UNIVERSITÉ DU QUÉBEC À RIMOUSKI

# PHÉNOLOGIE DE LA REPRODUCTION ET ALLOCATION DES RESSOURCES DANS LES ŒUFS CHEZ UN REPRODUCTEUR SUR ÉPARGNE, L'EIDER À DUVET (*SOMATERIA MOLLISSIMA*) NICHANT EN ARCTIQUE

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# AVANT-PROPOS

Ce mémoire est divisé en quatre parties. D'abord, une introduction générale fournit au lecteur une mise en contexte du sujet d'étude et présente les objectifs du mémoire. Les deux chapitres principaux présentent ensuite les résultats des travaux de recherche et sont écrits sous forme d'articles qui seront soumis à des revues scientifiques. Le mémoire se termine par une brève conclusion générale.

## CONTRIBUTION DES AUTEURS

Bien que Joël Bêty, Grant Gilchrist, Keith Hobson et Sarah Jamieson soient co-auteurs de l'un ou des deux chapitres principaux, le manuscrit doit être considéré comme le mémoire de l'étudiante. J. Bêty et G. Gilchrist ont fourni les données de 2002 à 2004 et ont guidé l'étudiante lors des analyses statistiques et de la rédaction du mémoire. K. Hobson et S. Jamieson ont collaboré en partie aux travaux en laboratoire. Édith Sénéchal a traité les données fournies, a planifié et effectué l'échantillonnage de 2007 et 2008, a fait des analyses en laboratoire et les analyses statistiques, et a rédigé le mémoire.

# RÉSUMÉ

Afin de maximiser leur valeur adaptative, les organismes vivants doivent balancer l’énergie qu’ils investissent dans les processus vitaux tels la survie, la croissance et la reproduction. Chez les oiseaux, les besoins énergétiques de la reproduction peuvent être assumés par les réserves endogènes des femelles ou par la nourriture ingérée au moment de la reproduction. Les contraintes énergétiques rencontrées par les femelles durant la période de ponte ainsi que la date et la taille de ponte peuvent potentiellement faire varier les stratégies d’allocation des nutriments dans la reproduction. Les eiders à duvet (*Somateria mollissima*) nichant en arctique sont considérés comme des reproducteurs sur épargne stricts, donc qui dépendent essentiellement de leurs réserves pour former et incuber leurs œufs. Les femelles jeûnent durant l’incubation et leur condition corporelle lors de l’éclosion des œufs est directement proportionnelle à leur capacité d’élever leurs jeunes. L’objectif principal de cette étude était de déterminer, chez les eiders à duvet se reproduisant sur l’île Southampton (Nunavut), l’importance relative des réserves endogènes des femelles pour la formation des œufs, et vérifier si les stratégies adoptées quant à l’allocation des nutriments dans les œufs variaient selon la date de ponte et la taille de la couvée.

Dans un premier temps, nous avons déterminé l’importance des réserves endogènes pour la formation des œufs en 1) caractérisant la dynamique des réserves endogènes des femelles de la pré-ponte jusqu’au début de l’incubation et 2) en quantifiant, à l’aide d’isotopes stables, la contribution des nutriments endogènes et exogènes retrouvés dans les œufs des eiders. Les signatures isotopiques ($\delta^{13}C$ et $\delta^{15}N$) des composantes des œufs (albumens et jaunes), des réserves endogènes des femelles (muscles pectoraux et graisses abdominales) et des proies des eiders (mollusques et crustacés) ont été analysées. La dynamique des réserves endogènes (masse totale, graisses abdominales, muscles pectoraux et pattes) suggère une mobilisation importante des réserves de graisses au moment de la ponte, et une faible mobilisation des protéines endogènes. De façon similaire, les résultats d’isotopes stables indiquent que les nutriments dérivés des invertébrés marins ingérés au moment de la formation des œufs contribuent fortement (>50%) à la formation des tissus protéiques des oeufs, alors que la composante lipidique des œufs semble être formés majoritairement à partir des réserves des individus. De plus, les femelles qui nichent tardivement semblent allouer à chaque œuf une plus grande proportion de nutriments endogènes que celles qui nichent tôt. Les eiders, comme d’autres espèces migratrices se reproduisant en Arctique, ne sont donc pas des reproducteurs sur épargne stricts et forment leurs œufs en utilisant un mélange de nutriments endogènes et exogènes.

Dans un deuxième temps, nous avons testé les prédictions d’un modèle théorique de combinaisons optimales de taille et de date de ponte (Rowe *et al.*, 1994). Selon ce modèle, une femelle en meilleure condition durant la ponte devrait augmenter son aptitude phénotypique en pondant plus d’œufs plutôt qu’en conservant un surplus de réserves pour les étapes subséquentes de la reproduction. Globalement, le modèle présume que la condition des femelles après la ponte devrait être indépendante de leur taille de couvée et de leur date de ponte. Les coûts de l'incubation peuvent cependant varier selon le nombre d'œufs à incuber, et des interactions pourraient exister entre les ressources endogènes investies dans la formation des œufs et celles conservées pour les phases subséquentes. Nous avons vérifié si la condition corporelle post-ponte des femelles (masse totale, graisses abdominales, muscles pectoraux et pattes) était reliée à l'investissement effectué dans la couvée ainsi qu'à la date de ponte. Nos résultats ont démontré que les réserves des femelles à la fin de la ponte étaient indépendantes ou négativement reliées à la taille de la couvée. La masse des pattes était positivement reliée à la date de ponte pour les trois années d'étude, alors que l'effet de la date de ponte sur la masse des graisses abdominales a varié annuellement. Nos résultats supportent donc partiellement le modèle condition-dépendant de combinaisons optimales. Les variations inter-individuelles de réserves endogènes au début de l'incubation semblent en grande partie déterminées, chez l'eider à duvet nichant dans l'Arctique, par d'autres facteurs que la taille de couvée et la date de ponte. Nous suggérons que ces variations sont plutôt causées par les conditions environnementales rencontrées par les femelles au moment de la ponte.

Combinées, les méthodes d'analyses isotopiques et de dynamique des réserves endogènes ont permis de mieux comprendre le rôle des réserves endogènes dans la reproduction d'un reproducteur sur épargne, l'eider à duvet, de même que les différentes stratégies utilisées par les femelles selon la phénologie de leur reproduction. Nous suggérons que les contraintes associées au vol pourraient limiter l'accumulation de réserves endogènes chez les individus en pré-ponte et en ponte, et expliquer l'absence de reproduction sur épargne stricte chez les oiseaux qui volent.

# TABLE DES MATIÈRES

# INTRODUCTION GÉNÉRALE

## REPRODUCTION ET ACQUISITION DE NUTRIMENTS

Afin de produire le plus grand nombre de descendants et de maximiser leur valeur adaptative, les organismes vivants doivent balancer l'énergie qu'ils investissent dans les processus vitaux telles la survie, la croissance et la reproduction (Stearns, 1989; Kisdi *et al.*, 1998; Tatar and Yin, 2001; McCoy *et al.*, 2007). La proportion d'énergie investie dans l'un ou l'autre de ces processus dépend en partie de l'âge et de la durée de vie des organismes, de même que des conditions environnementales rencontrées au cours de l'année (Kisdi *et al.*, 1998; Neuhaus *et al.*, 2004). Un individu peut, par exemple, investir davantage dans sa reproduction une année donnée s'il estime que les conditions sont favorables à la production et à l'élevage des jeunes (King and Allaine, 2002; Broussard *et al.*, 2008), ou si ses chances de se reproduire à nouveau sont plus faibles (ex: individus plus âgés, voir Strickland *et al.*, 2008). Dans les milieux saisonniers, l'accès aux ressources peut cependant varier au cours de la période de reproduction, et le succès reproducteur des individus dépend alors en grande partie de la phénologie de leur reproduction (Rowe *et al.*, 1994; Einum and Fleming, 2000; Thomas *et al.*, 2001).

Chez les oiseaux, les femelles qui initient la ponte tôt en saison produisent généralement des couvées de plus grandes tailles et des oeufs de meilleure qualité (en termes de composition des œufs et survie des jeunes), atteignant ainsi un meilleur succès reproducteur que celles qui se reproduisent plus tard (Daan *et al.*, 1988; Perrins, 1996; Monaghan and Nager, 1997; Nager *et al.*, 2000). Par contre, les femelles qui sont en moins bonne condition corporelle en pré-ponte (i.e. peu de réserves endogènes) peuvent possiblement retarder la reproduction et profiter du délai pour améliorer leur condition physique et ainsi augmenter la taille potentielle de leur couvée (Rowe *et al.*, 1994; Bêty *et al.*, 2003). Retarder la reproduction entraînerait donc des coûts (diminution de la qualité des jeunes) et des bénéfices (augmentation des ressources disponibles pour la production de jeunes). Les combinaisons optimales de date de ponte et de taille de couvée qui maximisent la valeur sélective des femelles pourraient, en théorie, varier selon leur condition physique au début de la période de reproduction, leur date d'arrivée au site de reproduction et leur taux d'acquisition de nutriments (Rowe *et al.*, 1994).

Afin d'amasser les nutriments nécessaires à la formation et à l'incubation des oeufs, différentes stratégies d'acquisition et d'allocation de l'énergie ont, en théorie, été sélectionnées chez différentes espèces au cours de l'évolution (Stearns, 2000). Ces stratégies peuvent être réparties le long d'un continuum allant des espèces se reproduisant « sur épargne » (*capital breeders*) à celles se reproduisant « sur revenu » (*income breeders;* (Jönsson, 1997; Meijer and Drent, 1999; Hobson, 2006; Houston *et al.*, 2006; Klaassen *et al.*, 2006). Les reproducteurs sur épargne extrêmes acquièrent de grandes quantités de réserves endogènes avant le début de la reproduction et puisent essentiellement dans celles-ci afin de combler l'ensemble des besoins énergétiques de la reproduction (voir Parker and Holm, 1990; Ankney *et al.*, 1991; Bonnet *et al.*, 1998). À l'opposé, les reproducteurs sur ressources exogènes se servent uniquement des nutriments acquis durant la période de reproduction pour satisfaire les dépenses énergétiques associées à la production des jeunes (ex: Morrison and Hobson, 2004; Langin *et al.*, 2006). Alors que les reproducteurs sur épargne peuvent possiblement transporter avec eux des nutriments nécessaires à la reproduction, le succès des reproducteurs sur revenu dépend principalement des ressources qu'ils trouveront au site de reproduction (Drent *et al.*, 2006).

La détermination des contributions relatives des ressources exogènes et endogènes utilisées dans la reproduction des organismes constitue un élément supplémentaire et crucial à la compréhension de l'effort et de la phénologie de la reproduction, et permet de mieux identifier les coûts et les bénéfices d'un délai de l'initiation de la ponte (ex: Varpe *et al.*, 2009).

## ALLOCATION DES NUTRIMENTS DANS LES ŒUFS : UTILISATION DES ISOTOPES STABLES

Des signatures d'isotopes stables (ex : $\delta^{13}C$, calculée à partir de : $^{13}C$ / $^{12}C$ et $\delta^{15}N$, calculée à partir de $^{14}N$ / $^{15}N$) peuvent être mesurées dans les tissus d'organismes vivants. Les conditions physico-chimiques de l'environnement d'un organisme sont responsables en grande partie des variations relatives des isotopes de carbone ($^{13}C$ / $^{12}C$) retrouvés dans ses tissus; alors que les différences dans les proportions d'isotopes d'azote ($^{14}N$ / $^{15}N$) sont principalement dues au régime alimentaire et au niveau trophique de l'organisme (Gannes *et al.*, 1998; Kelly, 2000). Les ratios d'isotopes présents dans les tissus d'un consommateur reflètent ceux de ses proies, auxquels un facteur de fractionnement est ajouté. Ce dernier tient compte de la perte de certains isotopes durant les processus métaboliques de l'ingestion et de l'assimilation des nutriments dans les tissus (Hobson and Clark, 1992; Pinnegar and Polunin, 1999; Ogden *et al.*, 2004; Becker *et al.*, 2007).

Les isotopes stables sont couramment utilisés pour caractériser le régime alimentaire d'une espèce, pour identifier un niveau trophique ou encore pour quantifier l'importance relative de différentes sources de nutriments utilisées par des individus (voir: Gannes *et al.*, 1998; voir: Kelly, 2000; Cherel *et al.*, 2005; Inger and Bearhop, 2008). Dans le cadre de cette étude, ces analyses seront employées afin de vérifier la contribution relative des réserves endogènes et des ressources exogènes dans la formation des œufs, tel qu'effectué chez d'autres espèces par Gauthier *et al.* (2003) et Bond *et al.* (2007).

Les oiseaux migrateurs peuvent fréquenter différents types d'habitats au cours de leur migration et s'alimenter dans des milieux caractérisés par des signatures isotopiques distinctes pour plusieurs éléments. Les réserves endogènes peuvent donc refléter des signatures isotopiques différentes de la nourriture ingérée au site de reproduction. Les nutriments acquis en pré-ponte sur le site de reproduction peuvent aussi être emmagasinés dans les réserves endogènes et utilisés ultérieurement, ou encore être utilisés par les femelles pour des besoins énergétiques immédiats (dont la formation des œufs). Chez les oiseaux, le foie, en plus de constituer le centre du métabolisme des nutriments, produit les précurseurs du vitellus (vitellogénine et lipoprotéines de très basse densité; Walzem *et al.*, 1999; Stevens, 2000). Ces derniers peuvent donc être synthétisés à partir de nutriments provenant de l'alimentation (ressources exogènes) ou du catabolisme des réserves endogènes. Finalement, l'allocation des nutriments exogènes dans les œufs chez un reproducteur sur épargne peut varier suivant les compromis de date de ponte et de taille de couvée effectués par les femelles, de façon à maximiser le succès reproducteur des individus (e.g.:Gauthier *et al.*, 2003).

## DYNAMIQUE DES RÉSERVES ENDOGÈNES AU COURS DE LA REPRODUCTION

Dépendamment du niveau de précocité des jeunes, les femelles doivent investir leur énergie de façon optimale entre la formation des œufs, la période d'incubation et l'élevage des jeunes (Nager, 2006). Certains tissus sont typiquement associés à l'accumulation de protéines ou de lipides. Par exemple, la masse des muscles pectoraux peut représenter un bon indicateur de la quantité endogène de protéines chez plusieurs espèces d'oiseaux (Jamieson *et al.*, 2006), et les muscles des pattes des canards plongeurs se propulsant grâce à leurs membres inférieurs sont particulièrement bien développés (Richman and Lovvorn, 2008) et peuvent aussi constituer une réserve de protéines. D'autres part, le contenu lipidique des réserves endogènes peut être estimé à partir de la masse des graisses abdominales (Jamieson *et al.*, 2006).

Contrairement au glycogène et aux protéines, l'accumulation de lipides dans les tissus nécessite un minimum d'eau, et la maintenance des tissus adipeux consomme très peu d’énergie (Jenni and Jenni-Eiermann, 1998). Les lipides constituent donc la source d’énergie optimale pour les oiseaux qui migrent sur de longues distances (Jenni and Jenni-Eiermann, 1998) et qui incubent de longues périodes (Klaassen, 2003). Or, les œufs sont principalement formés de lipides, de protéines et de minéraux (Williams, 1999). Les réserves des oiseaux migrateurs ne sont donc habituellement pas complètement adéquates à la formation des œufs, puisqu’elles sont typiquement déficientes en protéines (Klaassen, 2003) et en calcium (Drent, 2006). Les protéines et les minéraux constituent donc, chez les espèces migratrices, des nutriments présents en quantités limitées dans les tissus des femelles en pré-ponte, ce qui peut expliquer que ces dernières aient parfois besoin de se nourrir d’items riches de ces nutriments durant la formation des œufs.

En effectuant un suivi de la dynamique des réserves endogènes des femelles au cours de chacune des phases de la reproduction (ex : pré-ponte, ponte, incubation et élevage des jeunes), il est possible de vérifier la quantité relative de lipides et de protéines endogènes investie dans la reproduction et à quel moment l’investissement endogène est le plus important. Il est également possible de déterminer si l’investissement endogène varie selon la date et la taille de ponte d’une femelle.

