UNIVERSITÉ DU QUÉBEC À RIMOUSKI

ASPECTS MORPHOLOGIQUES ET PHYSIOLOGIQUES DES CAPACITÉS D'ENVOL CHEZ L'EIDER À DUVET (*SOMATERIA MOLLISSIMA*) EN PÉRIODE PRÉ-PONTE

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PAR

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AVANT-PROPOS

Le présent mémoire a été soumis comme exigence partielle pour l'obtention du diplôme de maîtrise du programme de Gestion de la faune et de ses habitats à l'Université du Québec à Rimouski. Il comprend une introduction générale, un seul chapitre central et une conclusion générale. Il traite du handicap d'envol des femelles eiders à duvet en période de pré-ponte examiné sous les aspects morphologiques, musculaires et métaboliques. Le chapitre central est rédigé en anglais sous la forme d'un article scientifique et a été formaté en vue de sa soumission au périodique *Physiological and Biochemical Zoology* publié par les Presses de l'Université de Chicago. Un résumé en français de cet article est présenté au début du chapitre. Les résultats préliminaires de l'étude concernée par ce mémoire ont été présentés au 71^{e} Congrès de l'Association Francophone pour le Savoir (ACFAS) tenu à Rimouski en mai 2003.

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RÉSUMÉ

Lors de la nidification, les femelles eiders à duvet assument seules l'incubation des œufs et jeûnent durant toute sa durée qui est d'environ 26 jours dans les colonies de l'estuaire du Saint-Laurent. Elles doivent par conséquent accumuler d'importantes réserves adipeuses au cours de la période de pré-ponte pour faire face à ce jeûne prolongé. La masse ajoutée de ces réserves impose aux femelles un grave handicap locomoteur. En effet, les femelles affichent, au cours de cette période, une nette propension à la plongée de fuite lors d'un dérangement tandis que les mâles s'envolent prestement. Des femelles sont même fréquemment vues échouer une tentative d'envol en absence de vent. L'objectif de cette étude était d'examiner comment le système locomoteur des femelles répond à leur gain de masse corporelle. Nous avons à cette fin formulé l'hypothèse qu'au cours de la période de pré-ponte, les femelles eiders à duvet adoptent des stratégies de compensation physiologique afin de retarder et de réduire leur handicap. Nous avons abordé cette étude à trois niveaux organisationnels : i) par des mesures morphométriques de l'appareil locomoteur (ailes et pattes); ii) par la pesée de la musculature locomotrice de vol et de nage et iii) par la mesure de l'activité des enzymes pyruvate kinase, lactate déshydrogénase et citrate synthase d'un muscle de vol (*pectoralis*), d'un muscle de nage (*iliotibialis*) et d'un muscle structural (*complexus*). Les variables ont été comparées entre les sexes et entre les femelles réparties en deux classes de charge alaire. Les résultats obtenus montrent que, comparativement aux mâles, les femelles possèdent des ailes surdimensionnées, une musculature de vol hypertrophiée ainsi qu'une protection des voies métaboliques de leur *pectoralis*. Toutefois, elles semblent atteindre les limites de leur flexibilité métabolique et nos résultats suggèrent pour la première fois l'existence d'un seuil minimal d'activité de la LDH pondérée à la masse corporelle pour l'envol. Les femelles de charge alaire élevée (masse corporelle $\times$ superficie alaire^{-1}) affichent davantage de compensation musculaire que les femelles de faible charge alaire. En contrepartie, comparativement aux mâles, les femelles ne présentent pas de prédispositions à la nage hormis des tarses proportionnellement plus longs et une musculature pédestre légèrement surdéveloppée. Nos résultats nous permettent de conclure que le principal handicap locomoteur des femelles se situe dans leur puissance métabolique insuffisante et dans leur superficie alaire restreinte.

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INTRODUCTION GÉNÉRALE

Problématique et objectif

L'eider à duvet (*Somateria mollissima*) est un canard plongeur marin à répartition circumpolaire. C'est le plus gros canard de l'hémisphère nord (Bellrose 1980) et il possède une charge alaire (masse corporelle × superficie alaire^{-1}) parmi les plus élevées qui soient chez les oiseaux aptes au vol (Rayner 1988; Guillemette 1994). Par conséquent, son envol est laborieux et son vo est rapide et direct. Cette espèce est probablement la moins terrestre de tous les ansériformes et vit dans les eaux froides où elle s'alimente d'épibenthos, principalement des moules bleues (*Mytilus edulis*) (Bellrose 1980; Guillemette et al. 1992). L'espèce affiche un comportement d'incubation rare chez les oiseaux : les femelles assument seules l'incubation des œufs et jeûnent durant toute sa durée, soit environ 26 jours dans l'estuaire du Saint-Laurent. Elles peuvent alors perdre jusqu'à 35% de leur masse corporelle initiale (Bolduc et Guillemette 2003; Guillemette et Ouellet, sous presses, a). Elles doivent conséquemment accumuler d'importantes réserves adipeuses au cours des semaines précédant la ponte et se trouvent obèses au moment de rejoindre leur colonie pour pondre leurs œufs (Parker et Holm 1990; Bolduc et Guillemette 2003). Cette espèce présente un dimorphisme sexuel prononcé dans ses aptitudes à l'envol au cours de la période de pré-ponte (de l'arrivée migratoire printanière à la ponte du premier oeuf) : alors que les mâles s'envolent prestement à l'approche d'un agent perturbateur, les femelles affichent une nette propension à la plongée de fuite (Guillemette et Ouellet, observations personnelles). Des femelles qui échouent leur tentative de décollage sont même

fréquemment observées à cette période (Guillemette et Ouellet, observations personnelles). Ce dimorphisme apparent suggère que le système locomoteur des femelles est incapable de produire suffisamment de portance pour assurer leur décollage.

L'objectif de la présente étude est d'examiner comment le système locomoteur des femelles eiders à duvet répond à leur gain de masse corporelle au cours de la période de pré-ponte. Pour atteindre cet objectif, il importe de comprendre comment est constitué le système locomoteur des oiseaux et de porter un regard global sur les mécanismes et phénomènes qui interagissent pour permettre le vol.

