résultats qui soulignent des variations de la vitesse de croissance des plumes de l'oie (chapitre 1), sont particulièrement novateurs puisque les travaux antérieurs (Lindholm *et al.* 1994 ; Hera *et al.* 2011) ont documenté peu de flexibilité intra-spécifique de la vitesse de mue.

En accord avec les résultats de Singer *et al.* (2012) sur la bernache cravant, nous montrons qu'il existe une période de temps incompressible entre l'éclosion des oisons et l'initiation de la mue des femelles adultes. Durant l'incubation, les possibilités d'alimentation des femelles sont très limitées (Poussart *et al.* 2001) et ce délai incompressible pourrait ainsi permettre la reconstitution des réserves énergétiques avant d'initier une activité énergétiquement coûteuse telle que la mue (Portugal *et al.* 2007). Nous avons observé une tendance à ce que le délai entre l'éclosion des jeunes et le début de la mue s'allonge les années où la reproduction est tardive, suggérant que les femelles pourraient avoir besoin de plus de temps pour refaire leur condition physique avant de débuter la mue durant ces années là.

Les changements physiologiques mis en place lors de la mue et la synthèse de tissus pour la croissance de nouvelles plumes sont des processus énergétiquement coûteux (Lindstrom *et al.* 1993). Il est donc plausible que l'augmentation de la vitesse de croissance des plumes lors des années tardives requiert une augmentation de l'activité métabolique et entraine des dépenses énergétiques accrues bien que dans notre étude des tendances opposées se dégagent, probablement en raison de biais dans le calcul de la date d'initiation de la mue. Cette idée est supportée par certains de nos résultats qui font ressortir une condition corporelle réduite chez les individus moins avancés dans leur mue et chez ceux présentant un niveau de stress plus élevé sur la base de leur niveau de corticostérone dans les plumes en croissance.

Nous montrons également que la sécrétion d'hormones thyroïdiennes, vraisemblablement un indice de l'activité métabolique, atteint des niveaux plus élevés durant la mue. Contrairement aux travaux réalisés par Groscolas et Leloup (1986) et Lien et Siopes (1993) qui rapportent tous les deux une diminution des niveaux de T3 en fin de mue, nos résultats soulignent une forte diminution de T3 durant la deuxième moitié de la mue. Ceci pourrait expliquer la diminution de la vitesse de croissance des plumes constatée durant la seconde partie de la mue de l'oie des neiges (chapitre 1). Par contre, nous n'avons pas trouvé d'évidence que ces niveaux d'hormones soient plus élevés chez les individus qui avaient initient la mue plus tardivement. Nous avons toutefois observé une réduction des niveaux de T3 chez les individus avec un niveau de corticostérone élevé ce qui suggère que l'intensité de la mue pourrait être réduite chez les individus les plus stressés.

Les résultats portant sur la rigidité flexionnelle des plumes n'ont pas permis de mettre en évidence une relation entre cette variable et le stress ou la condition physique des individus. Ceci suggère que les individus ne sont pas prêts à compromettre la qualité des plumes de vol produites quelles que soient les conditions environnementales. Ces résultats pourraient s'expliquer par l'importance majeure de produire des plumes de qualité afin de maintenir l'efficacité énergétique du vol chez un oiseau migrateur de longue distance comme l'oie des neiges. Pourtant, des travaux chez l'étourneau sansonnet ont démontré une diminution de la qualité des plumes en fonction de leur vitesse de croissance. Toutefois, les conditions expérimentales de cette étude (Dawson, 2000) pourraient induire des niveaux de stress qui ne se retrouvent que rarement en milieu naturel (i.e. seulement lorsque les conditions environnementales sont extrêmes). Il est aussi possible que des propriétés mécaniques non mesurées dans notre étude aient été affectées. En effet, les résultats d'une étude interspécifique chez les Anatidae soulignent les différentes stratégies et compromis possibles entre une augmentation de la vitesse de croissance des plumes, pouvant conduire à une diminution de leur qualité, et une diminution de la période d'incapacité de vol, réduisant le risque de prédation (Viain *et al.* 2014).