Le suivi de la dynamique des réserves endogènes permet de quantifier l’utilisation des réserves pour chacune des phases de la reproduction, sans toutefois déterminer leur rôle dans l’une ou l’autre des activités métaboliques. À l’opposé, les analyses isotopiques permettent d’établir dans quelles proportions les nutriments endogènes et exogènes sont utilisés pour la formation des œufs. Ces analyses sont toutefois associées à plusieurs incertitudes, tel que les estimés des facteur de fractionnement et l'identification des sources de nutriments utilisées par les individus (Phillips and Gregg, 2003; Moore and Semmens, 2008). Combinées, ces deux méthodes permettent de tirer des conclusions plus fiables sur la contribution des réserves endogènes des femelles à la formation des œufs.

## IMPORTANCES DES RÉSERVES ENDOGÈNES POUR LA REPRODUCTION DE L'EIDER À DUVET

Les eiders à duvet se reproduisant en Arctique sont typiquement considérés comme étant des reproducteurs sur épargne stricts, donc qui dépendent essentiellement de leurs réserves corporelles pour combler les besoins énergétiques de la reproduction (Parker and Holm, 1990; Meijer and Drent, 1999). Les femelles pondent en moyenne de trois à cinq œufs (Goudie *et al.*, 2000) et ne se nourrissent pas lors de l'incubation (Criscuolo *et al.*, 2002; Bolduc and Guillemette, 2003). L'éclosion se produit de façon synchrone, et les femelles amènent les jeunes à la mer peu de temps après l'éclosion. Elles se réunissent en crèches ou non, dépendamment entre autre de leur condition physique à l'éclosion (Ost *et al.*, 2003). Certaines femelles en mauvaise condition physique peuvent même abandonner leurs jeunes à d'autres femelles afin de se nourrir de façon intensive (Kilpi *et al.*, 2001). Les réserves endogènes jouent donc un rôle crucial pour la reproduction des eiders à duvet, et ils représentent conséquemment un bon modèle pour étudier les différentes stratégies d'allocation des nutriments endogènes adoptées par des femelles 1) hâtives et tardives, et 2) produisant de grandes et de petites couvées.

La majorité des individus qui composent la population étudiée dans le cadre de ce projet (essentiellement sous-espèce *S. m. borealis*) se reproduisent dans l'Est de l'Arctique canadien (île Southampton) et passent l'hiver au Sud-Ouest du Groenland (Merkel *et al.*, 2006). Ils arrivent au site de reproduction peu avant la ponte et des femelles ont été observées s'alimentant de façon intensive en pré-ponte et en ponte près du site de reproduction, révélant une contribution possible des ressources exogènes dans la reproduction des eiders à duvet.

## OBJECTIFS ET HYPOTHÈSES DE TRAVAIL

L'objectif principal de notre étude était de déterminer, chez les eiders à duvet, l'importance des réserves endogènes pour la formation des œufs, et vérifier si les stratégies adoptées quant à l'allocation des nutriments variaient selon la date de ponte et la taille de couvée. Dans un premier temps, nous avons effectué un suivi de la dynamique des réserves endogènes des femelles au cours de la période de reproduction. Nous avons également quantifié, avec des isotopes stables, la contribution relative de différentes sources de nutriments (endogènes et exogènes) potentiellement utilisés pour la formation des œufs. Combinées, ces deux méthodes nous ont permis i) d'identifier à quel moment les réserves endogènes sont mobilisées chez les eiders à duvet et ii) de déterminer la contribution relative des réserves endogènes dans les œufs.

Dans un deuxième temps, nous avons vérifié si les stratégies de gestion des réserves endogènes destinées à satisfaire les besoins énergétiques des femelles après la ponte différaient selon la date et la taille de ponte. Deux hypothèses alternatives ont été testées, soit : 1) la condition corporelle des femelles immédiatement après la ponte est similaire pour toutes les femelles (non corrélée à la date ou à la taille de ponte) et est équivalente à un seuil minimum nécessaire à l'incubation des œufs; et 2) la condition physique des femelles immédiatement après la ponte est positivement corrélée à la taille de la couvée.

Les permis suivants ont été obtenus pour effectuer l'échantillonnage des femelles eider à duvet et invertébrés dans le cadre de cette étude: Nunavut Research Permit WL 000159 en 2002, WL 000198 en 2003, WL 000523 en 2004, WL 000833 en 2007 et WL2008 1028 en 2008; Animal Care Permit 2002PNR008, 2003PNR008 et 2004PNR008.

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# CHAPITRE 1

# CAN FLYING BIRDS BE PURELY CAPITAL LAYERS? EVIDENCE OF EXOGENOUS CONTRIBUTION TO ARCTIC-NESTING COMMON EIDER EGGS

Manuscrit en préparation pour une publication

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# E. SÉNÉCHAL, J, BÊTY, G. GILCHRIST, K. A. HOBSON, AND S. E. JAMIESON. Can flying birds be purely capital layers? Evidence of exogenous contribution to arctic-nesting Common Eider eggs

**Abstract.** The strategy of relying extensively on stored resources for reproduction has been termed capital breeding and this tactic is in contrast to income breeding, where needs of reproduction are satisfied by exogenous resources. Most species likely fall somewhere between these two extremes and the position of an organism along this gradient can influence several key life history traits. Common Eiders (*Somateria mollissima*) are the only flying birds that are still typically considered pure capital breeders, suggesting that they depend exclusively on endogenous reserves to form their eggs and incubate. We investigated the annual and seasonal variation in contributions of endogenous and exogenous resources to egg formation in eider nesting in the Canadian Arctic. We collected females at different breeding stages, as well as their eggs and prey items and used two complementary approaches (body reserves dynamics and stable isotope [$\delta^{13}C$, $\delta^{15}N$] mixing models) to quantify resources mobilization and trace specific macronutrients invested in eggs. An index of protein stores remained stable from pre-laying to post-laying stages, while lipid reserves declined significantly during laying. Similarly, stable isotope analyses indicated that 1) exogenous nutrients derived from marine invertebrate strongly contributed to the formation of lipid-free egg constituents and 2) yolk lipids were constituted mostly from endogenous lipids. We also found evidence for a seasonal variation in the use of body stores, with early breeders using proportionally more exogenous proteins to form each egg

than late breeders. Although a strict capital breeding strategy could strongly reduce egg predation risk in eiders, take-off capabilities of pre-laying and laying individuals may limit their dependence on stored capital. This could explain the absence of known pure capital breeding flying birds.

**E. SÉNÉCHAL, J, BÊTY, G. GILCHRIST, K. A. HOBSON, AND S. E. JAMIESON. Can flying birds be purely capital layers? Evidence of exogenous contribution to arctic-nesting Common Eider eggs**

**Résumé.** Les organismes qui dépendent fortement de leurs réserves corporelles pour se reproduire sont considérés des reproducteurs sur épargne, alors que les reproducteurs sur revenu dépendent essentiellement des ressources exogènes pour combler les besoins énergétiques de la reproduction. La plupart des espèces adoptent une stratégie de reproduction intermédiaire, et la position d'une espèce le long de ce gradient peut influencer certains traits d'histoire de vie. Parmi les oiseaux qui volent, les eiders à duvet (*Somateria mollissima*) sont les seuls qui persistent à être considérés reproducteurs sur épargne stricts, donc qui dépendraient exclusivement de leurs réserves pour former et incuber leurs œufs. Nous avons examiné les variations annuelles et saisonnières de la contribution des ressources endogènes et exogènes dans la formation des œufs chez l'eider à duvet nichant dans l'Arctique canadien. Nous avons récolté des femelles à différents stades de reproduction, de même que leurs œufs et leurs proies; et nous avons utilisé deux méthodes complémentaires (suivi de la dynamique des réserves endogènes et modèles mixtes d'isotopes stables) afin de quantifier la mobilisation des réserves et de déterminer la source des nutriments investis dans les œufs. Nos résultats indiquent que les masses des réserves endogènes associées aux protéines demeurent stables de la période de pré-ponte à la période post-ponte, alors que les réserves de lipides diminuent significativement durant la ponte. De façon similaire, les modèles isotopiques ont démontré que 1) les nutriments

dérivés des invertébrés marins contribuent fortement à la formation des tissus protéiques des œufs, et que 2) les tissus lipidiques sont formés majoritairement des réserves de graisses des femelles. Nos résultats démontrent également une variation saisonnière dans l'utilisation des ressources; les femelles hâtives utilisant une plus grande proportion de protéines exogènes que les femelles tardives pour former chaque œuf. Nous concluons que les eiders utilisent une stratégie de reproduction mixte (épargne et revenu) et nous suggérons que les contraintes associées au vol pourraient limiter l'accumulation de réserves endogènes chez les femelles en pré-ponte et en ponte. Ceci pourrait expliquer l'absence de reproduction sur épargne stricte chez les oiseaux qui volent.

## INTRODUCTION

The availability of endogenous and exogenous resources to breeding organisms can influence several key life history traits such as timing of breeding (Rowe *et al.*, 1994; Perrins, 1996; Bêty *et al.*, 2003), number and quality of offspring (Brown and Shine, 2002; Sakai and Harada, 2005; Jardine *et al.*, 2008), degree of parental care (Lewis and Kappeler, 2005), as well as reproductive investment and lifespan (Festa-Bianchet *et al.*, 1998; Broussard *et al.*, 2005). Individuals should allocate available resources in order to maximise their fitness (Stearns 1992), and determining how and when organisms acquire resources needed for reproduction is crucial to understand their life-history strategies.

Animals breeding in environments where food is seasonally limited could increase their fitness by relying on stored resources acquired prior to breeding. Alternatively, organisms living in environments with reliable food resources could increase their reproductive success by rapidly responding to increases in local food supply (Drent and Daan, 1980; Jönsson, 1997; Houston *et al.*, 2006). These two strategies are respectively called "capital" (i.e., financed by stored capital) and "income" (i.e., based on concurrent food intake) breeding, and can be considered opposite ends of a continuum (Klaassen *et al.*, 2006).

Capital breeding has several potential energetic and survival costs, which can be counterbalanced by various benefits, such as breeding when the value of offspring peak and increasing the offspring production rate (Varpe *et al.*, 2009). Migratory birds that nest in

Polar Regions were first thought to rely extensively on endogenous reserves to breed successfully, given the unpredictability of nutrient abundance at breeding site and the short breeding period. However, recent studies have shown that many northern birds rely considerably on exogenous resources during egg formation (e.g.: Hobson *et al.*, 2004; Bond *et al.*, 2007; Gorman *et al.*, 2008), and incubation (e.g.: Klaassen *et al.*, 2001; Morrison and Hobson, 2004).

The Common Eider (*Somateria mollissima*, hereafter eider) is the only flying bird species that is still typically considered a pure capital breeder. Indeed, resources required for both producing and incubating clutches are generally assumed to be drawn entirely from endogenous reserves (Parker and Holm, 1990; Meijer and Drent, 1999; Stephens *et al.* 2009). However, females have been observed feeding intensively during the pre-laying and laying periods (Christensen, 2000; Guillemette, 2001; Mosbech *et al.*, 2006), making it unclear whether females allocate exogenous nutrients to egg production or if they store them for later use during incubation and chick rearing periods.

Using two complementary approaches, we investigated the annual and seasonal variation in contributions of endogenous and exogenous resources to egg formation in eider nesting in the Canadian Arctic. We first described the dynamics of body reserves from pre-breeding to post-laying reproductive stages. We then used stable isotope analyses to quantify the relative contribution of body stores and prey species to egg formation. Combining these methods provides a better assessment of the energetic reproductive strategy of individuals. Body stores dynamics provides information on resources mobilization, and stable isotopes help to trace sources of specific macronutrients invested in different egg components. We provide evidence that female eiders are strongly dependent on exogenous resources to produce the lipid-free egg constituents and suggest that take-off capabilities may prevent these flying birds from being exclusive capital layers.

## MATERIAL AND METHODS

### *Study site*

Our study was conducted on Mitivik Island (0.24 $km^2$) in the East Bay Migratory Bird Sanctuary, Southampton Island, Nunavut, Canada (64°02’N, 81°47’W), which is the largest known eider breeding colony in the Canadian Arctic (up to 8000 pairs annually). Female eiders arrive in the vicinity of the nesting island up to 3 weeks before laying (Mosbech *et al.*, 2006), and forage in river mouths and ice leads before laying (Abraham and Ankney, 1986).

### *Females and eggs collection*

Pre-breeding, pre-laying, and laying adult eider females (see below for definitions) were shot at foraging and resting sites located within 5 km from the nesting colony (from June 11 to July 11; Total N = 15 in 2002, 15 in 2003, and 14 in 2004). Post-laying females (i.e., sitting on a full clutch for 24 to 48h) and a few (≤2 per year) laying females were captured on their nest using nest traps (from June 18 to July 22; Total N = 15 in 2002, 17 in 2003, and 19 in 2004). Females were euthanized using halothane and their eggs were collected. and the. Birds were immediately dissected in the field and endogenous reserves were estimated by weighing wet breast muscle (pectoralis and supra-coracoid from the left side), abdominal fat, total leg mass (left side only, including all muscles that originate or insert in the femur or tibiotarsus bones) and body mass (following Jamieson *et al.*, 2006). Breeding stages of females were confirmed by inspecting follicles: females without developing or post-ovulatory follicles were considered in the pre-breeding stage (which could also include non-breeding birds); the presence of only developing follicles was associated with the pre-laying stage; females with both developing and post-ovulatory follicles were considered laying; while post-laying females had post-ovulatory follicles only. Prior to nest-trapping, we visited the nest every one or two days during laying to mark the eggs and determine the laying sequence. First and last laid eggs were collected at the same time as the female (only the first egg was collected for laying females). Frequently, the number of post-ovulatory follicles was higher than the number of eggs found in nests (33 cases out of 52). In those cases, we assumed that missing eggs were the first ones, given the low nest attendance of females at the beginning of laying and the high predation rate of first eggs (Andersson and Waldeck, 2006). In only two cases, the number of eggs found in nest was higher than the number of post-ovulatory follicles, which indicated nest parasitism. Eggs (boiled), breast muscle, abdominal fat and liver samples were kept frozen at -20$^{o}$C for subsequent laboratory analyses.

### *Prey collection*

Prey species consumed by pre-laying and laying eiders were identified by examination of feces and gizzards, as well as behavioral observations (see also Abraham and Ankney, 1986). These included the bivalves *Hiatella arctica, Serripes* spp., *Acmea testudinalis*, and amphipods (*Gammarus* spp.). We collected prey items by scuba-diving at 56 locations within East Bay (1-30m deep) in mid July 2007 (0 to 20 km from the nesting colony). Diving sites were associated with heavily used eider feeding areas identified by previous telemetry surveys (Authors, unpublished data). As prey species and female eiders were not collected the same year, and prey were not collected during the eider pre-laying period, we investigated potential annual and seasonal variations in prey isotopic ratios by collecting amphipods throughout 2003, 2007 and 2008 breeding seasons. We found no evidence of such variation and are thus confident that our sampling design did not generate bias in our analyses (see Appendix 1). All prey samples were kept frozen at -20$^{o}$C except for few small organisms that were preserved in 70% ethanol before laboratory analyses.

### *Laboratory analyses*

Breast muscle and liver samples, as well as egg components (albumen and yolk) and prey species (without exoskeleton for bivalves) were oven dried (60oC for 48 hours) and ground to powder. Abdominal fat samples were soaked in 2:1 chloroform:methanol for 24 hours and dissolved lipids were collected. Since endogenous and exogenous lipids and proteins can be allocated differently to egg formation, we separated our samples into lipid and lipid-free components. Lipids were extracted from prey samples, yolk, liver and breast muscles samples with successive rinses of the 2:1chloroform:methanol. Lipid extracts were conserved for every tissue except for breast muscle. Solvent was evaporated completely using a fume hood and the remaining lipid residue stored frozen.. Carbonates were also extracted from lipid-free marine organism samples by treating them with drops of 0.1N HCL without rinsing (Carabel et al., 2006). Those samples were then oven dried (60oC for 24 hours) and powdered with a mortar and pestle.

We loaded 1 ± 0.01 mg of each sample in a tin cup and combusted them in a Robo-Prep elemental analyzer (Europa Scientific, Crewe, UK). Resultant gases were delivered, using continuous-flow isotope ratio mass spectrometry (CFIRMS), to a Europa 20:20 mass spectrometer (Europa Scientific, Crewe, UK) for stable-carbon and nitrogen isotope ratio determination. Stable isotope ratios are expressed in delta (δ) notation relative to the Pee Dee Belemnite or AIR standards for carbon and nitrogen, respectively (see Hobson, 1995). Based on replicate within-run analyses of a keratin (BWB II) and egg albumen lab standards, Aanalytical error was estimated to be ±0.3‰ for δ15N and 0.1‰ for δ13C.