L'appareil de vol aviaire

En contrepartie des bénéfices qu'il procure, le vol est un mode de locomotion dispendieux en termes énergétiques (Schmidt-Nielsen 1972, Butler 1991). En effet, étant soumis aux fortes contraintes gravitationnelles, son coût énergétique est directement lié au poids de l'oiseau (i.e. masse corporelle × accélération gravitationnelle) (Pennycuick 1975). Théoriquement, un oiseau doit, pour s'envoler et demeurer en vol, générer avec ses ailes une force ascensionnelle supérieure à celle de la gravité terrestre : la portance. La puissance mécanique que la musculature de vol doit transmettre aux ailes pour produire cette portance est déterminée par le poids de l'oiseau, par sa géométrie alaire et par sa vitesse incidente (Pennycuick 1975). À son tour, cette puissance mécanique requise détermine l'intensité de la puissance métabolique qui doit être générée dans les myofibrilles pour soutenir le travail des contractions musculaires.

L'appareil de vol des oiseaux est constitué de membres antérieurs reptiliens modifiés en structures aérodynamiques et d'une musculature squelettique imposante (Hartman 1961; Feduccia 1999). Ce système locomoteur a été raffiné jusqu'à un haut niveau d'efficacité au cours de la longue histoire évolutive de la classe *Aves*. Cette classe regroupe environ 10 000 espèces qui se répartissent en une vaste diversité de niches écologiques sur tous les continents et jusqu'aux plus isolées des îles océaniques (Storer 1971). Puisque les oiseaux utilisent leurs ailes dans des activités vitales comme la quête alimentaire ou la fuite de prédateurs, les pressions sélectives sur la morphologie alaire sont très fortes (Norberg 1990). Conséquemment, il existe une géométrie alaire appropriée aux divers patrons de vol existants (Rayner 1988; Norberg 1990). Par exemple, les ailes elliptiques des passereaux forestiers facilitent les manœuvres parmi la végétation dense tandis que les ailes longues et étroites des oiseaux de mer pélagiques minimisent la résistance dans l'air et leur permettent de voler quotidiennement sur des distances considérables à faible coût énergétique (Norberg 1990).

Toutefois, il ne suffit pas d'avoir des ailes pour voler, encore faut-il que l'oiseau possède la musculature apte à leur transmettre la puissance mécanique nécessaire pour produire suffisamment de portance et de propulsion. La musculature locomotrice responsable du vol chez les oiseaux est répartie comme suit : i) le muscle *pectoralis* provoque le mouvement descendant de l'aile, il est ancré sur la face ventrale du sternum, il est généralement de taille importante et c'est le muscle le plus sollicité au cours du décollage et du vol battu; ii) le supracoracoïde participe au mouvement ascendant de l'aile, il est ancré sur le sternum sous le *pectoralis*; iii) la musculature marginale, comprenant

plusieurs muscles de petite taille ancrés sur les différents os de la ceinture pectorale, participe à la motricité fine de l'aile et des rémiges (Hartman 1961; Raikow 1985).

Les voies anaérobie et oxydative du métabolisme énergétique

Les divers patrons d'envol utilisés par les oiseaux sollicitent différemment la musculature de vol. Par exemple les canards barboteurs (*Anas sp.*), la gélinotte huppée (*Bonasa umbellus*) et le faisan à collier (*Phasianus colchicus*) effectuent un envol rapide sans vitesse incidente qui exige des pectoraux un effort intense mais de courte durée. À l'opposé, les canards plongeurs, les oiseaux de mer pélagiques et les grands oiseaux de proie effectuent une course d'envol ou se lancent d'un perchoir pour gagner la vélocité incidente nécessaire à leur décollage. Ceci suggère que la musculature de vol des oiseaux possède des capacités variables à effectuer un effort intense. Ces capacités sont directement tributaires de la composition des muscles en types de fibres musculaires (George et Berger 1966; Rosser et George 1986). Les muscles locomoteurs aviaires sont composés principalement de deux types de fibres : les glycolytiques et les glycolytiques-oxydatives (George et Berger 1966). Les fibres glycolytiques permettent un effort de type *sprint*, soit très intense mais de courte durée (Hochachka et Somero 2002). Dans la voie de la glycolyse, le glucose est transformé en pyruvate à l'issue d'une chaîne de réactions enzymatiques fortement exergonique et l'énergie biochimique libérée est fixée sous forme d'adénosine triphosphate (ATP). L'ATP est un métabolite hautement énergétique nécessaire aux contractions des fibres musculaires. En conditions anaérobies, comme dans les fibres glycolytiques ou toute autre fibre au cours d'un effort intense, le pyruvate est

transformé en lactate qui s'accumule dans le flux sanguin sous forme d'acide lactique. Ce dernier est toxique à forte concentration et son accumulation provoque la fatigue musculaire. Cette voie métabolique fournit instantanément une quantité importante d'énergie mais impose à l'organisme une dette d'oxygène (Hochachka et Somero 2002). Les fibres glycolytiques-oxydatives permettent pour leur part un effort aérobie qui peut être soutenu sans contracter de dette d'oxygène donc sans générer d'acide lactique. La voie oxydative est la voie de l'effort marathonien (Hochachka et Somero 2002). Elle peut être alimentée par les voies du catabolisme des protéines, des acides gras et du glucose. Dans ce dernier cas, le pyruvate issu de la glycolyse est transformé en acétyl-CoA qui intègre le cycle de Krebs. Ce dernier constitue un véritable moteur métabolique qui fournit à la chaîne respiratoire les électrons nécessaires à la production d'ATP. Cette voie produit davantage d'ATP que la glycolyse mais elle est limitée par la vitesse de l'approvisionnement en oxygène et autres substrats par la circulation sanguine (Hochachka et Somero 2002).