Perspectives d'avenir

Afin d'élargir notre compréhension des mécanismes de la mue, de sa plasticité et des coûts qui peuvent y être associés, différents aspects de notre étude mériteraient d'être approfondis. En effet, les contraintes logistiques durant l'échantillonnage nous ont obligé à travailler à une échelle populationnelle pour calculer des vitesses de mue annuelles. De la même manière, la phénologie de la reproduction a été calculée à partir de dates médianes annuelles. Cette approche ne permet donc pas de considérer avec précision la variabilité inter-individuelle et malgré les corrections apportées, des biais potentiels pourraient subsister dans notre étude, notamment à travers des effets confondants entre les années et la diminution de la vitesse de croissance des plumes en fin de mue. Sachant que des oies marquées et facilement identifiables (i.e. femelles à collier) sont relativement accessibles durant la période de ponte et d'incubation, des mesures spécifiques ainsi qu'un effort de recapture ciblé sur ces individus augmenterait certainement la précision de l'étude. De plus, si les mesures de longueur des plumes pouvaient être répétées sur les mêmes individus plus d'une fois dans l'été, cela permettrait d'obtenir des mesures de vitesse de croissance des plumes au niveau individuel plutôt que populationnel. Cet effort d'échantillonnage supplémentaire permettrait sans doute d'affiner nos résultats en mettant en relation, sur une échelle individuelle, la phénologie de la reproduction, le timing de la mue, la vitesse de croissance des plumes, la condition corporelle, les facteurs physiologiques et la qualité des plumes nouvellement produites. Ainsi, les coûts associés aux mécanismes de compensation (i.e ajustement de la vitesse de mue) en fonction de la phénologie et de l'environnement seraient plus précisément quantifiables.

Il pourrait aussi être particulièrement intéressant de répéter l'échantillonnage et les analyses physiologiques lors d'années contrastés et/ou extrêmes en termes de phénologie et de conditions environnementales. En effet, la phénologie de la reproduction, le timing et la vitesse de mue étaient non seulement très similaires entre 2012 et 2013 mais également assez typiques comparativement à l'ensemble des autres années de notre base de données. Ce faible contraste, conjugué à l'absence de conditions extrêmes, pourrait expliquer certaines relations non significatives que nous avons constatées lors de notre approche écophysiologique de la mue. D'autres dosages hormonaux tels que la prolactine et la thyroxine pourraient également permettre de préciser un élément clé de notre étude. Plusieurs travaux montrent en effet une diminution des niveaux de prolactine et une augmentation de T4 lors de l'initiation de la mue (Groscolas et Leloup, 1986, Lien et Siopes, 1993 ; Dawson, 2006). Enfin, pour des raisons pratiques et logistiques, nous avons choisi de travailler avec la rigidité flexionnelle comme proxi de la qualité des plumes mais de toute évidence, de nombreuses autres covariables pourraient être considérées comme indice de qualité (e.g. résistance aux parasites, à l'abrasion, mesure du Module de Young). Les propriétés mécaniques associées aux forces aérodynamiques durant le vol restent peu étudiées et les divers rôles joués par les plumes (e.g. le vol, l'isolation thermique, caractères sexuels secondaires durant la reproduction) complexifient grandement la détermination des éléments qui constituent une plume de haute qualité. Il serait donc intéressant d'approfondir ce sujet puisque notre étude fait ressortir une capacité d'augmentation de la vitesse de croissance des plumes lors des années tardives contrairement aux années hâtives où la vitesse est réduite. Ceci suggère la présence de coûts associés à une augmentation de la vitesse de mue qui pourraient apparaitre à travers une réduction possible de la qualité des plumes.

En conclusion, l'approche écophysiologique et intégrative de notre étude a permis de mettre en évidence des capacités d'ajustement de la mue chez la grande oie des neiges en fonction des conditions environnementales prévalant en début de reproduction. Pourtant, les limites de cette plasticité phénotypique et certains coûts qui pourraient y être associés n'ont pu être établis. Examiner ces questions permettrait d'élargir notre compréhension des mécanismes de plasticité de la mue et serait particulièrement pertinent dans un contexte de changement climatique marqué, dans les hautes latitudes, comme par exemple dans le régime des précipitations ou de la couverture neigeuse printanière (Hassol, 2004 ; Gauthier *et al.* 2013). Ces phénomènes pourraient affecter de façon marquée le cycle vital et ultimement la survie de plusieurs espèces de l'Arctique.