### *Isotope mixing model calculations*

We calculated relative endogenous and exogenous protein contributions to egg components using the Bayesian-based MixSIR model (version 1.0.4; Moore and Semmens, 2008; and Semmens et al., 2009) based upon δ13C and δ15N values of prey items, egg components and eider tissues. Six protein sources were included in these models: breast muscles (endogenous source) and five prey types (exogenous sources), all lipid-free. Protein models were generated for both lipid-free yolk and albumen samples.

The relative contribution of endogenous and exogenous lipids to yolk-lipid was calculated only from δ13C measurements, given the low nitrogen levels in adipose tissues. However, as endogenous lipid δ13C values overlapped those of prey items, we could not adequately quantify the specific contribution of all potential sources to yolk-lipid. We therefore included only two sources in lipid models (abdominal fat and liver lipids) to estimate the relative contributions of endogenous and exogenous lipids, respectively, and we used IsoError linear mixing model (Phillips, 2001). Carbon isotope values of liver lipids can be used as an integrative indicator of exogenous lipid ratios, as they provide short-term dietary information (Hobson and Clark, 1992). However, liver is also an organ where lipid catabolism occurs and where yolk precursors are synthesized. Yolk lipids and abdominal fat δ13C values were expected to differ if exogenous resources contribute to egg lipids (assuming no fractionation between abdominal fat and yolk lipids; see Gauthier et al., 2003). In such case, the greater the difference between δ13C values in fat reserves and those in yolk lipids would indicate a stronger contribution of prey items consumed during egg formation (see also Discussion section).

Through the process of isotopic discrimination, stable isotope values in egg components are expected to differ from those in contributing (endogenous or exogenous) nutrient pools. Discrimination factors between food and egg components have been determined in few bird species (Hobson, 1995; Ogden et al., 2004) . Like Gauthier et al (2003), we used a carnivore model of Hobson (1995) to estimate discrimination between endogenous reserves and egg components. This approach was necessary since isotopic discrimination factors between endogenous reserves and egg components have not been determined experimentally (Gauthier et al. (2003). We consequently assumed that lipid-free sources discriminate 1) from lipid-free yolk by +3.5 ± 0.35 ‰ for δ15N and 0 ± 0.5 ‰ for δ13C, and 2) from albumen by +3.1 ± 0.35 ‰ for δ15N and +0.9 ± 0.5 ‰ for δ13C. Given that yolk lipids are likely to be derived without discrimination either from the diet or from lipid stores (Hobson, 1995), and that lipids from every source have to pass through the liver before their transport to yolk precursors (Stevens, 2000), we assumed no δ13C isotopic discrimination between lipids of sources and the yolk.

A number of Bayesian-based isotope models are now available to calculate relative contributions of n+1 sources when measuring n isotopes. We thus compared our results obtained with the Bayesian MixSIR model to the outcomes generated by the non-Bayesian IsoSource (Phillips and Gregg, 2003) and the Bayesian SIAR model (Jackson et al., 2009; see Appendix 3).

## ***Statistical analyses***

### *Endogenous reserves dynamics*

We adjusted, when required, endogenous reserve estimates to body size using principal component analysis (Sedinger *et al.*, 1997). We used measurements (±0.01 mm) of the right wing chord length, right tarsus length, and total head length to establish the first principal component, which explained 47% of the variation observed in the original data. All eigenvectors ranged from 0.18 to 0.83 and were positive, suggesting that each measure increased with body size. PC1 scores were thus an appropriate index of structural size. Body and leg masses were significantly related with PC1 scores (general linear regressions: $P = 0.007$ and $P = 0.004$, respectively), so we used the residuals from these models in subsequent analyses. Body and leg masses are hereafter presented on their size-corrected form.

Variation in endogenous reserves between breeding stages and years were analysed with general linear models and Tukey-Kramer multiple comparisons tests. The interaction terms between year and breeding stage were non-significant and thus removed from the models (all $P > 0.05$). Within a given stage, we performed Pearson correlation tests to examine the relationships between body stores and number of follicles. We did not detect strong violations of assumptions of residual normality (Shapiro-Wilk test, all $P > 0.05$) and variance homogeneity (Levene's test, all $P > 0.05$ except for abdominal fat with $P = 0.005$).

In that case, non-parametric tests (Kruskal-Wallis one-way ANOVA) provided similar results.

### *Stable isotopes*

Inter-annual variation in δ13C and δ15N values of endogenous reserves and eggs were analyzed with one-way ANOVAs. We did not detect strong violations of the assumptions required for these analyses (Levene's test for homogeneity of variances, all P > 0.05 except for albumen δ13C of first eggs with P = 0.02; Shapiro-Wilk test of normality, all P > 0.05 excepts for yolk δ13C of first and last eggs with P = 0.002 and 0.03 respectively). In all cases, non-parametric tests (Kruskal-Wallis one-way ANOVA) provided similar results. Tukey-Kramer multiple comparisons tests were performed when inter-annual variations were significant.

We performed a MANOVA on the δ13C and δ15N values of potential egg protein sources, which were grouped in six categories: Serripes spp., Hiatella sp., Acmea testudinalis, amphipods collected at river mouths, amphipods collected offshore, and breast muscles. They all showed significantly different values (Wilks λ = 0.08, F10,184 = 47.17, P < 0.001) and we thus used them as independent sources in isotopic models. Likewise, a one-way ANOVA on δ13C of lipid sources (liver lipid and abdominal fat) showed that they were statistically different (F1, 101 = 15.2, P < 0.001).

To detect inter-annual variation in protein allocation to eggs, we ran MixSIR models for each of the three years separately. Similarly, to determine if there was a seasonal variation in protein allocation to eggs, we grouped females according to their relative lay date: early (≤ 5 days before the yearly median; N = 14), mid (yearly median ± 4 days; N = 23), and late breeders (≥ 5 days after yearly median; N = 15), and ran separate models. Lay dates of females were back-calculated according to the number of post-ovulatory follicles (assuming a 28-hour laying interval, see Watson et al., 1993). In order to avoid pseudo-replication, we included only one collected egg per clutch (the earliest in the laying sequence) in the models.

Finally, to determine if the source of nutrients changed within the laying sequence, we calculated the difference in δ13C and δ15N values between the last and the first egg collected in each clutch. The average position in the laying sequence of the first egg collected was 1.8, and 4 for last eggs (hereafter called first and last eggs). Using general linear models, we determined, for every isotope ratio, if the intra-clutch difference varied with the relative lay date. All statistical analyses were performed using SAS V 9.1 (SAS Institute 2002-2003) with a critical level of significance of 0.05.

# RESULTS

## *Endogenous reserve dynamics*

Endogenous reserve estimates varied significantly between reproductive stages and years (all $P \leq 0.02$). After controlling for reproductive stages, we found that females were on average heavier and had higher lipid stores in 2003, while the lowest protein stores were observed in 2002. Body stores were generally higher for females who had started follicle development (pre-laying) than for pre-breeding ones (which were in similar condition than post-laying females; Figure 1). From pre-laying to post-laying, significant differences were detected in total body weight and abdominal fat only, indicating an important mobilisation of fat reserves during the laying period (average loss of 16% in body mass and 53% in fat reserves). Conversely, index of protein stores (breast muscles and leg) did not vary significantly from the start of egg formation to the onset of incubation (Figure 1). This indicates that endogenous protein mobilization during egg formation was absent or weak (the observed non-statistically significant decrease in breast muscle mass was 5% on average). Within-stage correlation between endogenous reserve estimates and number of follicles (developing or post-ovulatory) were not significant ($P > 0.05$), except for leg mass of laying females ($r = 0.59$, $P = 0.03$), and total body mass ($r = -0.38$, $P = 0.005$) and breast muscle mass ($r = -0.30$, $P = 0.03$) of post-laying females.

### *Isotopic composition of eider somatic tissues and eggs*

Stable carbon and nitrogen isotope ratios of eider somatic tissues were similar between years ($\delta^{15}$N: breast muscles, $F_{2,49} = 0.66$, and liver lipid-free, $F_{2,46} = 1.82$; $\delta^{13}$C: breast muscles, $F_{2,49} = 2.39$, liver lipid-free, $F_{2,46} = 0.26$, liver lipids, $F_{2,48} = 1.72$ and abdominal fat, $F_{2,33} = 0.97$; all $p > 0.1$).

Stable carbon isotope ratios of lipid-free yolk differed between years (F2,47 = 5.15, P = 0.01 and F2,44 = 4.45, P = 0.02 for first and last eggs respectively), being both significantly more enriched in 2003 (Table 1). However, δ13C of albumen and yolk-lipid did not significantly vary between years (all $P \geq 0.35$). Stable nitrogen isotope ratios varied annually only for lipid-free yolk of the first egg, with the highest δ15N values observed in 2003, and the lowest in 2004 (F2,47 = 3.66, P = 0.03; $P > 0.18$ in other cases; Table 1).

### *Relative contribution of endogenous and exogenous sources to egg formation*

Based on isotopic models, protein allocation to eggs was derived mainly from local exogenous resources. Indeed, endogenous contributions to yolk and albumen proteins did not exceed 16% and 11% respectively, except for yolk proteins in 2003 (Table 2). Interestingly, the main exogenous protein source appeared to vary annually for the yolk but not for the albumen (always primarily derived from the clam *Hiatella arctica*: Table 2 and Figure 2). *Hiatella arctica* contributed the most to yolk proteins in 2002 and 2004 but very little in 2003, when *Gammarus sp.* were the main exogenous source.

On the other hand, stored lipids apparently contributed largely to egg lipids, reaching 74% (±0.4) in 2003 and 67% (±0.5) in 2004. The model was unable to generate estimates for 2002, given that the δ13C of yolk lipids was higher than both abdominal fat and liver-lipid δ13C values (Figure 3; see Discussion). Results from paired t-tests also suggested a strong contribution of endogenous lipids. In all years, yolk lipids and abdominal fat δ13C values were not significantly different for a given female (mean absolute differences observed in 2002: 0.85‰, df = 13, t = 1.63, P = 0.13; in 2003: 0.39‰, df = 9, t = -0.57, P = 0.58; in 2004: 0.72‰, df = 10, t = -1.76, P = 0.11; all years combined: 0.04‰, df = 34, t = 0.25, P = 0.80). Conversely, δ13C of yolk lipids and liver lipids of a given female were significantly different in 2003 and 2004, but similar in 2002 (mean absolute differences observed in 2002: 0.57‰, df = 13, t = 0.03, P = 0.97; in 2003: 1.83‰, df = 15, t = -3.34, P = 0.005; in 2004: 0.76‰, df = 18, t = -2.88, P = 0.01; all years combined: -0.39‰, df = 48, t = -3.34, P < 0.001).

### *Seasonal variations of source contributions*

Distributions of possible endogenous protein contributions to the first egg of early and mid breeders were similar and very low (the most likely endogenous contribution in lipid-free yolk and albumen ranged from 0.9% to 4.3%; Figure 4). However, late breeders apparently mobilized a higher proportion of endogenous proteins to form each egg (most likely contribution of 23.3% and 9.6% for lipid-free yolk and albumen respectively; Figure 4).

Given that δ13C values of abdominal fat overlapped those of exogenous resources (see Figure 3), it was not possible to detect seasonal differences in endogenous lipid investment between early, mid and late breeders. Nevertheless, the difference between abdominal fat and yolk lipid δ13C for a given female did not vary with relative lay date (after controlling for year: F1,31 = 0.82, P = 0.37), suggesting that endogenous lipid investment in eggs was similar among early and late nesters.

The difference between albumen δ13C and δ15N values of first- and last-laid eggs collected within a clutch did not vary with timing of breeding ($P \geq 0.66$). However, within a clutch, δ15N values tended to be systematically slightly higher in albumen of last-laid eggs compared to first-laid eggs (average of 0.58; P = 0.08), which may suggest a higher contribution of endogenous reserves at the end of the laying sequence (i.e., last egg closer to breast muscle δ15N values: Figure 2). On the other hand, we found evidence for a seasonal variation in the differences of lipid-free yolk isotope values between last and first eggs (Figure 5; δ13C: F1,45 = 3.12, P = 0.08; δ15N: F1,45 = 8.16, P = 0.007). This likely reflects seasonal changes in the accessibility of prey in the vicinity of the eider colony and suggests that early and late nesters feed on different prey items and partly change their diet during clutch formation (see Discussion).

## DISCUSSION

Our results derived from both body reserves dynamics and stable isotope analyses indicated that arctic-nesting Common Eiders produce their eggs mostly from stored lipids but exogenous proteins. Like other well studied waterfowl species (e.g.: Gauthier *et al.*, 2003; Hobson *et al.*, 2004; Hobson *et al.*, 2005; Bond *et al.*, 2007; Gorman *et al.*, 2008), eiders thus use a mixed capital-income strategy during egg formation.

Determining to what extent endogenous stores are used for reproduction involves the placement of a species along the capital-income continuum (Stephens et al. 2009). Given that mixed strategies are difficult to quantify, it is especially challenging to compare species studied using different methods. The approach we used (complementary methodological techniques and investigation of intra-population variations) greatly assist with this endeavour. Based on detailed stable isotope studies, Greater Snow Geese (Chen caerulescens atlantica; Gauthier et al., 2003) and Barrow's Goldeneyes (Bucephala islandica; Hobson et al., 2005) are the species closest to the capital end of the capital-income continuum, while Redhead (Aythya americana) and Harlequin Ducks (Histrionicus

histrionicus) were defined as being mostly income layers (respectively Hobson et al., 2004 and Bond et al., 2007). By combining egg formation and incubation strategies of Common Eiders (which fast during the entire incubation; Bottitta et al., 2003), we conclude that they remained the most extreme known capital breeders among flying birds. Nevertheless, they cannot be considered as pure capital breeders because the contribution of exogenous macronutrients in egg formation is unequivocal and is even higher than in some other species for the lipid-free components (see Gauthier et al., 2003).

### *Stable isotope models and uncertainty issues*

We recognize that our stable isotope approach involves uncertainty. For instance, discrimination factors (Wolf et al., 2009), proper representation of sources included in models (Phillips and Gregg, 2003), pretreatment of samples in laboratories (Soreide et al., 2006), and inherent variability between samples (Barnes et al., 2008) all represent sources of uncertainty which could be unintentionally included in models and affect conclusions. To strengthen our conclusions, we used Bayesian mixing models, which include a certain degree of uncertainty (i.e., incorporate standard deviations of source isotope ratios and discrimination factors, and take into account the variability among mixture data points: Inger and Bearhop, 2008; Moore and Semmens, 2008). We also carefully chose the diet sources included in models (i.e., based on direct observations). Finally, our results from stable isotope models were strongly supported by data on endogenous reserve dynamics.

### *Inter-annual variation in nutrient source contribution to egg formation*

Sea-ice extent can affect marine birds foraging conditions and prey selection, particularly during spring migration and just prior to egg formation (Gaston *et al.*, 2005; Mosbech *et al.*, 2006; Chaulk *et al.*, 2007). Our stable isotope models showed that yolk proteins were principally derived from clams in 2002 and 2004, but from amphipods in 2003, a year characterised by a late ice break-up (Love *et al.*, Submitted). Moreover, females were heavier upon return to the nesting colony in 2003 and they apparently increased their endogenous protein contribution to yolk in that year (Table 2). As suggested by Guillemette (1994) for wintering Common Eiders, heavy pre-laying females may have decreased their chance of flightlessness by feeding more intensively on small organisms, and this could have contributed to their higher use of amphipods (rather than clams) in 2003.

Yolk lipids were derived principally from endogenous fat reserves in 2003 and 2004, but the relative contribution could not be calculated in 2002 using stable isotopes. Stable carbon isotope ratios of yolk lipids of the first egg did not fall between those of liver lipids and abdominal fat δ13C values in that year (Figure 3a) but did for the last egg (Table 1). Given that females laid their first egg 4 to 5 days before they were collected, and that the half-life of carbon (turnover rate) in liver is 2.6 days (Hobson and Clark, 1992), it is possible that liver isotope ratios changed between the formation of the first egg and the female collection time. Our results may thus reflect a prey switch towards clams during egg formation, as such change would shift the liver δ13C values higher (see Figure 3).