La composition en types de fibres dans le *pectoralis* varie considérablement parmi les espèces aviaires selon leurs patrons de vol spécifiques (Rosser et George 1986; Tobalske 1996). De façon générale, on observe une nette dominance des fibres glycolytiques-oxydatives chez les espèces de petite taille et une tendance vers l'hétérogénéité chez les espèces plus grandes (Rosser et George 1986). Ceci est attribuable au fait que les fibres glycolytiques-oxydatives à elles seules génèrent suffisamment de puissance pour permettre le décollage des oiseaux de petite taille. Par contre, chez les espèces de grande taille pour lesquelles l'envol est plus coûteux, la puissance fournie par les seules fibres glycolytiques-oxydatives ne suffit pas et le décollage n'est possible qu'en sollicitant temporairement des

fibres glycolytiques (Rosser et George 1986). Cette alternance dans le recrutement des fibres musculaires est connue sous le nom anglais de *shift-gear hypothesis* (Goldspink 1977).

Les handicaps de vol, la flexibilité et la compensation

Les bénéfices que le vol apporte aux oiseaux sont considérables : 1) la migration entre les sites de reproduction et les aires d'hivernage les plus propices, 2) la dispersion des individus au-delà de barrières géographiques et sur des distances autrement infranchissables, 3) l'accès à des sources de nourriture qui ne peuvent être atteintes ou repérées que par voie aérienne et 4) une stratégie efficace de fuite des prédateurs (Pennycuick 1987; Rayner 1988; Hildebrand 1995).

Cependant, de nombreux cas plus ou moins graves et prolongés de difficultés d'envol ou d'inaptitude complète au vol ont déjà été documentés chez les oiseaux. Par exemple, la transition vers l'inaptitude au vol complète et permanente est un phénomène assez rare mais qui s'est tout de même déroulé de façon indépendante chez au moins 13 ordres taxonomiques aviaires depuis le Crétacé et dans toutes les régions zoogéographiques du globe (Raikow 1985; Feduccia 1999). L'inaptitude au vol permanente prouve que les avantages du vol ne sont pas universellement essentiels et, qu'en certaines circonstances, des espèces d'oiseaux réussissent à se perpétuer après avoir renoncé au vol (Livezey et Humphrey 1986; Livezey 1990, 1992). En plus du cas de l'eider à duvet en période de pré-ponte, un autre exemple d'inaptitude au vol temporaire s'observe annuellement chez les ansériformes en période de mue, lorsque les individus perdent simultanément toutes leurs

rémiges (Gates et al. 1993; Taylor 1995; Brown et Saunders 1998). Des cas moins extrêmes de simples difficultés d'envol sont aussi documentés chez certaines espèces en période de nidification ou pré-migratoire (Jehl 1997; Lind et al. 1999; Kullberg et al. 2002).

Ces difficultés d'envol sont généralement attribuables au fait que la musculature de vol est incapable de fournir la puissance mécanique ou métabolique nécessaire pour satisfaire l'importante demande énergétique imposée par une superficie alaire restreinte, une masse corporelle trop élevée ou un effet combiné de ces deux causes (Jehl 1997; Brown et Saunders 1998; Guillemette et Ouellet sous presses, b). Dans ces conditions, deux types de réponses sont rapportés dans la littérature. Dans un premier cas, les oiseaux subissent des phénomènes de compensation morphologique et physiologique propres à augmenter la portance. Ces phénomènes se résument en une morphologie alaire surdimensionnée, une hypertrophie musculaire, une amélioration des capacités anaérobies des muscles locomoteurs et un allègement des organes qui ne sont pas directement impliqués dans la locomotion (Fry et al. 1972; Marsh et Storer 1981; Saunder et Klemm 1994; Møller et al. 1995; Piersma et Gill 1998). Cette condition s'applique uniquement lorsque la flexibilité et la plasticité phénotypiques de la population le permettent et lorsque celle-ci n'est pas limitée en ressources. Alternativement, les oiseaux peuvent renoncer au vol et économiser ainsi d'importants investissements ontogéniques et énergétiques reliés à l'entretien de l'imposante musculature de vol et de l'intense régime métabolique (McNab 1994). Parallèlement, ces espèces développent habituellement des aptitudes spécifiques dans un mode de locomotion alternatif, comme la nage ou la course (Livezey et Humphrey 1983; Cubo et Arthur 2001). À partir de ces observations, nous avons formulé l'hypothèse qu'au

cours de la période de pré-ponte, les femelles eiders à duvet adoptent des stratégies de compensation physiologique afin de retarder et de réduire leur handicap.

Contribution de l'étude

L'originalité de la présente étude est de s'intéresser aux capacités d'envol des oiseaux en tenant compte de plusieurs niveaux organisationnels. Cette étude serait vraisemblablement la première à examiner les aptitudes locomotrices simultanément au niveau du véhicule (la morphologie alaire), du moteur (la musculature) et de la combustion du moteur (le métabolisme énergétique). Cette façon d'aborder ce sujet est la seule qui soit propre à fournir davantage que des réponses partielles et pourtant, jamais ces trois niveaux d'organisation n'ont été examinés simultanément (Ricklefs et Wikelski 2002).

À ce jour, la plupart des études traitant des effets de l'alourdissement sur les performances d'envol partagent les caractéristiques communes d'utiliser principalement des passereaux et de supposer que les espèces deviennent vulnérables face à la prédation (Chandler et Mulvihill 1992; Lind et al. 1999; Veasey et al. 2000, 2001; Kullberg et al. 2000, 2002; cependant voir Dierschke 2003). Cependant, en respect avec le concept de marge énergétique décrit par Pennycuick (1975), les passereaux ne constituent pas le groupe taxonomique le plus adéquat pour ce type de travaux. En effet, les oiseaux de petite taille sont pour la plupart des champions du décollage car ils subissent des contraintes gravitationnelles moins fortes que ceux de grande taille, donc la puissance pondérée qui leur est nécessaire à l'envol est plus faible. À preuve, le muscle *pectoralis* des passereaux est principalement constitué de fibres rouges oxydatives (George et Berger 1966; Rosser et

George 1986). Il semble donc que la marge énergétique des petits oiseaux, même en mode aérobie, soit suffisante pour permettre des manœuvres d'accélération et de freinage ainsi que des ascensions abruptes. À l'inverse, la musculature de vol des oiseaux de grande taille, comme l'eider à duvet, suffit tout juste à contrebalancer la gravité terrestre et n'a que peu de marge énergétique (et ultimement aucune). Par exemple, l'alourdissement causé par la simple ingestion de proies peut provoquer une perte temporaire de l'aptitude au vol chez cette espèce (Guillemette 1994). Il est probablement plus facile de détecter l'effet d'un alourdissement chez des oiseaux de grande taille que chez des passereaux.