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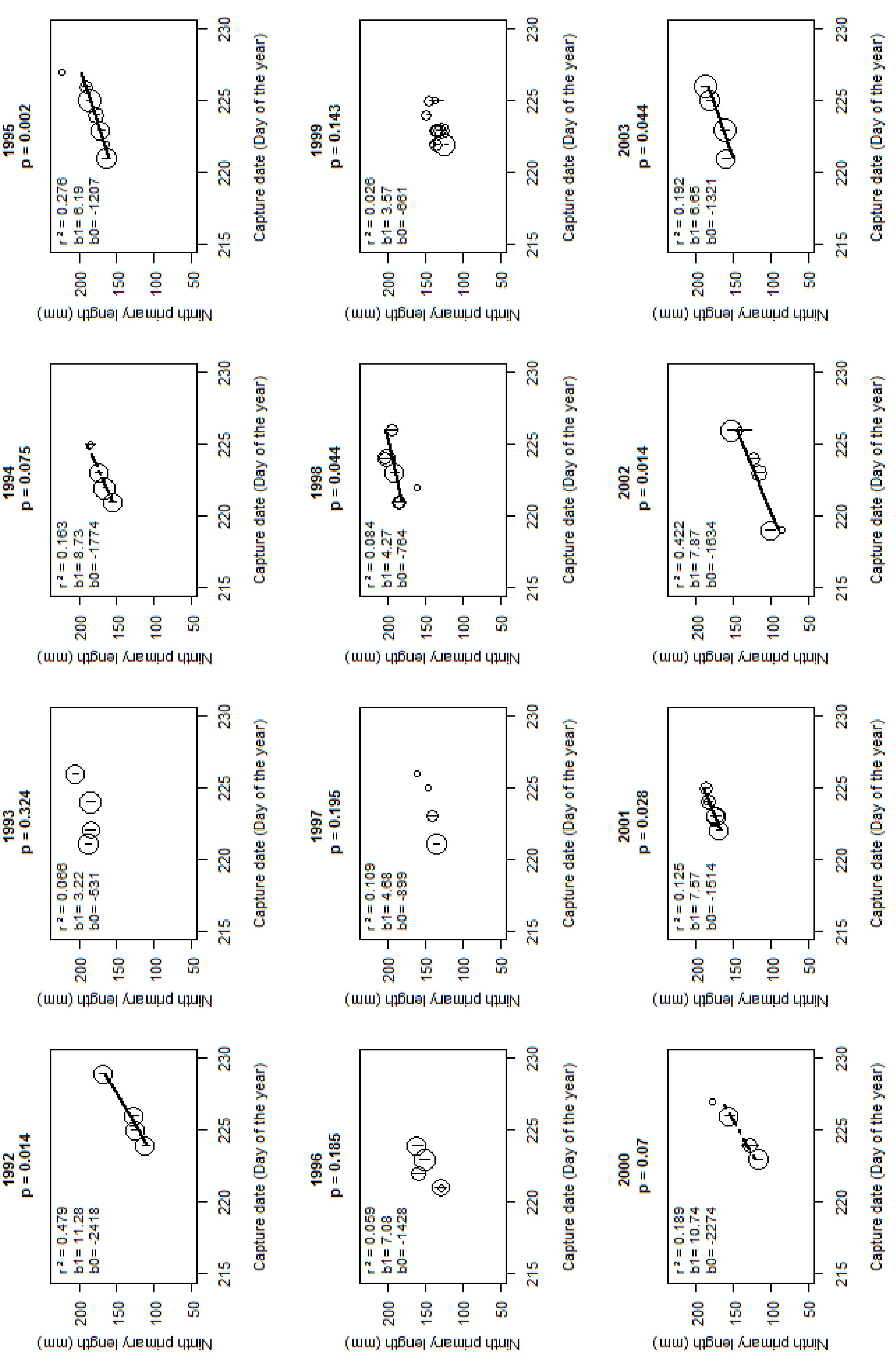
ANNEXES

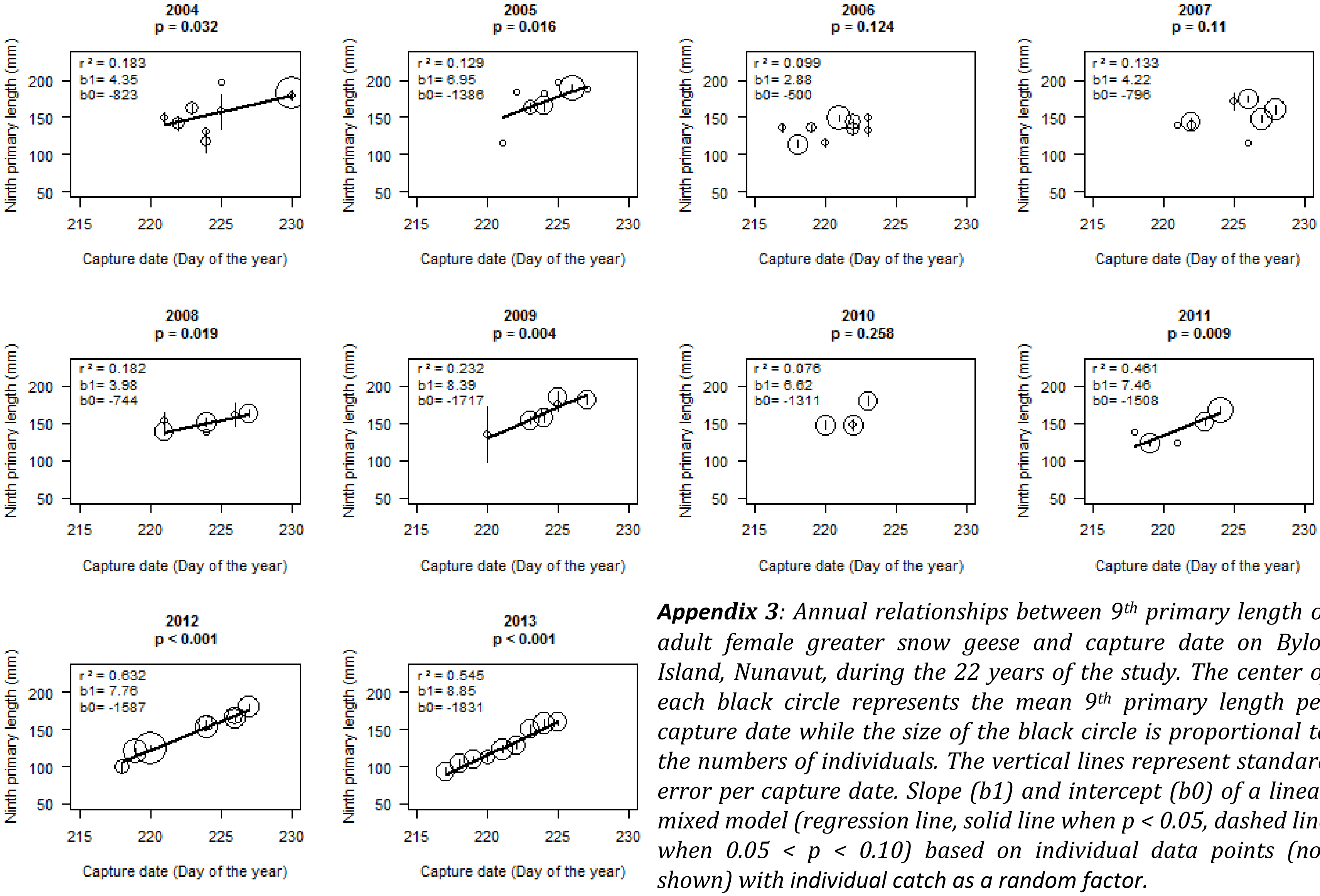
Appendix 1 : Summary table of median hatching date, capture date and mean 9th primary length during the 22 years of sampling (dates are in day of the year)