## ***Seasonal variations in sources contribution***

### *Inter-individual variation*

In seasonal environment, early born offspring generally have higher post-hatching survival than late born, and this typically leads to a seasonal decline in egg value (e.g.: Lepage *et al.*, 2000; Love *et al.*, 2009). Birds can, however, benefit from a delay in breeding to acquire more endogenous resources prior to breeding (Bêty *et al.*, 2003; Love *et al.*, 2009). In this context, optimization models suggest that birds arriving late or in poor body condition on their breeding grounds should lay later and fewer eggs in order to maximize their expected reproductive success (Rowe *et al.*, 1994). We found that endogenous protein contribution per egg increased in late breeders. This strongly suggest that, by laying fewer eggs (see Chapter 2), late breeders can afford to slightly increase the proportion of endogenous nutrients invested in each egg and therefore breed as early as possible (when offspring value is still high enough to successfully reproduce; Varpe *et al.*, 2009). A similar conclusion has been suggested in arctic-nesting snow geese (Gauthier *et al.*, 2003).

### *Intra-clutch variations*

The seasonal variation we found in the difference between the isotope values of the first and last laid egg may reflect switches in prey consumed during egg formation. As rapid follicular growth takes about nine days in Common Eiders (Robertson, 1995), nearly two weeks can separate the recruitment of the first follicle and the ovulation of the last one in a clutch of four eggs. Due to full ice cover in early June, eiders nesting early at our study site are likely forced to feed outside the bay while forming their first egg (i.e., at about 20 km off the nesting island). When their follicle development or laying period progresses in mid/late June, shorelines (river mouths and nesting island periphery) become available in the bay and females start feeding on amphipods, which is the prey first available close to the colony. This potential switch is consistent with the differences we found in δ13C and δ15N values of lipid-free yolk between last and first eggs (positive differences in δ13C and negative differences in δ15N in early breeders; Figure 2 and Figure 5). Late nesters showed the opposite trend in both δ13C and δ15N values (Figure 5), indicating a reverse switch. Indeed, late breeders may start follicle development while feeding on amphipods in the vicinity of the nesting site, and then switch to clams, which become available in the bay in late June/early July when ice starts breaking up. Alternatively, these females may allocate more endogenous reserves to yolk formation as the development of follicles progresses (as this would generate a similar trend is isotopic ratios). Finally, the systematic enrichment in albumen 15N during the laying sequence (regardless of the timing of breeding) could be explained by a higher endogenous investment in the last egg. Indeed, albumen of the last egg is formed 18 to 24 hours before clutch completion (Williams, 1999) and females tend to spend more time on the nest at the end of laying in order to protect the clutch against predators (Swennen et al., 1993; Hanssen et al., 2002). Further investigations are nonetheless needed to validate our conclusions and tease apart alternative explanations for intra-clutch variations.

### ***Capital breeding and flying constraints***

The acquisition of nutrient stores prior to reproduction may be a selected trait, especially for species breeding in unpredictable environments. Endogenous reserves can enable females to start clutch production regardless of local resources availability, and in turn increase their fecundity (Varpe et al., 2009). Moreover, egg predation is a major source of breeding failure in birds and increasing nest attentiveness can strongly reduce predation risk (Bêty et al., 2002; Hanssen et al., 2002). From this perspective, there should be a strong selection pressure to reduce the time spent foraging away from the nest and a pure capital breeding strategy could nearly eliminate nest predation in some cases (i.e., when parents can defend the nest against predators). However, heavier endogenous reserves also increase wing loading, and pre-laying eiders are known to be at the limit of flight capabilities, with high energetic costs of flight (Guillemette and Ouellet, 2005a; Guillemette and Ouellet, 2005b). Pectoral and flight muscle masses of pre-laying eider females do not keep up with the increase in body mass associated with body stores and egg formation (up to 40% higher than their winter mass; Guillemette and Ouellet, 2005b). The effects of an increase in wing loading and a decrease in relative flight muscle mass can lead to a temporary loss in flight capability among pre-laying females, which is an extreme case of impaired flight ability associated with reproduction (Guillemette and Ouellet, 2005a). The trade-off between maximizing the likelihood of successfully producing a large clutch in harsh environments and minimizing the flightlessness time period may explain why females do not rely exclusively on endogenous reserves to produce their eggs. Given the potential survival costs associated with temporary flightlessness, pure capital laying may not be an optimal strategy for eiders.

The loss of flight capabilities in several insect species permits females to allocate more resources to egg production (Zera et al., 1998; Socha and Sula, 2008). Similarly, the evolution of flightlessness among sea ducks and penguins could be the consequence of a change in resource allocation, required by limited available resources for crucial processes such as growth, survival or reproduction (McNab, 1994). Financing the reproduction may have enhanced the evolution of flightlessness of non-flying birds, and pure capital breeding may be possible (optimal) only for those species.

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## TABLES AND FIGURES

**Table 1**. Stable isotope composition (‰) of somatic tissues and components of the first and last egg of Common Eiders collected at Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada.

| | 2002 | | | 2003 | | | 2004 | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | Mean | SE | N | Mean | SE | N | Mean | SE |
| **Somatic Tissues** | | | | | | | | | |
| $\delta^{13}$C Breast | 15 | -16.9 | 0.21 | 17 | -17.3 | 0.11 | 20 | -17.4 | 0.17 |
| $\delta^{13}$C Liver lipid free | 15 | -17.2 | 0.28 | 15 | -17.1 | 0.15 | 19 | -17.3 | 0.26 |
| $\delta^{13}$C Liver lipid | 15 | -21.3 | 0.21 | 16 | -20.9 | 0.16 | 20 | -21.4 | 0.19 |
| $\delta^{13}$C Abdominal fat | 15 | -21.8 | 0.22 | 10 | -21.6 | 0.28 | 11 | -22.1 | 0.21 |
| $\delta^{15}$N Breast | 15 | 12.6 | 0.14 | 17 | 12.7 | 0.16 | 20 | 12.5 | 0.16 |
| $\delta^{15}$N Liver lipid free | 15 | 13.7 | 0.27 | 15 | 13.8 | 0.3 | 19 | 13.1 | 0.19 |
| | | | | | | | | | |
| **First Egg** | | | | | | | | | |
| $\delta^{13}$C Albumen | 15 | -16.6 | 0.45 | 16 | -16.2 | 0.24 | 20 | -16.8 | 0.35 |
| $\delta^{13}$C Yolk* | 15 | -17.8 | 0.37 | 17 | -16.2 | 0.22 | 18 | -17.8 | 0.4 |
| $\delta^{13}$C Yolk lipid | 14 | -21.3 | 0.35 | 17 | -21.4 | 0.23 | 19 | -21.9 | 0.32 |
| $\delta^{15}$N Albumen | 15 | 11.8 | 0.48 | 16 | 12.3 | 0.49 | 20 | 11.2 | 0.33 |
| $\delta^{15}$N Yolk* | 15 | 13.0 | 0.41 | 17 | 14.1 | 0.37 | 18 | 12.7 | 0.31 |
| | | | | | | | | | |
| **Last Egg** | | | | | | | | | |
| $\delta^{13}$C Albumen | 15 | -16.7 | 0.33 | 15 | -16.3 | 0.25 | 17 | -16.6 | 0.34 |
| $\delta^{13}$C Yolk* | 15 | -17.5 | 0.41 | 16 | -16.2 | 0.26 | 16 | -16.3 | 0.36 |
| $\delta^{13}$C Yolk lipid | 13 | -21.6 | 0.33 | 15 | -21.3 | 0.21 | 16 | -21.8 | 0.32 |
| $\delta^{15}$N Albumen | 15 | 12.7 | 0.39 | 15 | 13.2 | 0.45 | 17 | 12.1 | 0.48 |
| $\delta^{15}$N Yolk | 15 | 12.9 | 0.49 | 16 | 14.0 | 0.44 | 16 | 13.2 | 0.39 |

* : Indicates significant differences among years ($p < 0.05$).

**Table 2.** Values at 5th, 50th, and 95th percentiles of the distributions of possible contribution of endogenous reserves (breast muscles) and prey items to the formation of lipid-free egg components of Common Eiders (first egg collected in each nest).

| | **2002** | | | **2003** | | | **2004** | | |
|---|---|---|---|---|---|---|---|---|---|
| | 5% | 50% | 95% | 5% | 50% | 95% | 5% | 50% | 95% |
| **Yolk lipid-free** | | | | | | | | | |
| Breast Muscles | 0,5 | 5,9 | 15,7 | 24,6 | 32,6 | 40,7 | 0,2 | 2,4 | 8,8 |
| Hiatella arctica | 70,4 | 79,5 | 88,5 | 0,1 | 0,7 | 3,2 | 66,2 | 78,8 | 88,9 |
| Serripes sp. | 0,3 | 3,4 | 11,7 | 0,1 | 1,5 | 6,4 | 0,1 | 1,1 | 4,7 |
| Acmea testudinalis | 0,2 | 3,3 | 12,7 | 0,1 | 1,1 | 4,9 | 0,5 | 6,4 | 23,5 |
| Gammarus / offshore | 0,2 | 2,3 | 8,6 | 55,1 | 61,7 | 69,2 | 0,3 | 3,9 | 15,3 |
| Gammarus / river mouth | 0,1 | 1,4 | 5,3 | 0,0 | 0,5 | 1,8 | 0,2 | 2,4 | 8,0 |
| **Albumen** | | | | | | | | | |
| Breast Muscles | 0,1 | 1,8 | 6,9 | 0,3 | 3,5 | 11,0 | 0,1 | 1,2 | 4,8 |
| Hiatella arctica | 78,1 | 86,2 | 93,2 | 68,4 | 78,1 | 87,6 | 76,6 | 84,5 | 91,7 |
| Serripes sp. | 0,1 | 1,5 | 6,0 | 0,1 | 1,8 | 6,9 | 0,1 | 1,3 | 5,0 |
| Acmea testudinalis | 0,1 | 2,2 | 8,5 | 0,4 | 4,6 | 15,2 | 0,1 | 1,7 | 6,4 |
| Gammarus / offshore | 0,2 | 2,5 | 9,0 | 0,4 | 4,5 | 15,9 | 0,2 | 2,7 | 9,9 |
| Gammarus / river mouth | 0,2 | 2,7 | 8,7 | 0,2 | 2,9 | 9,4 | 0,8 | 6,1 | 13,4 |

**Figure 1**. Year-corrected masses of Common Eider females endogenous reserves from pre-breeding to post-laying stages, Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada. Dotted lines represent means for each stage. Stages accompanied by different letters differed significantly ($\alpha = 0.025$, Bonferroni correction).

**Figure 2.** Lipid-free stable isotope ratios (‰ mean ± SD) of egg components (first egg collected in each nest), endogenous reserves, and prey items of Common Eiders. Year of egg collection is indicated in each panel (a–c). Sample sizes of each food item range from 5 to 22. In some cases, only positive or negative standard errors are shown to avoid overlaps. Only egg component ratios are corrected for discrimination. Therefore, it is not appropriate to interpret, from this figure, prey contributions to body reserves.

**Figure 3.** Lipid δ13C (‰ mean ± SD) of egg components (first egg collected in each nest), endogenous reserves, and liver of Common Eiders (a-c). Prey lipid ratios did not allow discriminating endogenous reserves and exogenous resources (d). Sample sizes of each food item range from 5 to 22, except for Serripes spp. (N=1). In some cases, only positive or negative standard errors are shown to avoid overlaps.

**Figure 4**. Seasonal variation of endogenous contribution to a) lipid-free yolk and b) albumen formation (first egg collected in each nest) of Common Eiders (grouped into early, mid and late breeders according to their relative lay date).

**Figure 5**. Lipid-free yolk δ13C and δ15N (‰) differences between last and first eggs laid in the laying sequence, according to the relative lay date of females. Dotted lines separate early, mid and late breeders (see methods).

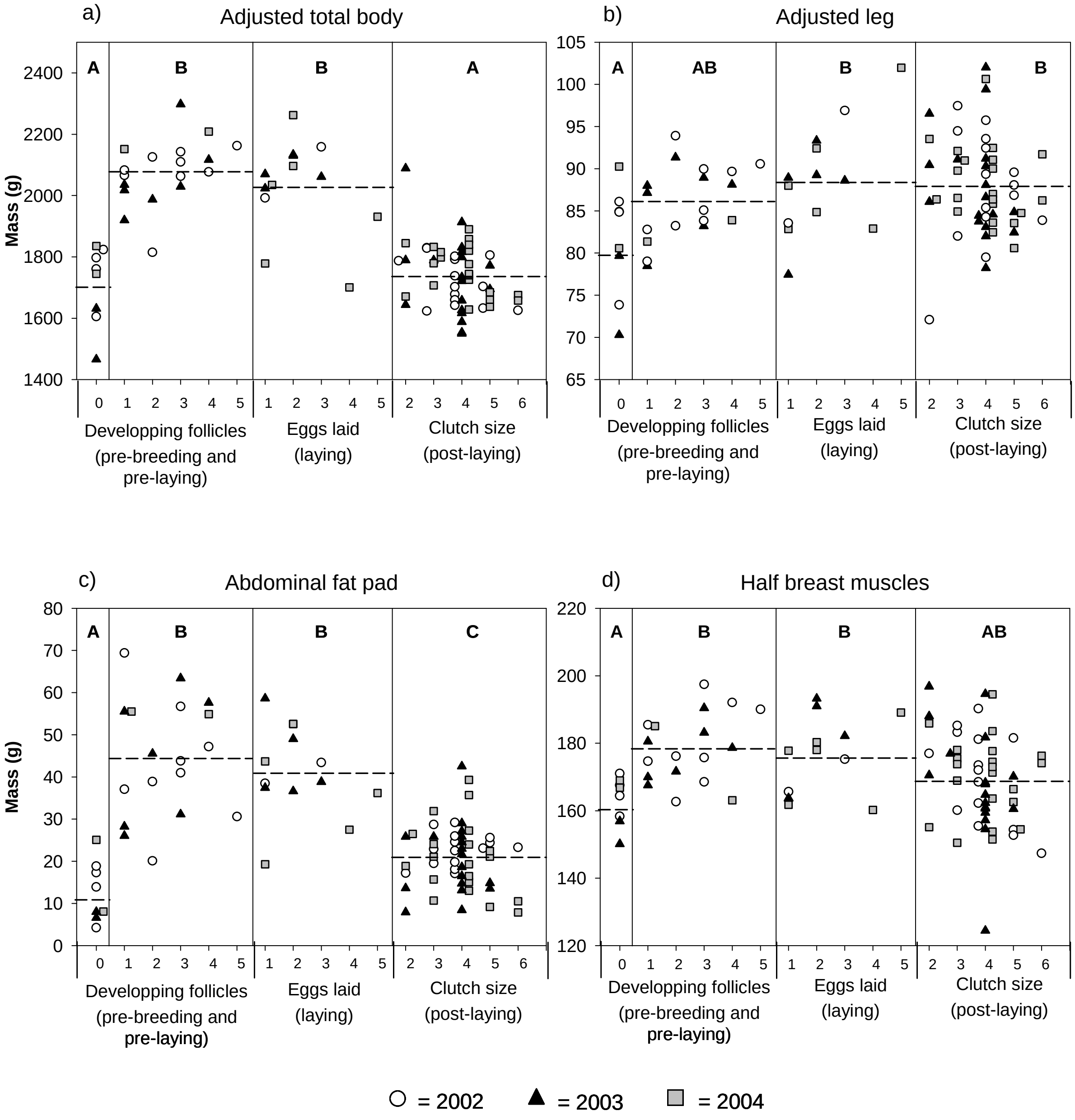
a)
Adjusted total body
A
B
B
A
Mass (g)
2400
2200
2000
1800
1600
1400
0 1 2 3 4 5
1 2 3 4 5
2 3 4 5 6
Developping follicles (pre-breeding and pre-laying)
Eggs laid (laying)
Clutch size (post-laying)
b)
Adjusted leg
A
AB
B
B
105
100
95
90
85
80
75
70
65
0 1 2 3 4 5
1 2 3 4 5
2 3 4 5 6
Developping follicles (pre-breeding and pre-laying)
Eggs laid (laying)
Clutch size (post-laying)
c)
Abdominal fat pad
A
B
B
C
Mass (g)
80
70
60
50
40
30
20
10
0
0 1 2 3 4 5
1 2 3 4 5
2 3 4 5 6
Developping follicles (pre-breeding and pre-laying)
Eggs laid (laying)
Clutch size (post-laying)
d)
Half breast muscles
A
B
B
AB
220
200
180
160
140
120
0 1 2 3 4 5
1 2 3 4 5
2 3 4 5 6
Developping follicles (pre-breeding and pre-laying)
Eggs laid (laying)
Clutch size (post-laying)
○ = 2002
▲ = 2003
▨ = 2004