Plusieurs études ont spéculé sur les aptitudes à l'envol des oiseaux à partir de mesures de la seule masse musculaire. Or, une fluctuation de la masse musculaire n'a pas le même effet sur la puissance nette selon que ce sont des fibres oxydatives ou glycolytiques qui sont impliquées.

De surcroît, un ajustement du régime métabolique musculaire peut affecter la puissance du muscle sans qu'aucun effet ne soit mesurable dans sa masse (Saunders et Klemm 1994). L'eider à duvet offre un modèle très approprié à l'étude des capacités d'envol des oiseaux parce que les femelles subissent d'importantes fluctuations de masse corporelle au cours d'un cycle annuel (Guillemette 1994; Criscuolo et al. 2002; Bolduc et Guillemette 2003). À l'opposé des passereaux, elles accusent en pré-ponte davantage qu'une perte de vélocité au décollage, elles font face à une incapacité d'envol (Guillemette et Ouellet, obs. personnelles). De plus, ce phénomène étant observé chez un seul sexe, ceci permet des

comparaisons intraspécifiques qui offrent l'avantage d'éviter les variables confondantes fréquentes dans les études interspécifiques.

Ces difficultés d'envol font de la pré-ponte une période critique du cycle annuel de l'eider à duvet qui demeure mal connue. Il est pertinent de documenter un phénomène dont les implications présumées sur la survie et le succès reproducteur de l'espèce sont importantes. Afin de répondre à notre objectif, un échantillon d'eiders à duvet des deux sexes a été récolté en avril et mai 2001 et 2002 près des îles du Bic et Saint-Barnabé. La morphologie alaire et pédestre des spécimens a été mesurée (superficie alaire et palmée, longueur des ailes et des tarses, envergure), la musculature locomotrice (de vol et de nage) a été pesée et l'activité d'enzymes-clés des voies oxydative et glycolytique anaérobie du métabolisme énergétique a été mesurée.

CHAPITRE 1

MORPHOLOGICAL AND PHYSIOLOGICAL ASPECTS OF TAKEOFF APTITUDES OF FEMALE COMMON EIDERS (*SOMATERIA MOLLISSIMA*) DURING THE PRE-LAYING PERIOD

RÉSUMÉ DU CHAPITRE

Les femelles eiders à duvet subissent un important gain de masse corporelle durant la période de pré-ponte. Cette masse ajoutée leur impose un grave handicap d'envol. L'objectif de la présente étude est d'examiner comment le système locomoteur des femelles répond à ce gain de masse et nous avons à cette fin formulé l'hypothèse qu'au cours de la période de pré-ponte, les femelles eiders à duvet adoptent des stratégies de compensation physiologique afin de retarder et de réduire leur handicap. Nous avons abordé la question à trois niveaux organisationnels: i) par la mesure de la morphologie locomotrice, ii) par la mesure de la masse des musculatures de vol et de nage et iii) par la mesure de l'activité de la pyruvate kinase, de la lactate déshydrogénase et de la citrate synthase dans un muscle de vol (*pectoralis*), un muscle de nage (*iliotibialis*) et un muscle structural (*complexus*). Toutes les variables ont été comparées entre les sexes ainsi qu'entre les femelles de charge alaire faible et élevée. Nos résultats supportent notre première hypothèse de travail. Comparativement aux mâles, les femelles affichent une superficie alaire surdimensionnée, une musculature de vol hypertrophiée et une protection des voies métaboliques de leur *pectoralis*. Les femelles semblent toutefois atteindre la limite de leur flexibilité métabolique et nos résultats suggèrent pour la première fois l'existence d'un seuil minimal de capacité glycolytique (reflétée par l'activité de la LDH) pour l'envol. Les femelles de charge alaire élevée affichent davantage de compensation musculaire que les femelles de faible charge alaire. En contrepartie, comparativement aux mâles, les femelles ne présentent pas de meilleures prédispositions à la nage hormis des tarses proportionnellement plus

longs et une musculature pédestre légèrement surdéveloppée. Nos résultats nous permettent de conclure que le principal handicap locomoteur des femelles se situe dans leur puissance locomotrice en partie limitée par la puissance métabolique du muscle et dans leur superficie alaire restreinte.

ABSTRACT

During the pre-laying period, female common eiders experience an important increase in body mass resulting in a dramatic sex-specific takeoff impairment. We investigated how their locomotor apparatus respond to this mass increase and tested the hypothesis that pre-laying female common eiders compensate physiologically in order to diminish or retard their takeoff impairment. We addressed the question at three organizational levels: i) measurement of locomotor morphology, ii) weighing locomotor musculature, iii) measurement of the activity of pyruvate kinase, lactate dehydrogenase and citrate synthase in two locomotor muscles and one structural muscle. Our results support our hypothesis. Compared to males, females show an enlarged wing area, an hypertrophied flight musculature and a protection of their energy metabolism pathway in *pectoralis* muscle. The *pectoralis* muscle of females of higher wing-loading further compensates for their weigh gain. However, they seem to reach their upper limit to metabolic power and our results suggest for the first time the existence of a glycolytic capacity threshold (reflected by body mass-specific LDH activity) to takeoff aptitudes in large birds. On the other hand, females do not show better aptitudes at swimming than males aside from longer tarsi and enlarged leg musculature.