Year	Median hatching date	First day of capture	Last day of capture	Median date of capture	Mean 9th primary length (mm)	Total number of females measured
1992	197	224	229	226	132.1	78
1993	184	221	226	224	188.5	82
1994	188	221	225	222	164.4	63
1995	188	221	227	224	175.6	96
1996	193	221	224	223	147.8	77
1997	188	221	226	221	138.3	32
1998	185	221	226	223	188.9	80
1999	193	222	225	223	133.8	101
2000	195	223	227	224	135.8	57
2001	190	222	225	223	175.7	81
2002	192	219	226	224	124.4	73
2003	187	221	226	224	168.5	92
2004	189	221	230	230	170.0	125
2005	189	221	227	224	175.0	69
2006	191	217	223	221	137.1	103
2007	192	221	228	226	155.9	95
2008	188	221	227	224	148.9	66
2009	190	220	227	224	168.4	85
2010	190	220	223	222	156.2	65
2011	189	218	224	223	149.7	73
2012	191	218	227	224	142.3	185
2013	191	217	225	221	126.9	189

Appendix 2: Eigenvalues and loading extracted from Principal component Analysis output

		Axis 1	**Axis 2**	**Axis 3**
Eigenvalues	**Variance**	2.04	0.73	0.23
	Percentages of variance	67.9	24.2	7.8
	Cumulative percentage of variance	67.9	92.2	100
Factor loadings	**Tarsus length**	0.65	0.76	0.03
	Head length	0.91	-0.23	-0.35
	Culmen length	0.89	-0.32	0.33


1992
p = 0.014
r² = 0.479
b1= 11.28
b0= -2418
1993
p = 0.324
r² = 0.066
b1= 3.22
b0= -531
1994
p = 0.075
r² = 0.163
b1= 8.73
b0= -1774
1995
p = 0.002
r² = 0.276
b1= 6.19
b0= -1207
1996
p = 0.185
r² = 0.059
b1= 7.08
b0= -1428
1997
p = 0.195
r² = 0.109
b1= 4.68
b0= -899
1998
p = 0.044
r² = 0.084
b1= 4.27
b0= -764
1999
p = 0.143
r² = 0.026
b1= 3.57
b0= -661
2000
p = 0.07
r² = 0.189
b1= 10.74
b0= -2274
2001
p = 0.028
r² = 0.125
b1= 7.57
b0= -1514
2002
p = 0.014
r² = 0.422
b1= 7.87
b0= -1634
2003
p = 0.044
r² = 0.192
b1= 6.65
b0= -1321
Ninth primary length (mm)
50
100
150
200
Capture date (Day of the year)
215
220
225
230