**Figure 1**.

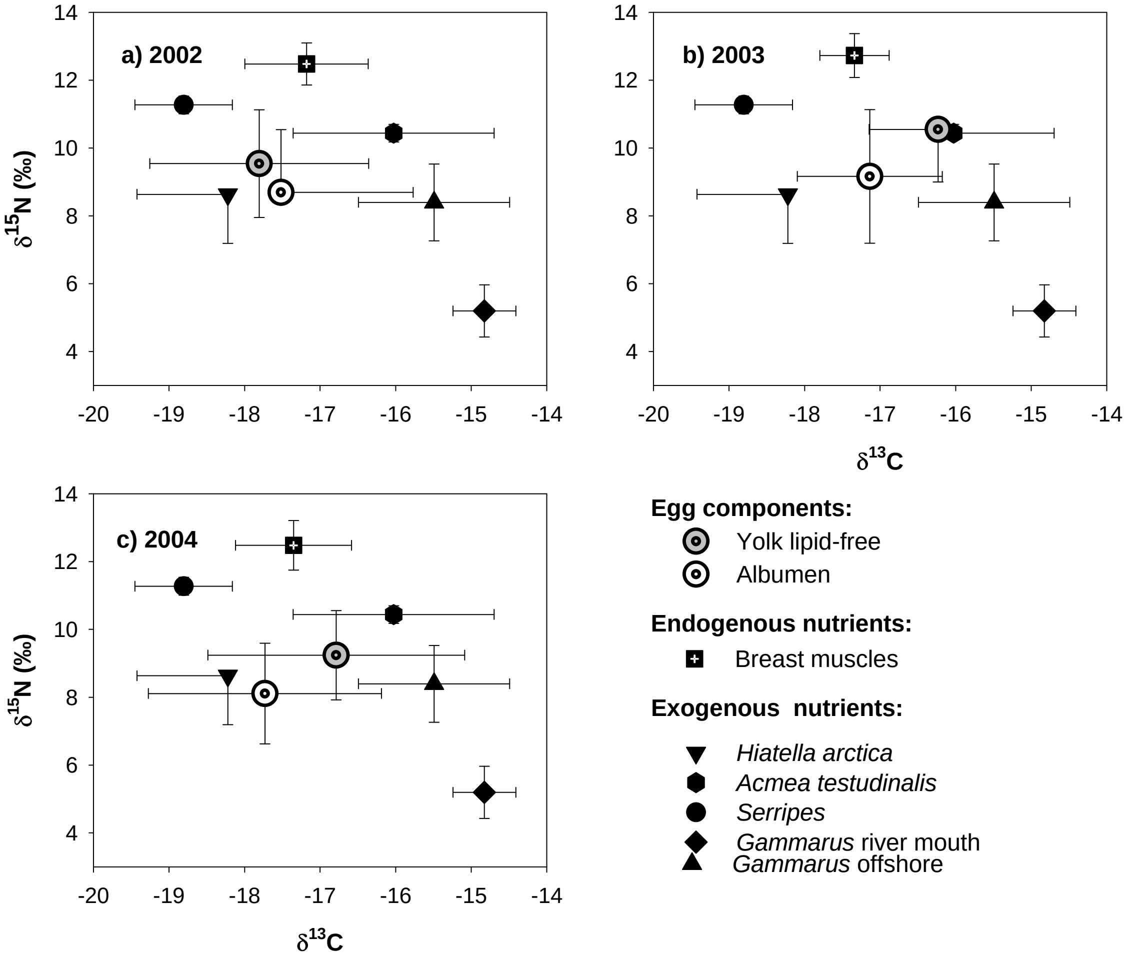
a) 2002
b) 2003
c) 2004
$\delta^{15}N$ (‰)
$\delta^{13}C$
14
12
10
8
6
4
-20
-19
-18
-17
-16
-15
-14
Egg components:
Yolk lipid-free
Albumen
Endogenous nutrients:
Breast muscles
Exogenous nutrients:
Hiatella arctica
Acmea testudinalis
Serripes
Gammarus river mouth
Gammarus offshore

**Figure 2.**

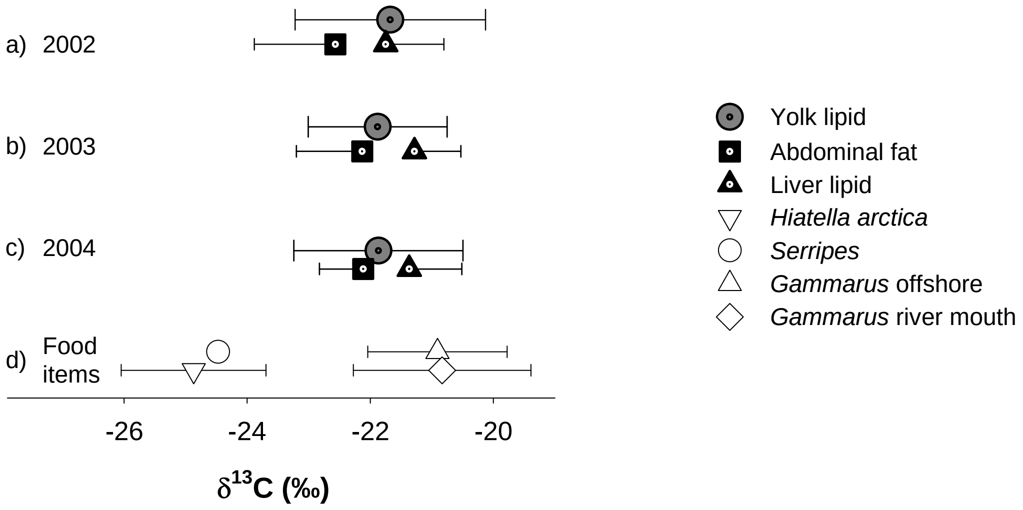
a) 2002
b) 2003
c) 2004
d) Food items
-26
-24
-22
-20
δ13C (‰)
Yolk lipid
Abdominal fat
Liver lipid
*Hiatella arctica*
*Serripes*
*Gammarus* offshore
*Gammarus* river mouth

**Figure 3.**

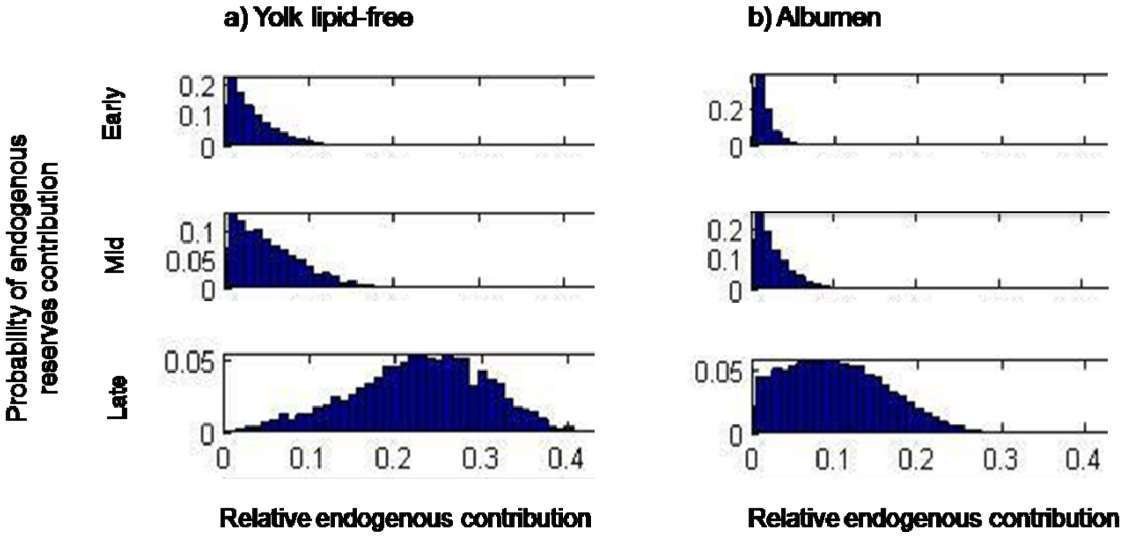
a) Yolk lipid-free
b) Albumen
Probability of endogenous reserves contribution
Early
Mid
Late
0.2
0.1
0
0.1
0.05
0
0.05
0
0
0.1
0.2
0.3
0.4
Relative endogenous contribution
0.2
0
0.2
0.1
0
0.05
0
0
0.1
0.2
0.3
0.4
Relative endogenous contribution

**Figure 4.**

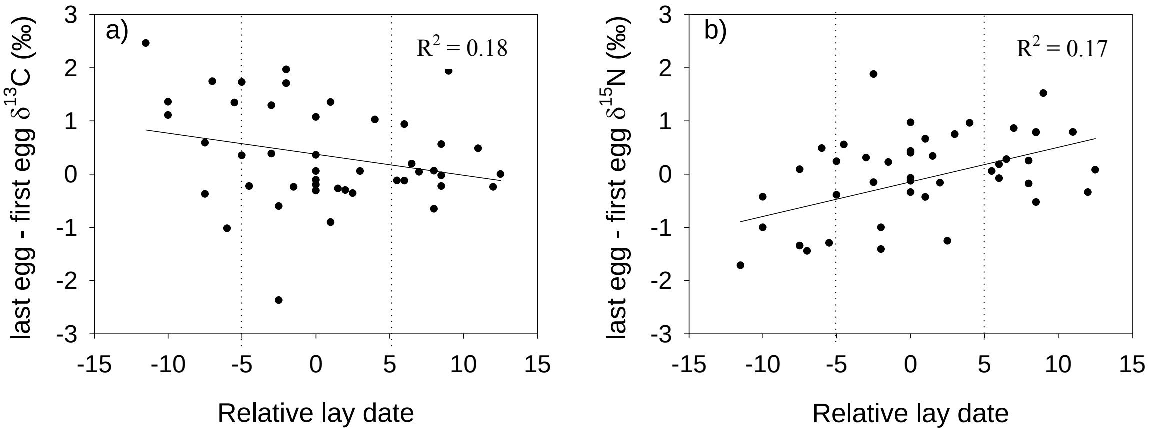
a)
R$^2$ = 0.18
last egg - first egg δ$^{13}$C (‰)
3
2
1
0
-1
-2
-3
-15
-10
-5
0
5
10
15
Relative lay date
b)
R$^2$ = 0.17
last egg - first egg δ$^{15}$N (‰)
Relative lay date

**Figure 5**

# APPENDIXES

## Appendix 1: Amphipods collection throughout 2003, 2007 and 2008 breeding seasons.

### *Methods*

Due to logistical constraints, most marine organisms were collected at the end of eider incubation (following ice break up), and in a different year than female and egg collections. Annual and seasonal variations in prey signatures could potentially bias our estimates of egg nutrient sources. Given that amphipods likely show an isotope turnover faster than other eider prey items (Gorokhova and Hansson, 1999), we assumed that potential intra- and inter-annual variations observed in their isotope ratios would be larger than for other prey species. Therefore, we collected amphipods ($n > 10$ individuals per sampling date most of the time) on the shore of Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada in three different years (2003, 2007 and 2008). Depending on ice conditions around the island, we tried to sample from the eiders pre-laying period until the end of July (which corresponds to the prey sampling period in 2007). By performing ANCOVAs, we examined the annual and seasonal variation in isotope ratios of lipid-free tissues ($\delta^{13}C$ and $\delta^{15}N$) and lipids ($\delta^{13}C$ only). The interaction (year and date) was first included in the models, and removed because it was not significant (all $P > 0.20$).

### *Results*

Carbon and nitrogen isotope ratios of amphipods did not significantly vary over time, suggesting that the seasonal variation in isotope composition of marine organisms maybe negligible at East Bay from eiders pre-laying period to the end of the prey sampling period in this study (effect of date: $F_{1,17} = 0.01$, $P = 0.93$ for $\delta^{13}C$ of lipid-free tissues; $F_{1,17} = 1.20$, $P = 0.29$ for $\delta^{15}N$ of lipid-free tissues; $F_{1,15} = 0.05$, $P = 0.82$ for $\delta^{13}C$ of lipids; Figure 1). The annual variation in amphipod isotope ratios was also not significant (effect of year: $F_{2,17} = 2.85$, $P = 0.09$ for $\delta^{13}C$ of lipid-free tissues; $F_{2,17} = 2.85$, $P = 0.09$ for $\delta^{15}N$ of lipid-free tissues; $F_{2,15} = 0.69$, $P = 0.52$ for $\delta^{13}C$ of lipids; Figure 1). Given that isotope models do not give an exact contribution for every source, but a range of possible contributions, and that uncertainty associated with isotope values (sources and mixtures) and discrimination factors were incorporated into mixing models, we are overall confident that the small variations observed are biologically not significant.

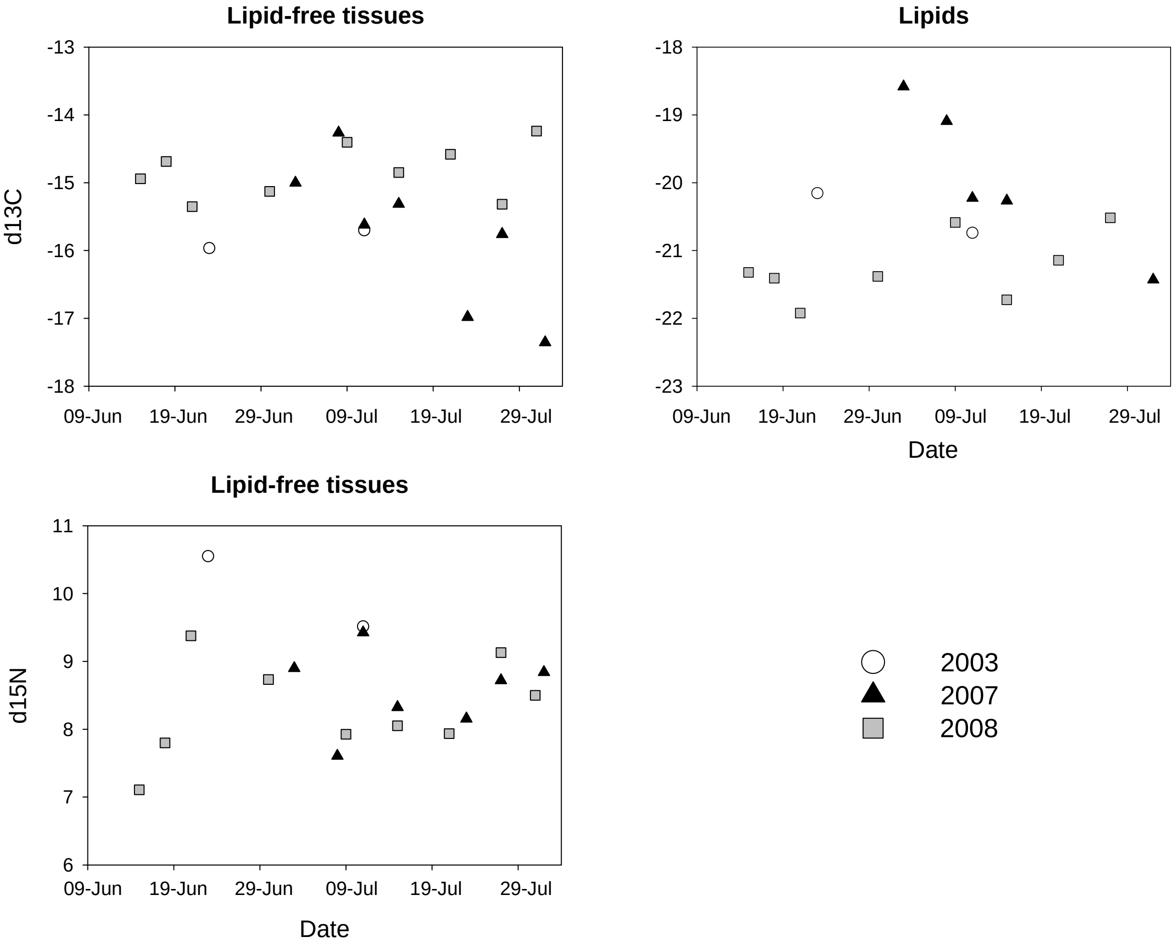

**Figure 1**. Annual and seasonal variation of isotope ratios of amphipods collected at Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada.