INTRODUCTION

Most studies addressing avian flight aptitudes have identified excessive wing-loading and insufficient mass of flight muscles as main causes of recurring events of takeoff impairment. Excessive wing-loading (body mass per unit wing area) results from a reduced wing area as during wing molt of aquatic birds or from an increased body mass associated with improved body condition in pre-laying or pre-migratory period. Theoretically, gains in wing-loading increase the power required to fly (Pennycuick 1975; Marden 1994) as well as the stalling speed (Norberg 1995). In empirical studies, detrimental effects of high wing-loading on takeoff aptitudes were mostly observed through reduced angle of ascent (Marden 1987; Witter et al. 1994, Lee et al. 1996, Lind et al. 1999) and reduced speed of ascent and acceleration (Kullberg et al. 2000; Swaddle et al. 1999; but see Veasey et al. 1998) and extreme cases where a rise in wing-loading led to temporary flightlessness have also been reported in free-ranging species (Guillemette 1994; Jehl 1997; Guillemette and Ouellet in press, b). Insufficient relative mass of flight muscles (flight muscle mass per unit total body mass) can be associated with simultaneous gains in body mass and/or muscle atrophy (Gaunt et al. 1990; Veasey et al. 2000). Atrophy of flight muscles arises, for example, through disuse and translocation of proteins (Parker and Holm 1990; Houston et al. 1995). Much like excessive wing-loading, relative flight muscle mass may reach critical levels resulting in temporary flightlessness (Gaunt et al. 1990). Using an experimental design, Marden (1987) showed that the relative flight muscle ratio (flight muscle mass per unit body mass, FMR) must exceed the critical value of 0.16 for a bird to overcome gravity in still air by the sole action of its wings. In a study of common eider takeoff ability during

the pre-laying period, Guillemette and Ouellet (in press, b) observed that relative flight muscle mass of females decreases with increases in body mass but, even in flightless individuals, never reached the critical FMR threshold and suspected that wing-loading and FMR interact in their effects. Brown and Saunders (1998) came to a similar conclusion while studying the locomotor capacities of molting blue-winged teal.

The mechanical output transmitted to the wings by the muscles is directly related to the amount of metabolic power generated by the myofibrils (with a muscle efficiency factor). Therefore, if its metabolic machinery does not meet the needed output, a bird is unlikely to achieve lift, would it have the optimal wing morphology and an adequate FMR. The avian flight musculature is composed of three kinds of twitch fibers, namely the white fast glycolytic fibers (FG) that power a short burst effort and the red and intermediate fast oxidative-glycolytic fibers (FOG) that enable a marathonian-type of effort (Rosser and George 1986). The glycolytic pathway produces adenosine triphosphate (ATP) from glucose through catabolic processes. In anaerobic conditions, the end-product of glycolysis, pyruvate, is transformed into lactate and the latter accumulates in its reduced form causing muscular fatigue (Hochachka and Somero 2002). This pathway generates a readily available amount of energy but cannot be sustained in a prolonged period. In the oxidative pathway, pyruvate is further transformed and integrates the citric acid cycle which provides the respiratory chain with electrons (Hochachka and Somero 2002). This pathway generates less ATP, thus less power, than glycolysis per time and mass unit since it is restrained by the rate of oxygen and metabolite supplies through blood stream. Takeoff in medium and large-sized birds is known to be anaerobically powered and the relative importance of FG

fibers in *pectoralis*, which are rare in small species, increases interspecifically with body mass (Rosser and George 1986). Changes in muscle mass will have different effects on net power output depending on wether FG or FOG fibers are involved.

Common Eider (*Somateria mollissima*) (hereafter, eider) is an interesting model for the study of takeoff aptitudes. This species is the largest duck of the northern hemisphere (Goudie et al. 2000) and has among the highest wing-loading found in volant birds (Rayner 1988; Guillemette 1994). It has therefore a strong and steady flight and a labored takeoff typical of the sea ducks. In addition, female eiders fast during egg incubation (ca. 26 days) and can lose up to 35% of their pre-laying body mass (Bolduc and Guillemette 2003, Guillemette and Ouellet, in press, a). They must therefore build up large body reserves through hyperphagia (Guillemette 2001), and are obese at the onset of laying (Parker and Holm 1990; Bolduc and Guillemette 2003). During the pre-laying period (spring arrival to laying of the first egg), the species shows a clear sexual dimorphism in takeoff aptitudes. When disturbed at sea, males take off promptly but females are frequently observed failing attempts to do so in still air and show a neat propensity toward escape-dives (Guillemette and Ouellet, pers. obs.). This apparent sex-specific inability or reluctance to take wing suggests that the energetic demand at takeoff exceeds the mechanical or metabolic power that heavy females can generate. This breeding strategy is therefore conflicting with flight requirements since the added weight of the endogenous reserves required to lay eggs and survive through the incubation fast brings the cost of flight to excessive levels.

We hypothesized that female eiders during the pre-laying period respond to their takeoff impairment by diminishing or retarding their impairment through physiological compensation. Expected outcomes of this are an enlarged flight musculature as frequently observed in individuals improving their body condition (Fry et al. 1972; Marsh and Storer 1981; Marsh 1984; Driedzic et al. 1993) and maintained or improved metabolic power in *pectoralis* muscle as occurs upon seasonal changes in frequency and duration of flight (Lundgren and Kiessling 1985; Saunders and Klemm 1994). In addition they could minimize their overweight by reducing the size of organs not directly involved in flight, such as digestive tract (Piersma and Gill 1998). Otherwise, they could temporarily abdicate flight as they do annually during wing molt. In this case, females could present unchanged or deteriorated features in flight apparatus but enhanced aptitudes in an alternate type of locomotion such as surface-swimming and diving (Cubo and Arthur 2001; Livezey 1992, 1995a, Saunders and Klemm 1994, Brown and Saunders 1998).

In most studies addressing reduced avian takeoff aptitudes, it is assumed that flight impairment is associated with increases in the probability of predation and a decrease in survival (Guillemette and Ouellet, in press, a). Although tests for this assumption would be welcome in most studies, it is noteworthy difficult to do such tests. In almost every cases, the presumed increased vulnerability is inferred from passerines studies where individuals show reduced takeoff performances (regardless of possible behavioral compensatory strategies) (Chandler and Mulvihill 1992; Lind et al. 1999; Veasey et al. 2000, 2001; Kullberg et al. 2000, 2002; but see Dierschke 2003). However, these reduced takeoff performances presumed severe enough to put the individuals at higher risk are reportedly

not as bad as the complete lack of flight ability seen in female eiders (Guillemette and Ouellet, pers. obs.). If such costs do exist in passerines, it is likely to be considerable in female eiders who are known to fall victims of predators competent in securing prey at or under the water surface such as seals and eagles (Moore 2001, Watson et al. 1992, Ouellet and Guillemette, pers. obs.).