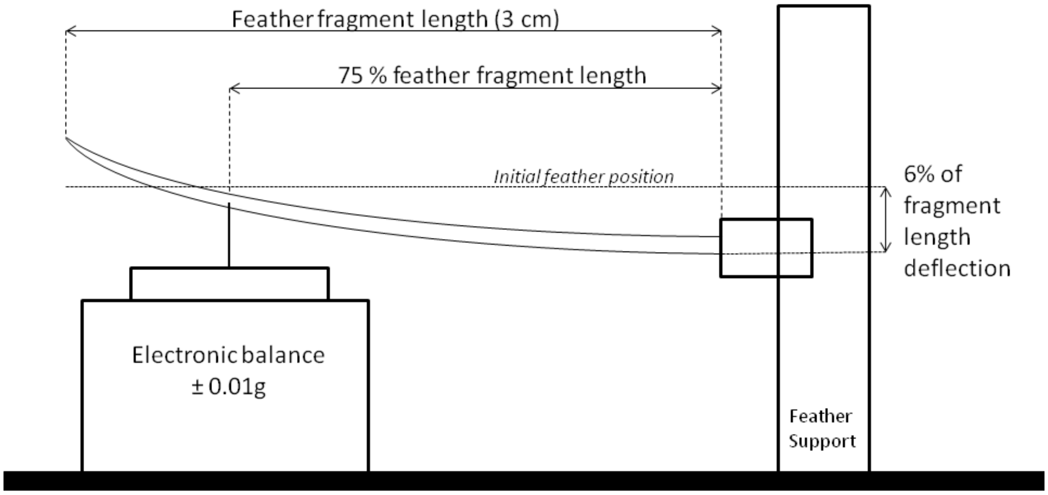


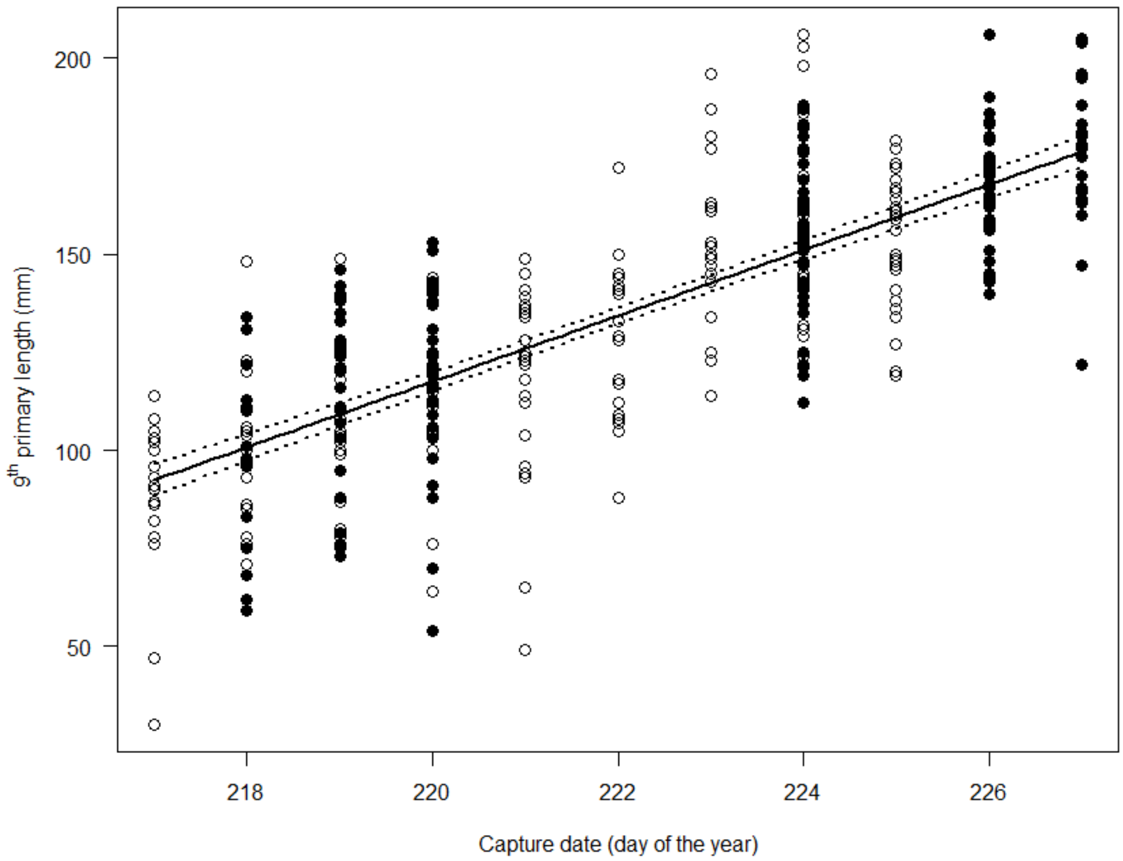
Appendix 3: *Annual relationships between 9th primary length of adult female greater snow geese and capture date on Bylot Island, Nunavut, during the 22 years of the study. The center of each black circle represents the mean 9th primary length per capture date while the size of the black circle is proportional to the numbers of individuals. The vertical lines represent standard error per capture date. Slope (b1) and intercept (b0) of a linear mixed model (regression line, solid line when $p < 0.05$, dashed line when $0.05 < p < 0.10$) based on individual data points (not shown) with individual catch as a random factor.*

Appendix 4: Model selection for the effect of capture Date , Year and their interaction on 9th primary lentgh of molting adult female greater snow geese (mixed linear model with catch size as the random factor; n = 1412 individuals during 15 years).