## Appendix 2: Isotope ratios determination of albumen (2004) and amphipods (2008).

### *Methods*

We had to ship samples at two different laboratories to generate our database of isotope ratios. Samples of albumen from 2004 and amphipods from 2008 have been sent to the Stable Isotopes in Nature Laboratory (SINLAB), at the University of New Brunswick (UNB) in Fredericton, New Brunswick, Canada, while all the other samples were sent to the stable isotope laboratory of the National Water Research Institute (see methods described in Chapter 1). At the SINLAB, approximately 0.2 mg of the samples were loaded in tin capsules and combusted in a NC2500 Elemental Analyzer. Resultant gazes ($CO_2$ and $N_2$) were delivered via continuous flow to a Finnigan Delta Plus mass spectrometer and analyzed for stable isotopes of carbon and nitrogen.

Ten samples of various tissues were sent to both laboratories in order to compare the results. We performed paired t-tests on $\delta^{13}C$ lipid-free, $\delta^{15}N$ lipid-free, and $\delta^{13}C$ lipid to compare isotopic ratios obtained from different laboratory.

### *Results*

Both laboratories found similar values of $\delta^{15}N$ ($t = -1.80$, df = 9, $P = 0.11$), but slightly different values in $\delta^{13}C$ of lipid-free tissues ($t = 4.74$, df = 9, $P = 0.001$) and lipid ($t = 11.99$, df = 3, $P = 0.001$). However, differences observed between $\delta^{13}C$ values of lipid-free tissues were, most of the time, smaller than the error predicted by laboratories, and therefore not biologically significant (average difference = 0.25‰ ± 0.05, and error predicted by laboratories = 0.3 ‰). Differences observed in lipids were higher (average difference= 0.63‰ ± 0.05). However, given that albumens are lipid-free and that we did not use the lipid extracts of amphipods (we used the liver isotopic ratio as an indicator of exogenous contribution), we think that this difference between labs (calculated from a small sample size) did not influence our conclusions. We therefore kept our samples of albumens 2004 and amphipods 2008 in our analyses, even if the provenance of isotopic results differed.

## Appendix 3: Sources contributions to lipid-free yolk and albumen using other mixing models.

New programs using Bayesian methods to calculate source contributions to a mix have been developed, but to date, they have been rarely used. We calculated the calculated endogenous and exogenous contributions to lipid-free yolk and albumen using three different programs (IsoSource (Phillips and Gregg, 2003) and Bayesian based MixSIR (see Chapter 1 for results) and  SIAR (Jackson *et al.*, 2009)) and compared the results.

### IsoSource

This mixing model has been extensively used in different fields of ecology (e.g: Cucherousset *et al.*, 2007; Samelius *et al.*, 2007; Farina *et al.*, 2008), and is based on the geometry and the similarity of mean signatures of sources and mixture. We ran the program with an increment of 1% and a tolerance of 0.3. The tolerance is the only measure of uncertainty incorporated to the model, and corresponds approximately to the standard error associated to the means of sources.

**Table 1**. Values at 1st, 50th, and 99th percentiles* of endogenous reserves (breast muscles) and prey items contributions to the formation of lipid-free egg components of Common Eiders using IsoSource program.

| | 2002 | | | 2003 | | | 2004 | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1%* | 50% | 99% | 1% | 50% | 99% | 1% | 50% | 99% |
| **Lipid-free yolk** | | | | | | | | | |
| Breast Muscles | 0 | 6 | 25 | 1 | 21 | 50 | 0 | 12 | 41 |
| Hiatella arctica | 3 | 41 | 70 | 0 | 2 | 12 | 0 | 15 | 41 |
| Amphipods / offshore | 0 | 7 | 30 | 0 | 8 | 36 | 0 | 20 | 62 |
| Serripes sp. | 1 | 29 | 63 | 0 | 3 | 15 | 0 | 14 | 41 |
| Limpet | 0 | 6 | 25 | 17 | 57 | 87 | 0 | 15 | 47 |
| Amphipods / river mouths | 0 | 6 | 23 | 0 | 4 | 20 | 0 | 16 | 34 |
| **Albumen** | | | | | | | | | |
| Breast Muscles | 0 | 4 | 17 | 0 | 9 | 31 | 0 | 1 | 8 |
| Hiatella arctica | 15 | 54 | 78 | 0 | 28 | 56 | 72 | 85 | 97 |
| Amphipods / offshore | 0 | 8 | 35 | 0 | 15 | 52 | 0 | 1 | 6 |
| Serripes sp. | 0 | 11 | 46 | 0 | 18 | 51 | 0 | 9 | 21 |
| Limpet | 0 | 5 | 22 | 0 | 10 | 37 | 0 | 1 | 5 |
| Amphipods / river mouths | 0 | 13 | 30 | 0 | 14 | 33 | 0 | 1 | 5 |

* : IsoSource outputs do not provide values at 5th and 95th percentiles.

## SIAR

This program is based, like MixSIR, on Bayesian techniques. Therefore, those two programs best incorporate sources of uncertainty such as variability in isotopes signatures and isotopic fractionation (Inger and Bearhop, 2008; Moore and Semmens, 2008), but differs quite fundamentally in that 1) MixSIR uses Sample Importance Resampling to fit the model whereas SIAR uses Markov Chain Monte Carlo; and 2) SIAR has a residual error term and MixSIR does not. SIAR results consequently have wider confidence intervals.

**Table 2**. Values at 5th, 50th, and 95th percentiles of endogenous reserves (breast muscles) and prey items contributions to the formation of lipid-free egg components of Common Eiders using SIAR program.

| | 2002 | | | 2003 | | | 2004 | | |
|---|---|---|---|---|---|---|---|---|---|
| | 5% | 50% | 95% | 5% | 50% | 95% | 5% | 50% | 95% |
| **Lipid-free yolk** | | | | | | | | | |
| Breast Muscles | 0 | 14 | 30 | 5 | 26 | 46 | 0 | 17 | 29 |
| Hiatella arctica | 2 | 23 | 45 | 0 | 2 | 18 | 0 | 20 | 33 |
| Amphipods / offshore | 0 | 4 | 28 | 0 | 23 | 38 | 0 | 20 | 33 |
| Serripes sp. | 2 | 25 | 43 | 0 | 2 | 22 | 0 | 19 | 31 |
| Limpet | 0 | 4 | 29 | 2 | 26 | 55 | 0 | 17 | 31 |
| Amphipods / river mouths | 0 | 6 | 23 | 0 | 3 | 22 | 3 | 19 | 31 |
| **Albumen** | | | | | | | | | |
| Breast Muscles | 0 | 3 | 26 | 0 | 15 | 28 | 0 | 1 | 16 |
| Hiatella arctica | 2 | 23 | 42 | 2 | 24 | 40 | 9 | 29 | 68 |
| Amphipods / offshore | 0 | 17 | 31 | 0 | 13 | 30 | 0 | 2 | 27 |
| Serripes sp. | 0 | 21 | 35 | 0 | 22 | 35 | 0 | 13 | 33 |
| Limpet | 0 | 3 | 28 | 0 | 9 | 30 | 0 | 2 | 20 |
| Amphipods / river mouths | 2 | 21 | 33 | 0 | 15 | 28 | 6 | 25 | 39 |

Overall, even if contributions of exogenous sources to lipid-free yolk and albumen sometimes vary between models, endogenous maximum contribution is always ≤ 50% for lipid-free yolk and never exceeded 31% for albumen. Our conclusions regarding endogenous protein contributions to egg components are thus comparable for the three models available.

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# CHAPITRE 2

## INTERACTIONS BETWEEN TIMING OF BREEDING, EGG PRODUCTION AND POST-LAYING ENERGETIC NEEDS IN A CAPITAL BREEDER

Manuscrit en préparation pour une publication

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## E. SÉNÉCHAL, J. BÊTY AND G. GILCHRIST. Interactions between timing of breeding, egg production, and post-laying energetic needs in a capital breeder

Condition-dependent model of individual optimal clutch size and lay date assumes that, before producing eggs, birds must reach a minimum condition threshold dictated by levels of stored nutrients needed during subsequent breeding phases. Once the threshold is exceeded, females reaching the optimal combination of lay date and clutch size in good body condition should not save extra body stores for later stages but should lay more eggs than females in poor condition. Consequently, post-laying condition is predicted to be independent of clutch size or lay date. However, incubation costs could increase with clutch size, and females investing more in current reproduction (i.e., larger clutch) could secure more body reserves for subsequent breeding stages in order to increase their capacity to successfully incubate eggs and rear young. The main goal of this study was to determine if the post-laying body condition of female arctic-nesting Common Eiders (*Somateria mollissima*) was affected by their timing of breeding and clutch size. Female eiders partly rely on endogenous reserves to produce their eggs, they fast during the incubation, and their body condition at hatching influences brood rearing success. During a three-year study, we collected females at incubation onset and used total weight, abdominal fat, leg and breast muscles masses as indicators of body condition. Our results showed that body stores at the end of laying were either independent or negatively related to clutch size. Leg mass was positively related to lay date in all years, whereas the effect of timing of breeding on fat stores varied annually. Overall, our results partly support predictions of the condition-

dependent model and indicate that most individual variation in post-laying body condition does not reflect a strategic adjustment determined by timing of breeding or energetic investment in egg production. We suggest that differences in body condition at the onset of incubation are mostly caused by the unpredictability in foraging and environmental conditions encountered by laying individuals.

## E. SÉNÉCHAL, J. BÊTY AND G. GILCHRIST. Interactions between timing of breeding, egg production, and post-laying energetic needs in a capital breeder

Le modèle condition-dépendant de combinaisons optimales de tailles de couvées et de dates de ponte présume qu'avant de produire leurs œufs, les individus doivent d'abord atteindre un seuil minimal de condition corporelle qui est déterminé par la quantité de réserves endogènes nécessaires pour les stades subséquents de la reproduction. Une fois ce seuil dépassé, les femelles en meilleures conditions devraient pondre plus d'œufs que les femelles en moins bonnes conditions et ne devraient pas conserver des réserves pour les stades subséquents de la reproduction. Conséquemment, selon le modèle condition-dépendant, la condition corporelle des femelles en post-ponte devrait être indépendante de la taille de la couvée et de la date de ponte. Cependant, les coûts de l'incubation peuvent augmenter selon le nombre d'œufs à incuber, et les femelles qui investissent davantage dans leur reproduction une année donnée (grande taille de ponte) pourraient conserver une plus grande quantité de réserves corporelles en prévision de la période d'incubation et d'élevage des jeunes. L'objectif principal de cette étude était de déterminer, chez l'eider à duvet (*Somateria mollissima*) nichant en arctique, si la condition corporelle post-ponte des femelles était affectée par la phénologie de la reproduction et par la taille de la couvée. Les eiders à duvet dépendent en partie de leurs réserves endogènes pour former leurs œufs, jeûnent durant l'incubation et leur condition corporelle lors de l'éclosion est directement proportionnelle à leur capacité d'élever leurs jeunes. Au cours de trois saisons de reproduction, nous avons récolté des femelles en début d'incubation et nous avons utilisé la masse corporelle, de même que la masse des graisses abdominales, des muscles pectoraux et des pattes comme indicateurs de la condition corporelle. Nos résultats ont démontré que les réserves à la fin de la ponte étaient indépendantes ou négativement reliées à la taille de la couvée. La masse des pattes était positivement reliée à la date de ponte pour les trois années, alors que l'effet de la date de ponte sur la masse des graisses abdominales a varié annuellement. Nos résultats supportent donc partiellement le modèle condition-dépendant, et indiquent que les variations individuelles de réserves endogènes au début de l'incubation ne reflètent pas un ajustement stratégique déterminé par la phénologie de la reproduction ou le degré d'investissement dans la couvée. Nous suggérons que les différences observées sont plutôt causées par les conditions environnementales rencontrées par les femelles au moment de la ponte.

## INTRODUCTION

Reproduction involves major life-history trade-offs and parents should invest energy in order to maximise their fitness (Stearns 1992). In birds, strategic parental decisions regarding the number of eggs laid may act during three distinct phases: egg production, incubation, and brood rearing stages (Monaghan and Nager, 1997; Nager, 2006). In precocial species, it is generally recognised that clutch size limitation can operate at the egg-laying stage (Lack, 1967; Bêty *et al.*, 2003). However, the energetic investment in egg formation could potentially interact with investments in subsequent stages (Moreno and Sanz, 1994; Erikstad and Tveraa, 1995; Kilpi and Lindstrom, 1997; Reid *et al.*, 2000; Bustnes *et al.*, 2002). Although such interactions in energetic allocation could be especially critical in capital breeders, they are rarely investigated in a single framework.

Rowe *et al.* (1994) proposed a model where individual optimal combinations of clutch size and lay date depend on pre-laying body condition, rate of condition gain and arrival date on the breeding grounds. The model predicts a seasonal decline in clutch size and is essentially based on the outcome of a conflict between the advantage of breeding early (greater offspring value) and the advantage of a delay in breeding (increase in body condition through energy acquisition and hence potential clutch size). According to this condition-dependant model, a female arriving late at the breeding site or with a poor body condition should strategically produce a smaller clutch in order to maximise her fitness (Bêty *et al.*, 2003). The model assumes that a minimum condition threshold must be reached to produce eggs and that such threshold should include the energy requirement needed to incubate and rear the eggs, relatively to the degree of precocity of offspring (Rowe *et al.*, 1994). The basic model presumes that the condition threshold does not vary over time (i.e., independent of lay date) and is not affected by clutch size (i.e., no interaction between energetic investment in egg formation and energy requirement needed for subsequent breeding phases). Once the minimum threshold is exceeded, females reaching the optimal combination of lay date and clutch size in good condition should not save extra body stores for subsequent breeding stages but should lay more eggs than females in poor condition (Figure 1). Consequently, post-laying condition should be independent of clutch size or lay date (Figure 1).

Optimal breeding decisions could however involve a flexible threshold condition associated with current reproductive effort and there could be an interaction between the allocation of body reserves in egg formation, incubation and parental care. Females producing larger clutches could have to deal with higher costs of incubation than females laying smaller broods (Thomson *et al.*, 1998; Hanssen *et al.*, 2005; de Heij *et al.*, 2006). The cost of incubation hypothesis thus predicts that females laying larger clutches should secure extra resources to compensate for higher costs of incubation, and start incubating in better body condition (Erikstad *et al.*, 1993; Erikstad and Tveraa, 1995). Moreover, as the expected fitness benefit of large clutches is typically higher, females laying more eggs could also start incubating in better condition in order to increase the likelihood of *i*) successfully completing incubation (higher condition leads to higher nest attendance and lower nest predation risk; Wiebe and Martin, 2000; Criscuolo *et al.*, 2002; Gorman and

Nager, 2003), and *ii*) successfully rearing their young (higher condition reduces the likelihood of brood abandonment; Kilpi *et al.*, 2001; Bustnes *et al.*, 2002; Ost *et al.*, 2003; Robinson *et al.*, 2005; Green *et al.*, 2007).

We investigated the potential relationships between energetic allocation of body reserves in egg production and subsequent breeding phases among Common Eiders (*Somateria mollissima*, here after eider) nesting in the Arctic. Eiders are precocial birds that produce their eggs mostly from stored lipids but exogenous proteins (Chapter 1), and rely extensively on stored nutrients to incubate (Bottitta *et al.*, 2003 - same colony). Females in better body condition during incubation show better nest attendance, and are less vulnerable to nest predation (Hanssen *et al.*, 2002; Andersson and Waldeck, 2006). Parental care is generally shared among individuals in a multi-female brood-rearing coalition. However, mothers with greater body reserves at hatching are more likely to care for their ducklings and are less prone to give them up to other females (Ost *et al.*, 2003; Ost *et al.*, 2008), which increases survival prospects of juveniles and in turn the mother's reproductive success (Ost and Back, 2003). Therefore, eiders appear to be a good model species to examine potential interactions between the investment in egg production, incubation and parental care.