Our goal was to investigate whether pre-laying female eiders experience physiological compensation to cope with their seasonal weight gain. We conducted our investigation at three organizational levels, namely the locomotor morphology (wings and legs), the locomotor musculature (flight and swim muscles) and the energy metabolism in locomotor muscles (glycolytic and oxidative pathways).

MATERIAL AND METHODS

Specimen collection

Twenty three female and 38 male eiders (*S. mollissima dresseri*) were collected under license (SC-1536) in April and May 2001 and 2002 in the St. Lawrence river estuary around Île du Bic (48°24'N, 68°52'W) and Île Saint-Barnabé (48°28'N, 68°34'W), Quebec, Canada. Immediately after collection the specimens were numbered. Within one hour of collection, the anterior half of one *pectoralis*, one *iliotibialis* and one *complexus* muscles were removed, labeled and stored separately in an ice bath kept at –20°C with the addition of sodium salt. *Pectoralis* and *iliotibialis* are locomotor muscles and were chosen for their action in flight and swimming, respectively. *Complexus* is a postural muscle attached to cervical vertebrae and we assume its action not being involved in locomotion. This muscle was therefore chosen as a control. Back in the laboratory, these tissues were stored at –80°C until enzyme assays whereas the carcasses were frozen at –20°C until dissection.

Specimen dissection

Throughout the process of dissection, we took care to minimize water losses from the carcasses through evaporation. Before dissection, the carcasses were thawed wrapped in plastic bags for ca. 18-20 hours and weighed. Total body mass was reconstituted by adding the mass of muscles dissected in the field and the amount of blood and water leaked out in the bags. All body masses reported in this study are corrected by subtracting the mass of the gut content since variable amount of food in the gut would introduce noise in the analysis.

Of course, the load of the gut content is a part of the total weight the bird must overcome to be airborne, but it fluctuates over a daily basis whereas the physiological adjustments sought herein result from processes acting at a longer time scale.

The locomotor musculature from one side of the specimens was weighed: the intact *pectoralis* muscle, one *supracoracoideus* and the wing musculature attached on the pectoral girdle, humerus, radius and ulna (following Hartman 1961). The intact leg musculature attached on the pelvic girdle including the femur and the tibiotarsus was also removed and weighed. The mass of the muscles was doubled assuming bilateral symmetry. The mass of the heart was recorded. Flight muscle ratio (FMR) was obtained by dividing the mass of total flight musculature by body mass. The digestive tract was cut off near the larynx and at the cloaca. Esophagus (including proventriculus), gizzard and intestine (excluding pancreas) were freed of fat and connective tissue and weighed separately. They were weighed empty but the mass of their content was recorded. Specimen dissection was performed by JFO or by a single assistant under the direct supervision of JFO.

Locomotor morphology and Flight capability

Wing span was measured as a straight line between the tips of the 10^{th} remiges on the specimens lying ventral side down with fully extended wings. Then for each specimen, one intact wing (i.e. without broken bones, neither lacking remiges) was removed from the body at the humero-coracoid joint. The wing area was determined by pinning the wing underside up on a sheet of paper and outlining the supporting area. The outline was then run with a digital planimeter. Wing length was also measured on the outline from the tip of

the 10^{th} remige to the mark on the leading edge. The measurements of area and length do not include the area between the wings since, as Marden (1987) correctly pointed out, only the wings produce lift at takeoff. We used the doubled area of one wing as a measure of total wing area. Ouellet and Guillemette (unpublished data) showed that the apparent asymmetry between the wings of eiders falls within the measurement error of the method. Wing-loading was determined as the ratio of body mass to wing area ($g \cdot cm^{-2}$) and aspect ratio as the ratio of squared wing length to wing area. Paddle area was also determined with a digital planimeter on the contour line of the fully extended webbing. As for wing area, we used doubled area of a single foot. The length of one tarsometatarsus (hereafter, tarsus length) was measured with a digital caliper.

Body size and Scaling

Eiders are sexually dimorphic in body size (see results). Quantitative comparison of organs and structures between sexes thus requires factoring out the effect of the structural size of the specimens. This is made possible in two ways: 1) through the analysis of covariance (ANCOVA) with a body size indicator as a concomitant variable (Blem 1984) and 2) by dividing every measurement by a body size indicator (Rising and Somers 1989). Since ANCOVA is incompatible with model II regressions (used with two random variables, Ricker 1973), the second way was chosen in this study. Hence, the following skeletal variables were measured : 1) body length with specimen lying ventral side down, 2) coracoid bone length, 3) sternum length and 4) keel arc length. Body and keel arc lengths were measured with a measuring tape whereas coracoid and sternum lengths were

measured with a digital caliper with the bones removed separately from the pectoral girdle. We conducted a principal component (PC) analysis of the correlation matrix of these four variables and PC1 scores of each individual were used as a body size indicator. Each variable had positive loadings on the first principal component (PC1) and eigenvalues for PC1 explained 70.2% of total variance (sexes pooled). Morphological variables (organs and muscle masses and locomotor morphometry) were corrected for structural size by dividing the value of every individual by its PC1 scores (hereafter referred to as corrected values). We are aware of the critique brought up by Blem (1984) about this procedure but we believe this is the best way allowing quantitative comparisons. PC1 scores as well as corrected values followed normal distribution as recommended by Blem (1984) (Kolmogorov-Smirnov Lilliefors, $P > 0.070$).

If abdication of flight was to occur in eiders, it should be most likely detected in females of high wing-loading since they are the ones facing the highest energy demand at takeoff. In order to compare the locomotor apparatus of females along a gradient of takeoff capacities, the females were classified in regards to their wing-loading in the following fashion: low wing-loading (LWL < 2.40 $g \cdot cm^{-2}$) and high wing-loading (HWL > 2.40 $g \cdot cm^{-2}$). Wing-loading was chosen since it represents an appropriate expression of relative weight and flight capabilities. Structural body size of females was found homogenous between the two wing-loading categories (one way ANOVA, $F_{1,22} < 1.35$, $P > 0.27$) thereby allowing inter-class comparison of females with un-corrected variables.