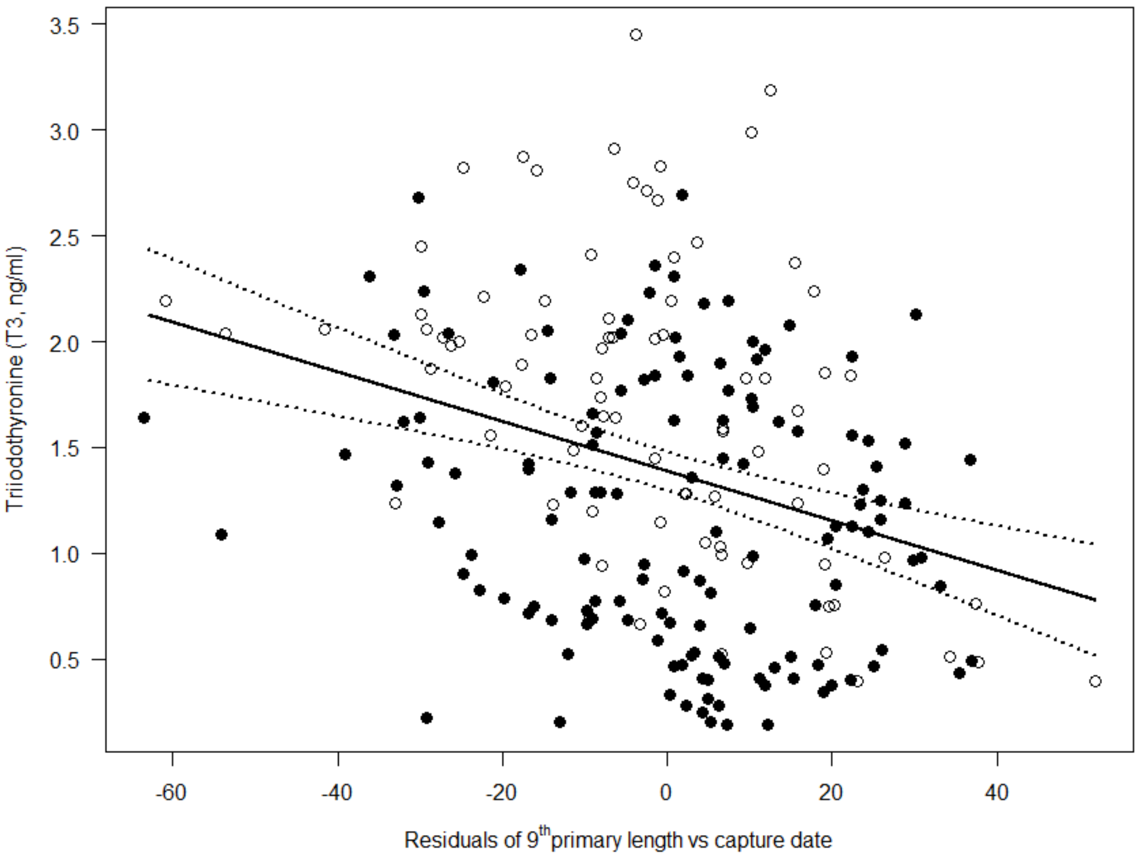
Variables	**K**	**Log-Likehood**	**Δ_AICc**
Date + Year + Date*Year	32	-6409.1	0
Date + Year	18	-6435.2	23.13
Year	17	-6499.9	150.54
Date	4	-6798.4	721.07
Null	3	-6876.1	874.44