Based on a three-year study, we tested whether individual variation in endogenous reserves at incubation onset were *i*) driven by individual investment in egg formation, and *ii*) affected by the timing of breeding. We specifically tested predictions derived from the basic individual optimization clutch size model (Rowe *et al.*, 1994), which suggest that female post-laying body condition should not be related to timing of breeding or clutch size.

## METHODS

### *Study design*

This study was conducted from 2002 to 2004 on Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada ($64^{o}$ 02’N, $81^{o}$ 47’W), where up to 8000 eider pairs breed annually. Nests were found during the early laying period and females were trapped on their nest at the end of laying (N = 14 in 2002, 16 in 2003 and 17 in 2004). Each year we attempted to collect females regularly throughout the laying period. Females were euthanized using halothane and dissections were done within 24 hours from collection following Jamieson *et al.* (2006). We took morphometric measurements (tarsus, total head, and wing chord lengths; ± 0.01 mm) and weighted total body mass (food items and eggs were respectively subtracted from gizzards and oviducts) using pesola scales (± 10g). We also weighted wet masses of abdominal fat pad (without intestinal fat), left breast muscle (pectoralis and supra-coracoid), and total leg mass (left side only, including all muscles that originate or insert in the femur or tibiotarsus bones) using electronic scale (± 0.1g). These proxies are strongly correlated with total endogenous reserves in wintering eider females and mostly reflect either protein (breast and leg) or fat stores (abdominal fat and total body mass; Jamieson *et al.*, 2006). Clutch size was determined by the number of post-developed follicles, which represents the genuine number of eggs laid by a female. The beginning of incubation was validated by the absence of remaining developing follicles. Lay date was back-calculated according to the number of post-ovulatory follicles, assuming a 28 hours interval between laid eggs (Watson *et al.*, 1993).

### *Statistical analysis*

We used measurements of the right wing chord length, right tarsus length, and total head length to run a principal component analysis and adjust, when necessary, endogenous reserve masses to body size (Sedinger *et al.*, 1997). The first principal component (PC1) explained 46% of the variation and eigenvectors were all positive, ranging from 0.18 to 0.69. PC1 scores were used as an integrated index of individual structural size. General linear regression models were used to examine the relationship between the PC1 and the different proxies of endogenous reserves. As individual variation in body mass, abdominal fat and leg was partly explained by PC1 ($P \leq 0.07$), we adjusted those three dependent variables with body size using residuals from the regression models (i.e., size-corrected values).

We used least-squares general linear models to examine the influence of lay date, clutch size and year on post-laying abdominal fat, leg, breast muscles and body masses. To account for annual variation, lay dates were expressed as deviation from the yearly median (i.e., relative lay date). All possible interactions between explanatory variables (clutch size, lay date and year) were tested and sequentially removed according to their p-values (type III sum of squares). Including year in the model allowed us to test for annual changes in the slope of the studied relationships. Annual differences in endogenous reserves and clutch sizes were estimated with one–way ANOVAs, and annual lay dates were compared with a non-parametric median one-way analysis. Post hoc comparisons of least mean squares were performed with Tukey-Kramer pairwise tests, and we used the Dunn method of pairwise non-parametric comparisons to compare median lay dates. Residuals from our models indicated no strong violation of the assumptions of normality (all $p > 0.05$; Shapiro-Wilk test) and homogeneity of variance (all $p > 0.05$, except for body mass: $p = 0.01$, likely due to two heavy females captured in 2003; Levene's test). The covariates lay date and clutch size were correlated but the relationship was not strong enough to generate collinearity in statistical models (following Quinn and Keough, 2002). All statistical analyses were performed with the software SAS V 9.1 (SAS Institute 2002-2003), and significance levels were set at 0.05 unless other levels are specified.

## RESULTS

The median lay date of collected birds varied annually ($\chi^2 = 7.28$; df = 2; P = 0.03) while average clutch size was similar between years (F = 0.38; df = 2; P = 0.69; Table 1). Average post-laying abdominal fat did not vary significantly between years, but females showed lower breast muscles, leg and total body masses in 2002, which was the earliest breeding season (Table 1 and Table 2).

For 28 females (60%), the number of post-ovulatory follicles was higher than numbers of eggs found in nests, suggesting partial nest depredation. Evidence of nest parasitism (number of post-ovulatory follicles lower than number of eggs found in nest) was detected for only 2 females (4%). Interestingly, the seasonal decline in clutch size was stronger when using the number of eggs found in nests ($r = -0.49$, $P < 0.001$) rather than the genuine clutch size (estimated using post-ovulatory follicles; $r = -0.26$, $P = 0.07$). As we are confident in our post-ovulatory follicle counts, the difference likely resulted from a higher partial predation rate in late breeders. However, estimates of post-laying body reserves did not differ between females with intact or partially depredated clutches (all $P > 0.50$). We thus combined all females in subsequent analyses.

Post-laying body condition was slightly lower in females that laid larger clutches (negative slopes for all proxies of endogenous reserves) but the relationships were significant only for total body mass and breast muscles (Table 2 and Figure 2; effect of clutch size on: abdominal fat, $F_{1,47} = 0.14$, $P = 0.71$; leg, $F_{1,45} = 1.30$, $P = 0.26$). After controlling statistically for clutch size, timing of breeding was systematically related to only one body store estimate, with late breeders having significantly heavier post-laying leg mass than earlier breeders (Figure 3). Lay date also had a significant effect on post-laying abdominal fat but the strength and the type of relationship (positive or negative) varied between years (Figure 3). During the earliest breeding season (2002), late breeders had higher post-laying fat reserves than early breeders (slope ± 95%CI = 0.51 ± 0.16), while the opposite relationship was observed during the latest breeding season (2004: slope ± 95%CI = -0.51 ± 0.24). Interestingly, no effect was detected in 2003 (slope ± 95%CI = 0.19 ± 0.26), which corresponded to an average season in terms of breeding phenology. Total body mass and breast muscles did not vary with timing of breeding (Table 2 and Figure 3; effect of lay date on: body mass, $F_{1,47} = 0.08$, $P = 0.77$; breast muscles, $F_{1,47} = 1.63$, $P = 0.21$). Results were similar when the number of eggs found in nests was included in models instead of the genuine clutch size (based on post-ovulatory follicles).

## DISCUSSION

The results allow us to generate four main conclusions. First, we reject the cost of incubation hypothesis, which predicted that females laying larger clutches should have secured extra resources to compensate for higher costs of incubation. Although weak or non-significant, we observed the exact opposite trends for every post-laying body reserve estimates. Second, we also reject the hypothesis that females adjust their post-laying condition according to the expected fitness benefits of the clutch (i.e., females laying earlier or more eggs did not start incubating in better condition in order to increase the likelihood of successfully incubating and rearing the young). Third, after controlling for clutch size, it appears that individual timing of breeding can affect post-laying body nutritional reserves but the relationships (positive/negative) may differ depending on the environmental conditions (early or late breeding season). Finally, our data partially support the predictions of the condition-dependent individual optimization model of clutch size (see below). Overall, it appears that the large individual variation in endogenous reserves at the onset of incubation is mostly driven by factors other than clutch size and lay date in arctic-nesting Common Eiders. We suggest that such variation is mostly caused by the unpredictability in foraging and environmental conditions experienced by laying females, and is not reflecting a strategic adjustment determined by timing of breeding or energetic investment in egg production. We will discuss these conclusions in turn as well as potential alternative mechanisms that could explain our results.

### *Clutch size and cost of incubation*

The condition-dependent optimization model predicts that females reaching the optimal combination of lay date and clutch size in better body condition should lay more eggs rather than saving stores for incubation and brood rearing (Rowe *et al.*, 1994). Our results are generally consistent with this prediction (i.e., post-laying fat stores were independent of clutch size), but nonetheless suggest that females investing less in clutch production had higher post-laying protein stores. Proteins are known to be one main limiting nutrient during egg formation for several bird species (Meijer and Drent, 1999; Klaassen, 2003). For eiders nesting at our study site, most egg proteins are derived from exogenous nutrients acquired during egg formation, while body stores contribute to a lesser extent (maximum possible endogenous protein contribution of 40%; Chapter 1). Based on an average egg mass of 104g (Parker and Holm, 1990) and a dry protein content of 20% (Williams, 1999), the mean body mass decrease of 31.8g per egg observed in post-laying females could be partly explained by the endogenous investment in egg formation (Table 2). Females that laid small clutches may have started egg production with similar protein stores than females laying large clutches, which allowed them to end laying in better condition. Alternatively, females that laid large clutches may have started egg production in better condition but were not able to acquire enough exogenous nutrients to cover the full costs of laying the extra eggs. Even if the real start of incubation (embryonic development) does not appear to be related to clutch size in eiders (Hanssen *et al.*, 2002), most precocial birds tend to increase the time spent at the nest during the laying period (Poussart *et al.*, 2000; Andersson and Waldeck, 2006). Female eiders laying large clutches may thus have spent more time at their nest during the laying period, which could have lowered their foraging rate and increased endogenous energetic investment during egg formation. Although the exact mechanisms leading to lower post-laying stores in female laying large clutches need further investigations, it is consistent with recent observations indicating that an increase in clutch size decreases the immune function in eiders, with potential cascading effects on future fitness prospects (Hanssen *et al.*, 2004; 2005; Descamps *et al.*, 2009).

Our results do not support previous studies suggesting that female eiders producing large clutches are in better body condition at the start of incubation than females producing small clutches (Erikstad *et al.*, 1993; Erikstad and Tveraa, 1995). Erikstad and Tveraa (1995) also found no effect of clutch size on body condition measured during the early incubation period (typically at day 5). They nonetheless argued, based on increasing incubation costs with clutch size, that it was likely that females producing large clutches were in better body condition at the start of incubation than females producing small clutches. Our study design allowed us to better test such hypothesis because *i*) we measured body condition at the very beginning of incubation (on the first day in most cases), ii) we simultaneously tested for seasonal and annual variation, and iii) we used different proxies of body condition. Although energetic costs of incubation may considerably increase with clutch size in altricial birds (Thomson *et al.*, 1998), such costs appear to be lower in precocial birds such eiders (20.5% mass loss for females incubating 6 eggs vs. 18% for females incubating 3 eggs: Hanssen *et al.*, 2005). This likely explain our results showing that females producing larger clutches do not strategically save endogenous reserves during laying to cover potential extra incubation costs.

Kilpi *et al.* (2001) found that body condition at hatching was not related to clutch size or timing of breeding. They also suggested that optimal decisions of females (on brood abandonment) would be more likely driven by energetic considerations rather than the value of the brood (given their long lifetime, numerous breeding opportunities, and small clutch size variation). Our findings also indicate that birds laying larger clutch size do not save extra endogenous stores during egg production to increase the likelihood of successfully incubating and rearing the brood. However, if the large individual variation we observed in post-laying condition generates variation in post-hatching female energetic status, it suggests that events occurring during egg production could subsequently affect body condition at hatching, and hence the likelihood of brood abandonment.

### ***Timing of breeding and inter-annual variations***

Our results showed that late breeders typically start incubation with similar breast muscle and total body masses as early breeders (as predicted by the condition-dependant model), but they systematically had heavier leg mass, and either greater or smaller fat stores, depending on the breeding seasons. We suggest that seasonal variation in leg mass may reflect differences in the main prey consumed by eiders at our study site. Females arriving early at the breeding site feed extensively on amphipods found in shallow water (river mouths and shores) during their pre-laying period (Chapter 1), as extensive ice-cover restricts access to benthic invertebrates such as clams and limpets at this time. As the season progresses and ice cracks appear, females can increase the consumption of their preferred prey and dive in deeper water to acquire exogenous resources critically needed for egg formation (Chapter 1). As eiders employ extensively foot propulsion to forage on the sea floor (Heath *et al.*, 2006), late breeders could benefit from stronger leg muscles. As post-laying total body mass was similar between early and late breeders, the difference in leg mass may simply reflect an energy reallocation in breeding females (i.e., an adjustment of organ sizes to ecological conditions), as detected in other species (e.g., European starlings: Vézina and Williams, 2003).

Moreover, annual differences in seasonal trend of post-laying fat stores may reveal the role of environmental factors encountered by females during the egg formation period. However, as total body mass was similar between early and late breeders in all years (indicating similar level of total body reserves; Figure 3), we must be cautious with our interpretation. In 2002, early breeders showed lower abdominal fat stores at the beginning of incubation compared to late breeders, while the opposite trend was observed in 2004. Early breeders may have started egg production in relatively lower body condition in 2002 or may have invested more fat reserves in egg production than in 2004. Summer 2002 was characterized by an early ice break-up and investing more fat reserves in egg production could have been advantageous for early breeding females as egg value (juvenile survival prospect) is typically higher in such case (Love *et al.*, Submitted). Moreover, endogenous reserves of females were generally smaller in 2002 (Table 1), which may indicate that birds faced more difficult wintering and/or migrating condition that year (Lehikoinen *et al.*, 2006; Descamps *et al.*, Submitted). Late breeding females may have benefited from important open water areas and higher food resource availability before and during laying, which allowed them to partly save endogenous fat (contrary to early nesters). In contrast, the 2004 breeding season was particularly late, with thicker ice and snow cover near the breeding site during the egg formation period. Late breeding females consequently could not take advantage of higher food availability near the colony and may have used extra endogenous fat stores to produce their eggs early enough during the breeding season. Such seasonal pattern has been shown in geese and eiders using stable isotopes (Gauthier *et al.*, 2003; Chapter 1).

### *Post-laying body condition: strategic adjustment or good fortune?*

There is growing evidence that environmental factors can play an important role in breeding trade-offs such as nest site selection (Robertson, 1995), nest desertion (Bourgeon *et al.*, 2006), yolk hormones concentration (Love *et al.*, 2009), and immune function (Descamps *et al.*, 2009). A small proportion of the variation in females post-laying body condition appears to be explained by timing of breeding and clutch size, suggesting that it may be more influenced by environmental factors such as food availability, egg predation rates (during laying), nest site quality and weather conditions (during or before the breeding season). Female intrinsic quality or previous experience may be another source of variation in laying behaviour and post-laying condition. For instance, Hanssen *et al.* (2002) found that eider females that start incubation earlier during the laying sequence are in poorer condition at the onset of incubation. However, factors generating such behavioural differences remain unknown.

Following the optimal decision curve of the condition-dependent model, a female in better pre-laying body condition is predicted to increase her fitness by laying extra eggs rather than keeping reserves for subsequent reproductive stages such as incubation and brood rearing (Figure 1). Our results generally support this rationale, although females that laid fewer eggs apparently had some extra protein stores available at the end of laying. Based on small sample size, Spaans *et al*. (2007) reached a similar conclusion in Dark-bellied Brent Geese (*Branta bernicla bernicla*). Moreover, an experimental reduction of female eiders pre-laying body condition conducted at our study site generated a delay in lay date but did not affect the condition measured during incubation (Descamps *et al.* unpublished manuscript). This further support the hypothesis that females adjust their breeding decisions before laying in order to achieve the same post-laying body mass. Finally, we conclude that there is no strategic adjustment of post-laying body condition associated to (potential) higher costs of incubation or reproductive value of larger broods in Common Eiders.

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## TABLES AND FIGURES

**Table 1**. Inter-annual variation in lay date, clutch size and post-laying body reserves of arctic-nesting Common Eiders collected from Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada. Years accompanied by different letters differed significantly (α = 0.025, Bonferroni correction).

| | 2002 (N = 14) | 2003 (N = 16) | 2004 (N = 17) |
|---|---|---|---|
| **Breeding information** | | | |
| Lay date * | 178.0 (171-190)$^{A}$ | 181.5 (170-201)$^{AB}$ | 185.0 (170-195)$^{B}$ |
| Clutch size § | 4.1 ± 0.2 $^{A}$ | 3.9 ± 0.2 $^{A}$ | 3.9 ± 0.2 $^{A}$ |
| **Body reserves (g) §** | | | |
| Total body weight | 1691.1 ± 20.9 $^{A}$ | 1777.0 ± 27.0 $^{B}$ | 1761.1 ± 19.0 $^{AB}$ |
| Half breast muscles | 144.4 ± 3.7 $^{A}$ | 169.3 ± 3.7 $^{B}$ | 171.0 ± 2.9 $^{B}$ |
| Abdominal fat | 21.6 ± 1.1 $^{A}$ | 26.6 ± 2.0 $^{A}$ | 22.3 ± 1.8 $^{A}$ |
| Leg | 83.4 ± 1.5 $^{A}$ | 89.8 ± 1.6 $^{B}$ | 88.5 ± 1.2 $^{B}$ |

*: Median (5th – 95th percentile), expressed in Julian date, January 1 = 1.