Scaling of the locomotor musculature was examined with the reduced principal axis method on $\log_{10}$ transformed values with alternatively PC1 scores and body mass on abscissa. The mass of the dependent variable was subtracted from body mass to account for part-whole correlation. Confidence intervals of the regression coefficients were obtained after Ricker (1973). We used for each analysis the largest number of valid specimens. But due to sampling difficulties, some specimens have missing values in specific variables and were thus excluded from the analysis of these variables. This reason explains the uneven size of the samples.

Enzyme assays

Three enzymes were assayed in all three muscle samples, namely pyruvate kinase (PK), lactate dehydrogenase (LDH) and citrate synthase (CS). PK is a key enzyme in the glycolytic pathway of which it is an obligate step and indicates the overall regime of carbohydrates catabolism. LDH is located downstream from PK in the glycolysis. It is a strict indicator of the anaerobic glycolytic regime and thus of short-burst effort capacity. CS is the first enzyme of the citric acid cycle and is herein used as an indicator of muscular aerobic capacities. Our selection of enzymes therefore allows us to compare the metabolic regime diverted to the anaerobic branch off with the one that goes through the glycolytic mainstream to the citric acid cycle.

Pectoralis samples dissected out upon specimen collection were too voluminous (ca. 45 g) to be efficiently homogenized. They were thus sub-sampled by coring them through at three places in accordance with Deaton et al. (1996). Muscle samples and sub-samples

were minced on ice with a scalpel and homogenized in 10 $ml \cdot g^{-1}$ of ice cold Tris-HCl buffer (100 mM, pH 7.5) with a homogenizer Polytron (Tekmar, Cincinnati, USA). Homogenization was performed at 50% maximal power in three periods of 10 s. with 60 s. intervening rest periods on ice preventing the homogenate to warm up. Lactate dehydrogenase and citrate synthase were assayed after modification of Thibeault et al. (1997) and pyruvate kinase after Pelletier et al. (1994).

Assays were run with UV/Visible spectrophotometers (Perkin-Elmer Lambda 11 or Ultrospec 3100 pro) fit with a desktop and a circulating water bath (VWR Scientific 1186). Changes in absorbance were monitored in duplicates at 25 ± 0.5°C and 340 nm wavelength except citrate synthase, which was assayed at 412 nm. Preliminary experiments allowed us to adjust the homogenate concentrations in order to obtain a linear response during at least two min., and the reactions were monitored during the first four minutes. Enzyme activities are expressed as μmol of substrate $transformed \cdot min^{-1} \cdot g\ proteins^{-1}$. Protein contents of the homogenates were determined using the bicinchoninic acid method (Smith et al. 1985). Biochemicals were supplied by Sigma Chemical (Oakville, Ontario, Canada) and all other chemicals were analytical grade.

Enzymes were assayed in the following order and with these reaction mixture compositions: *Citrate synthase* (CS) : 100 mM imidazole-HCl, 0.1 mM 5,5' dithiobis-2-nitrobenzoic acid (DTNB), 0.1 mM acetyl coenzyme A, 0.15 mM oxaloacetate, pH 8.0. *Pyruvate kinase* (PK) : 50 mM imidazole-HCl, 10 mM $MgCl_2$, 100 mM KCl, 5 mM ADP, 0.15 mM NADH, 5.0 mM phosphoenolpyruvate, 0.6 $unit \cdot ml^{-1}$ LDH, pH 7.4. *Lactate*

dehydrogenase (LDH) : 100 mM potassium-phosphate, 0.16 mM NADH, 0.4 mM pyruvate, pH 7.0. Extinction coefficients for NADH and DTNB were 6.22 and 13.6 $ml \cdot cm^{-1} \cdot \mu mol^{-1}$, respectively. All pH values were adjusted at room temperature.

RESULTS

Body size and Locomotor morphology

Pre-laying female eiders are nearly 20% heavier than males in average, a striking difference given their significantly smaller skeleton. Indeed, the females have the lowest means in all four skeletal measurements (Table 1).

TABLE 1. Comparison of body mass (g), body length (mm) and length of selected bones (mm) between sexes of pre-laying common eiders. Relative difference is calculated as the difference between means of each sex divided by the mean value of males. Note the opposite sexual dimorphism between body mass and skeletal measurements. Values are means ± SD, one-way ANOVA $P < 0.001$, $F_{1, 59} > 30$.

	Females (n = 23)	Males (n = 38)	Δ (%)
Body mass	2504.9 ± 199.4	2093.0 ± 171.8	19.7
Body length	584.1 ± 17.5	604.7 ± 12.9	-3.4
Sternum	99.9 ± 2.9	104.3 ± 2.9	-4.2
Carina	122.4 ± 5.2	129.7 ± 3.7	-5.6
Coracoid	63.5 ± 1.9	66.1 ± 1.5	-3.9

Surprisingly, females have wings of similar area as males (Table 2) in spite of their smaller structural body size. This disproportion in female wing morphometry was highlighted by factoring out the body size of the specimens. At equal body size, females

TABLE 2. Comparison of locomotor morphology, locomotor musculature and digestive organs (g) between sexes of pre-laying common eiders with corrected and uncorrected means. Except for aspect ratio, relative difference is calculated on the corrected means only (see Methods) which are values corrected for the structural size of the specimens.