Appendix 5: Experimental device used to measure bending stiffness of feathers,

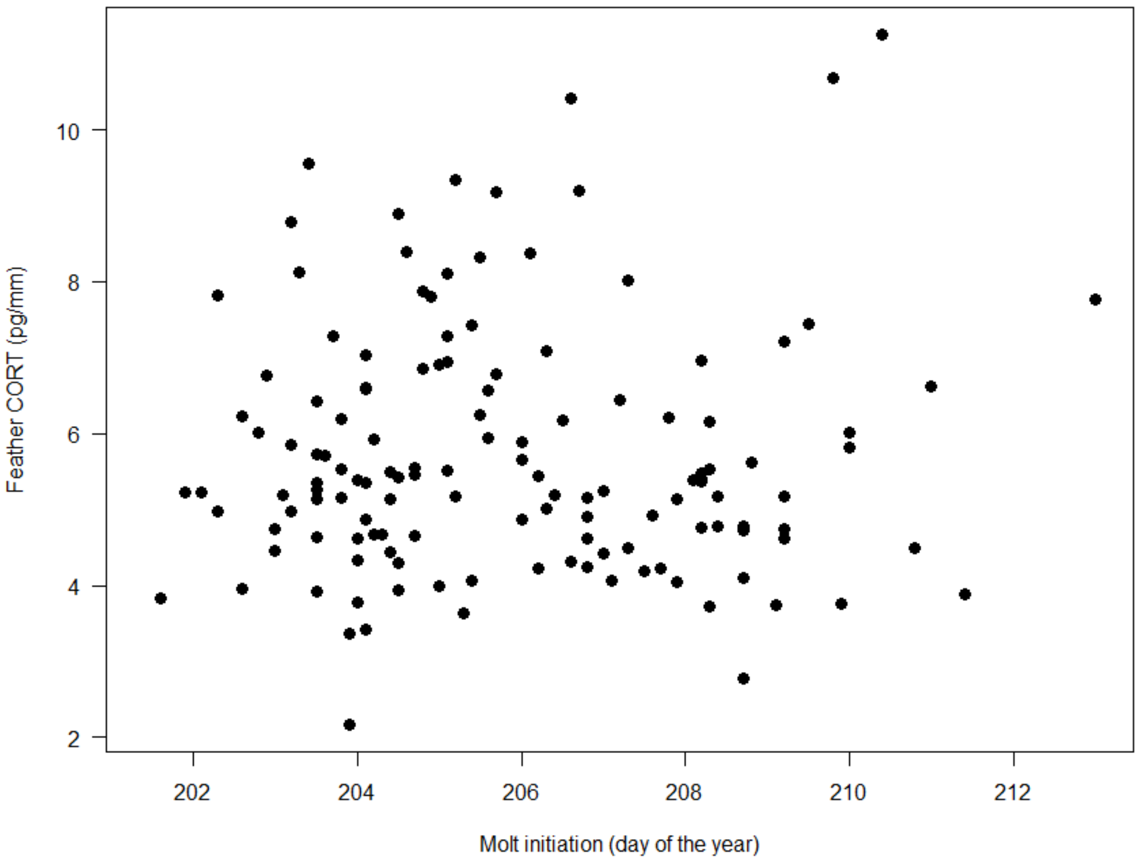




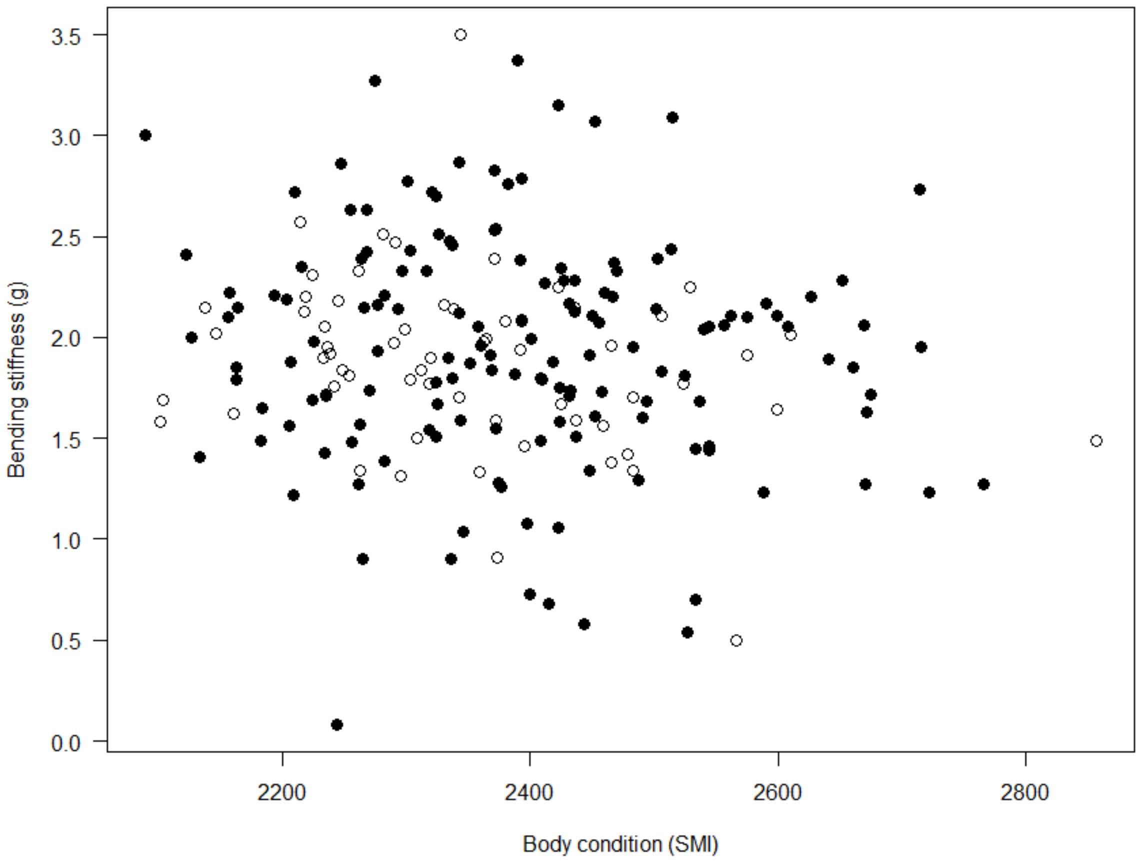
Appendix 6: *Relationship between* 9^{th} *primary length and capture date of molting adult female greater snow geese. Black dots represent 2012 and white dots 2013. The solid line represents the linear regression (b1 = 8.37, SE = 0.35,* $r^2 = 0.61$*, p < 0.001) and dotted lines the 95% confidence interval.*