§: Mean ± SE

**Table 2**. Relationship between lay date or clutch size and post-laying endogenous reserves of eider females collected in 2002, 2003 and 2004. Covariates and interactions (denoted by *) were reported only when significant ($P < 0.05$).

| | Model | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Body reserves** | **$r^2$** | **df error** | **F** | **P** | **Source** | **partial $r^2$** | **Estimate** | **SE** | **df** | **F** | **P** |
| Body Mass[a] | 0.23 | 43.0 | 4.2 | 0.01 | Year | 0.15 | | | 2.0 | 3.4 | 0.04 |
| | | | | | Clutch Size | 0.08 | -31.8 | 15.1 | 1.0 | 4.4 | 0.04 |
| Abdominal Fat[a] | 0.25 | 41.0 | 2.7 | 0.04 | Year | 0.10 | | | 2.0 | 2.6 | 0.09 |
| | | | | | Lay date | 0.00 | -0.5 | 0.2 | 1.0 | 0.2 | 0.67 |
| | | | | | Lay date * Year | 0.15 | | | 2.0 | 4.0 | 0.03 |
| Breast Muscles | 0.50 | 43.0 | 14.3 | < .0001 | Year | 0.45 | | | 2.0 | 17.5 | < .0001 |
| | | | | | Clutch Size | 0.05 | -4.6 | 2.3 | 1.0 | 4.0 | 0.05 |
| Leg[a] | 0.41 | 43.0 | 14.3 | < .0001 | Year | 0.19 | | | 2.0 | 7.1 | 0.002 |
| | | | | | Lay Date | 0.22 | 0.4 | 0.1 | 1.0 | 16.0 | < .001 |

[a] Corrected for structural size, see methods.

**Figure 1**. Graphical representation of the condition-dependent optimization model of clutch size and lay date (modified from Rowe *et al.*, 1994). Letters represent individuals with different initial body condition or arrival dates on breeding grounds (upper case) and illustrates the predicted post-laying condition (lower case). Dashed lines represent the increase in body condition before egg laying; the thick line illustrates the optimal combinations of clutch size and lay dates assuming a trade-off between the costs (decreasing offspring value) and the benefit (increasing condition and hence clutch size) of a delay in lay date; dotted lines connect optimal lay dates and clutch sizes for individuals reaching the optimal curve at different times. Before producing a clutch, individuals must first reach the minimum threshold condition, which should include the energy needed to incubate and rear the eggs.

**Figure 2**. Relationships between clutch size and endogenous reserves of post-laying female Common Eiders from Mitivik Island, East Bay Migratory Bird Sanctuary, Nunavut, Canada. Values were corrected for the effect of other variables, when significant (Table 2). Circles, triangles and squares represent respectively data from 2002, 2003, and 2004. Some points are offset in order to display full sample size.

**Figure 3**. Relationships between lay date (relative to the yearly median) and endogenous reserves of females. Values were corrected for the effect of other variables, when significant (Table 2). Circles, triangles and squares represent respectively data from 2002, 2003, and 2004. Some points are offset in order to display full sample size.

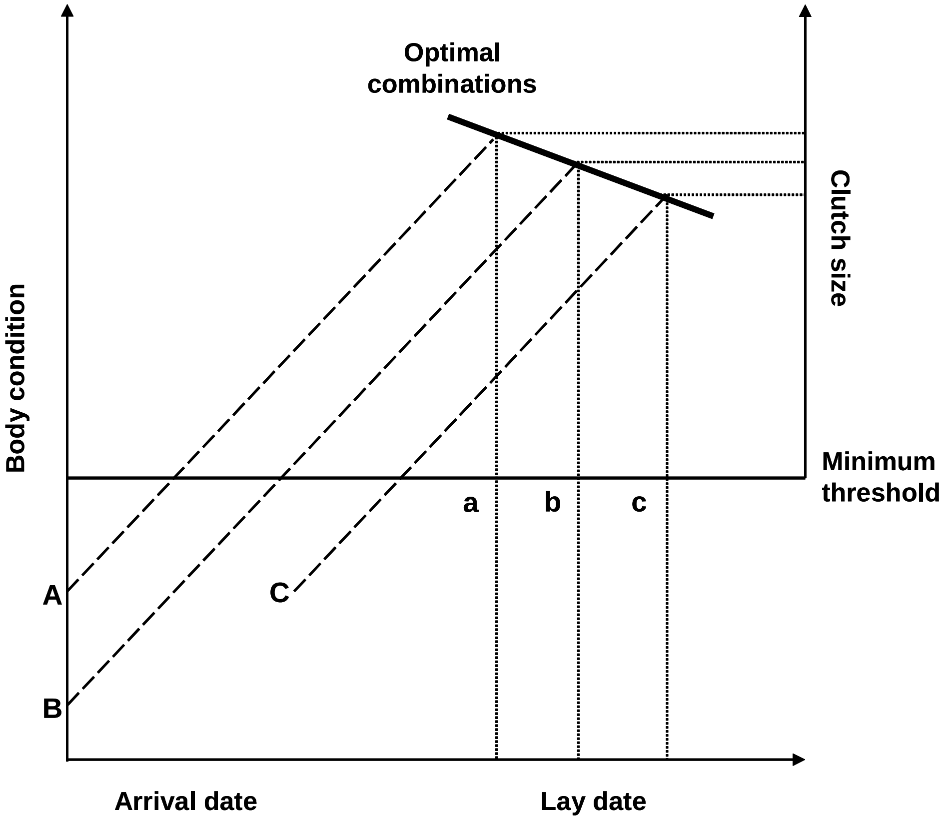
Optimal combinations
Clutch size
Body condition
Minimum threshold
a
b
c
A
C
B
Arrival date
Lay date

**Figure 1.**

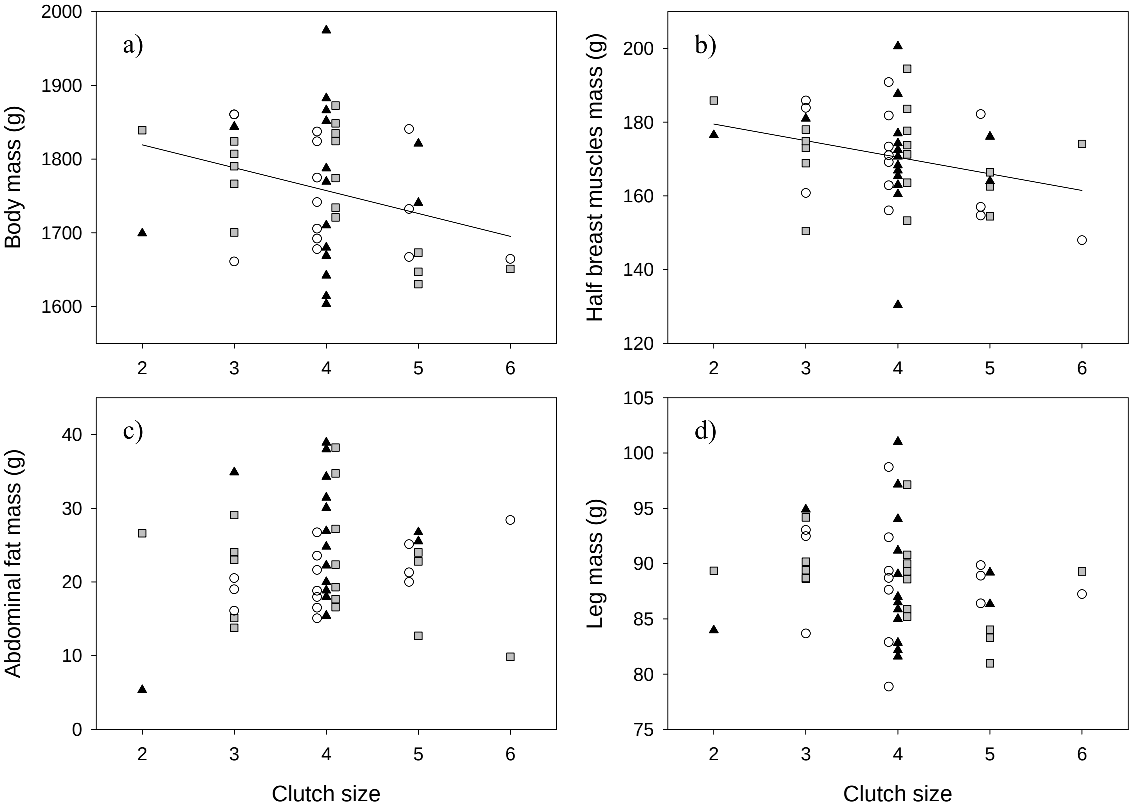
a)
Body mass (g)
2000
1900
1800
1700
1600
b)
Half breast muscles mass (g)
200
180
160
140
120
c)
Abdominal fat mass (g)
40
30
20
10
0
d)
Leg mass (g)
105
100
95
90
85
80
75
2
3
4
5
6
Clutch size

**Figure 2.**

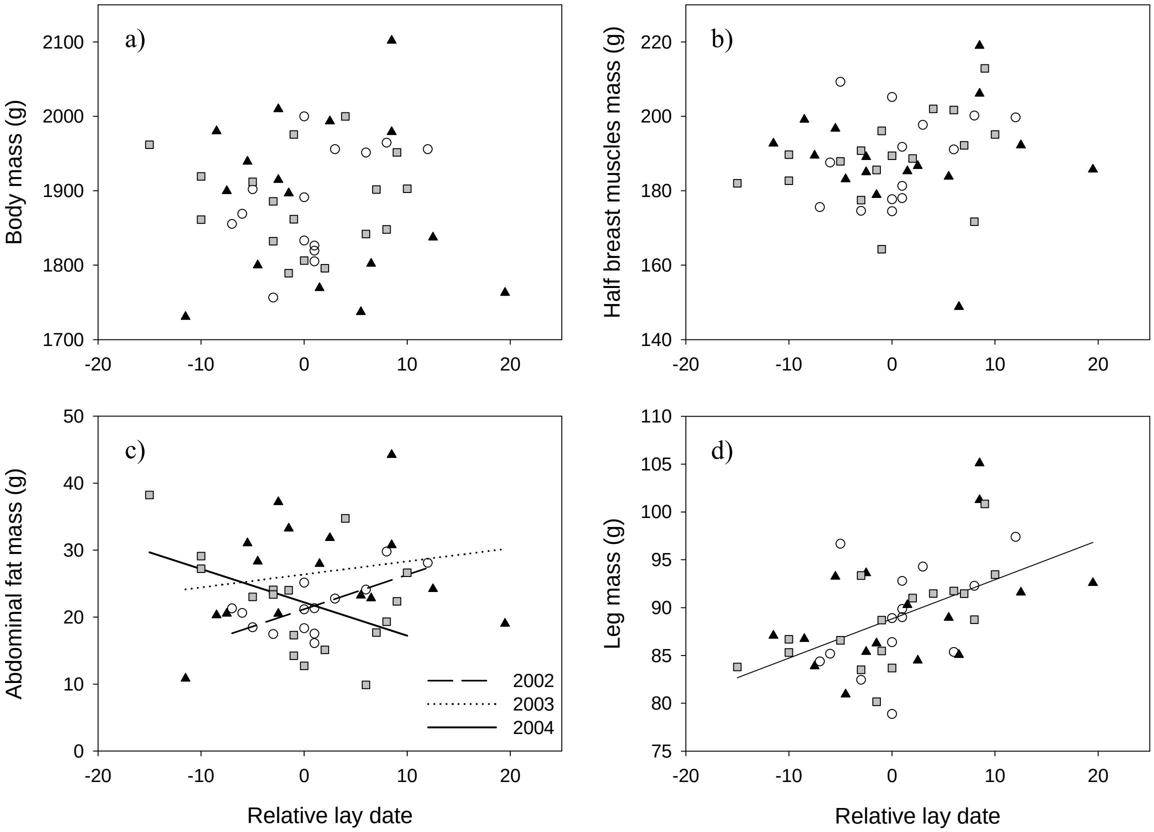
a)
Body mass (g)
2100
2000
1900
1800
1700
-20
-10
0
10
20
b)
Half breast muscles mass (g)
220
200
180
160
140
-20
-10
0
10
20
c)
Abdominal fat mass (g)
50
40
30
20
10
0
-20
-10
0
10
20
2002
2003
2004
Relative lay date
d)
Leg mass (g)
110
105
100
95
90
85
80
75
-20
-10
0
10
20
Relative lay date

**Figure 3.**

# CONCLUSION GÉNÉRALE

## CONTRIBUTIONS

De façon générale, notre étude a permis de comprendre le rôle essentiel mais non exclusif des réserves endogènes dans la reproduction de l'eider à duvet, de même que les différentes stratégies d'allocation des nutriments dans les œufs utilisées par les femelles selon la phénologie de leur reproduction. Les résultats issus de ce travail permettent de mieux comprendre certains mécanismes pouvant influencer l'allocation de nutriments endogènes aux besoins énergétiques d'un reproducteur sur épargne.

Notre étude se distingue par l'utilisation combinée de deux approches méthodologiques différentes pour déterminer la contribution des nutriments endogènes et exogènes dans la formation des œufs. À notre connaissance, la comparaison simultanée des résultats provenant d'analyses isotopiques et du suivi de la dynamique des réserves sur des mêmes individus n'a jamais fait l'objet d'une publication. Nos résultats suggèrent que les femelles utilisent majoritairement des ressources exogènes pour former les tissus protéiques de leurs œufs, et puisent principalement dans leurs réserves de graisses pour les besoins en lipides. De plus, les femelles qui nichent tardivement semblent allouer à leurs œufs une plus grande proportion de nutriments endogènes. Ces résultats constituent une avancée significative dans notre compréhension des stratégies de reproduction chez les oiseaux, puisque l'eider à duvet est considéré, parmi les oiseaux qui volent, comme l'espèce utilisant le plus ses réserves endogènes pour formés ses oeufs. Les résultats de notre étude portent donc à croire que la reproduction sur épargne stricte ne serait pas possible chez les oiseaux qui volent, étant donné les contraintes physiques engendrées par l'accumulation de réserves.

Dans un deuxième temps, notre étude a permis de clarifier les mécanismes qui déterminent le niveau de réserves corporelles disponible aux femelles durant la période d'incubation. Il semblerait que les femelles en début d'incubation n'ajustent pas leur condition corporelle selon les coûts anticipés de l'incubation (qui pourraient augmenter avec la taille de la couvée) ou selon la date de ponte. Leur condition corporelle au début d'incubation serait d'abord influencée par les conditions environnementales rencontrées lors de la période de ponte. Ce résultat pourrait considérablement améliorer la compréhension des facteurs impliqués dans les compromis rencontrés par les reproducteurs sur épargne et des choix optimaux que les individus effectuent afin d'augmenter leur valeur adaptative.

## PERSPECTIVES

La suite logique de notre étude serait probablement de réaliser le même genre d'étude sur des espèces d'oiseaux 1) qui ne volent pas; et 2) qui ne se nourrissent pas durant la ponte. Ces études pourraient permettre de positionner les espèces les unes par rapport aux autres sur le continuum des stratégies de reproduction, et de mieux comprendre les facteurs physiques et environnementaux qui favorisent une stratégie de reproduction sur épargne stricte.

Par ailleurs, les schémas conceptuels englobant les principaux facteurs pouvant influencer les compromis effectués par les individus en reproduction facilitent beaucoup la compréhension et font avancer rapidement les idées. Cependant, nous invitons les chercheurs à inclure les variations environnementales dans ces schémas, car leur rôle est, de toute évidence, primordial dans les choix effectués par les individus.

Finalement, dans un contexte de changements globaux, l'abondance et la nature des organismes marins présents à East Bay pourraient varier au cours des prochaines années. Ce sera nécessairement un facteur à inclure lors de prochaines études portant sur le succès reproductif des eiders à ce site, étant donné la grande importance des nutriments exogènes dans la formation des œufs des eiders. Idéalement, un suivi de l'abondance des principales espèces proies des eiders devrait être effectué au site d'étude, en parallèle au suivi déjà effectué sur la reproduction des eiders. Avec du temps, de la persévérance et certains moyens, même les plus grandes difficultés techniques associées aux études en milieux éloignées peuvent être contrées! À qui la chance?