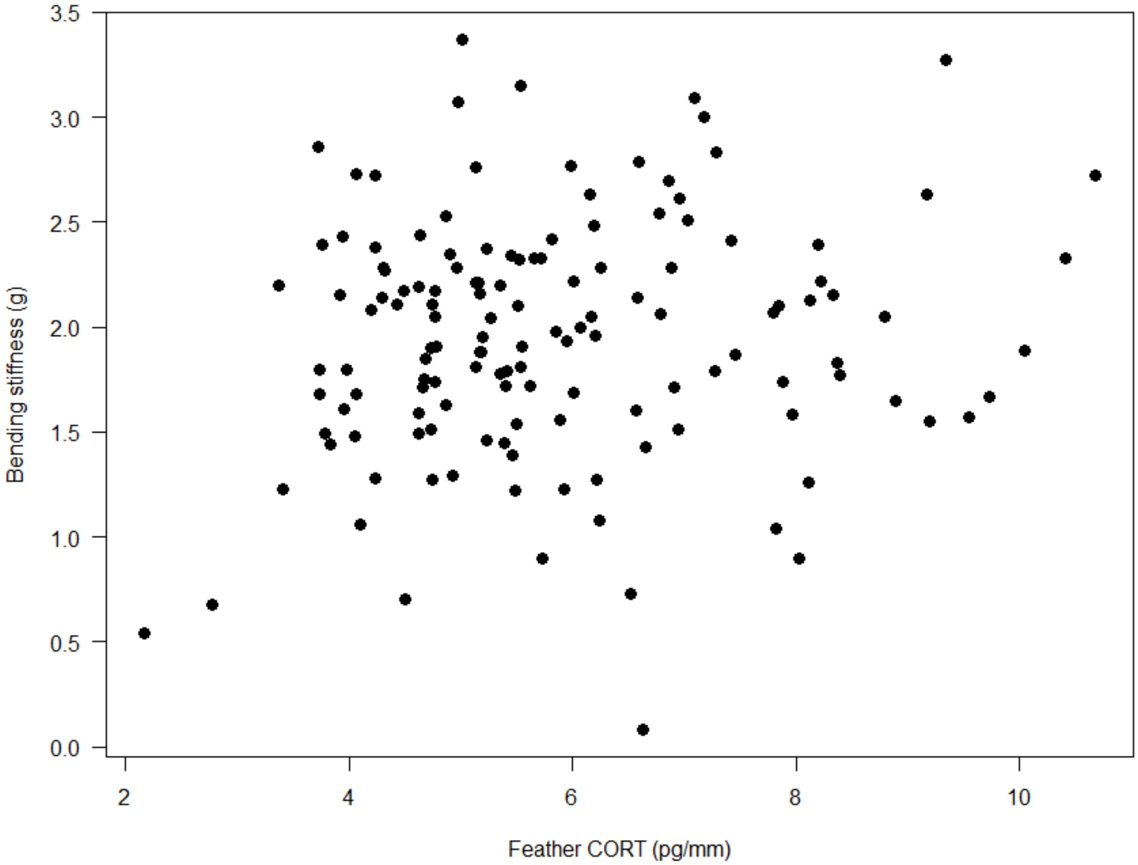
Appendix 7: *Relationship between T3 and residuals of 9th primary length vs capture date in molting adult female greater snow geese. Black dots represent 2012 and white dots 2013. The solid line represents the linear regression (b1 = -0.01, SE = 0.002, r^2 = 0.09, p< 0.001) and dash lines the 95% confidence interval.*



Appendix 8: *Relationship between corticosterone (CORT) measured in feather of molting adult female greater snow geese and molt initiation date* (b1 = 6.66×10^{-3}, SE = 5.69×10^{-2}, p = 0.91).



Appendix 9: *Relationship between bending stiffness of growing feathers and body condition (Scale Mass Index; see methods for a description of this index) of molting adult female greater snow geese. Black dots represent 2012 and white dots 2013 (b1 =* -4. 85×10^{-4}, *SE = 2.58×*10^{-4}, $r^2 = 0.01$, $p = 0.06$).



Appendix 10: *Relationship between bending stiffness of growing feathers and corticosterone (CORT) measured in feathers of molting adult female greater snow geese (b1 = 0.04, SE = 0.03, r^2 = 0.01, p = 0.13).*