	Uncorrected means ± SD		Corrected means ± SD				
						One-way ANOVA	
	Females	Males	Females	Males	Δ (%)[a]	P	F (df)
Locomotor morphology							
Wing area (cm^2)	1045.1 ± 47.1	1048.7 ± 48.2	115.9 ± 9.51	103.3 ± 4.75	12.1	<0.001	45.3 (1, 57)
Wing length (cm)	80.7 ± 2.1	82.1 ± 2.0	8.96 ± 0.79	8.09 ± 0.2	10.8	<0.001	40.6 (1, 57)
Tarsus length (mm)	59.7 ± 2.2	62.9 ± 2.1	6.62 ± 0.52	6.19 ± 0.19	6.9	<0.001	21.2 (1, 58)
Wing span (cm)	93.6 ± 2.4	95.0 ± 1.8	9.92 ± 2.37	9.36 ± 0.18	6.0	0.184	1.8 (1, 52)
Aspect ratio	6.24 ± 0.23	6.44 ± 0.23	-	-	-3.0	0.002	10.4 (1, 52)
Paddle area (cm^2)	87.4 ± 6.5	96.1 ± 5.5	9.67 ± 0.77	9.47 ± 0.54	2.1	0.260	1.3 (1, 53)
Locomotor musculature							
Heart (g)	20.3 ± 3.1	19.7 ± 2.8	2.24 ± 0.29	1.94 ± 0.27	15.5	<0.001	16.6 (1, 59)
Pectoralis (g)	314.4 ± 33.7	306.4 ± 33.6	34.73 ± 3.25	30.2 ± 3.31	15.0	<0.001	27.2 (1, 59)
Supracoracoideus (g)	45.4 ± 4.7	44.4 ± 3.9	5.02 ± 0.53	4.37 ± 0.39	14.9	<0.001	30.6 (1, 59)
Swim musculature (g)	183.1 ± 17.9	181.7 ± 15.2	20.26 ± 1.95	18.16 ± 2.13	11.6	<0.001	14.8 (1, 57)
Digestive organs							
Gizzard (g)	61.9 ± 24	91.8 ± 18.5	6.81 ± 2.38	9.05 ± 1.83	-24.8	<0.001	17.0 (1, 59)
Intestine (g)	56.8 ± 14.8	59.2 ± 15.1	6.29 ± 1.64	5.83 ± 1.47	7.9	0.259	1.3 (1, 59)
Esophagus (g)	27.3 ± 5.9	29.2 ± 5.2	3.03 ± 0.68	2.87 ± 0.52	5.6	0.310	1.0 (1, 59)

[a]calculated as in Table 1

have wings 12% larger and 10% longer than males. It is then not surprising that aspect ratio is significantly lower in females. Corrected tarsus length is also significantly longer in females but corrected paddle area is equally proportioned (Table 2).

Locomotor musculature

Inter-sex— Masses of locomotor muscles are sexually dimorphic ($P < 0.001$; Table 2). Accounting for structural size, the female heart, *pectoralis* and *supracoracoideus* are in average nearly 15% larger than those of males. The same pattern was observed in the corrected swim musculature with a significant difference of 11.6% (Table 2).

Interclass— Comparisons between females of low (LWL) and high (HWL) wing-loading reveal that heart, *pectoralis* and swim muscles are significantly larger in HWL females (Table 3). The largest difference is observed in the heart (14.1%) and the smallest is observed in the *supracoracoideus* (8.4%).

Muscle scaling

Locomotor muscles are significantly correlated with both body size and body mass, with males heart and swim muscles as the only exceptions. But except for males *supracoracoideus*, the relationships were stronger when locomotor muscles were regressed against body mass instead of body size (Table 4). *Pectoralis* scaled with body mass in a slight positive allometry (i.e. coefficient >1) and the relationship is stronger in females than in males. When regressed against body mass, neither *supracoracoideus* or swim

TABLE 3. Comparison of locomotor musculature and digestive organs (g) between females of high (HWL) and low (LWL) wing-loading. Relative difference is calculated as the difference between means divided by the mean value of LWL.

	Uncorrected means ± SD				
	LWL (n=12)	HWL (n=11)	Δ (%)	One-way ANOVA	
				P	F (df)
Locomotor musculature					
Heart	19 ± 2.6	21.7 ± 3.1	14.1	0.035	5.053 (1, 22)
Pectoralis	299.8 ± 31.5	330.3 ± 29.5	10.2	0.026	5.742 (1, 22)
Supracoracoideus	43.7 ± 4.7	47.3 ± 4.1	8.4	0.062	3.898 (1, 22)
Swim musculature	175.2 ± 17.9	191.7 ± 14.1	9.4	0.024	5.949 (1, 22)
Digestive organs					
Gizzard	61.9 ± 22.3	61.9 ± 26.7	0.0	0.994	0.000 (1, 22)
Intestine	55.2 ± 14.8	58.6 ± 15.3	6.3	0.585	0.031 (1, 22)
Esophagus	27.2 ± 5.3	27.4 ± 6.8	0.8	0.929	0.008 (1, 22)

musculature differed significantly from an isometric condition and in the latter case, the relationship is stronger in males. Females heart scaled with body mass in a steep positive allometry with a highly significant correlation coefficient. In contrast, males heart was not correlated with body mass. In the case of females, the strongest relationship was in heart and weakest in swim musculature.

Locomotor metabolism

Inter-sex— No significant differences were found in enzyme activities in neither muscles, with PK in *complexus* as the only exception (Table 5). Similarly, no sexual dimorphism was found in LDH activity relative to PK activity in *pectoralis* (females: 1.086

TABLE 4. Inter-sex comparisons of reduced major axis regressions relating locomotor muscle mass to body size (PC1) and body mass (Bm, g), separately (see Methods). N = 23 females and 38 males except for swim musculature. Values are $\log_{10}$-transformed. CI are slope confidence intervals at 95% level. PC1 are scores on the first axis obtained with a principal component analysis performed on the correlation matrix including four skeletal measurements. Body mass was corrected for part-whole correlation.

	Females				Males			
	Regression	CI	Correlation		Regression	CI	Correlation	
			$R_{Pearson}$	P			$R_{Pearson}$	P
Predictor: Body size								
Pectoralis	1.14PC1 + 1.41	0.80 - 1.61	0.617	0.004	1.94PC1 + 0.50	1.45 - 2.61	0.475	0.029
Supracoracoideus	1.10PC1 + 0.60	0.74 - 1.64	0.454	0.054	1.68PC1 + 0.70	1.25 - 2.25	0.480	0.051
Swim muscles[a]	1.02PC1 + 1.29	0.70 - 1.49	0.519	0.024	1.59PC1 + 0.63	1.18 - 2.14	0.490	0.898
Heart	1.54PC1 - 0.17	1.08 - 2.20	0.592	0.014	2.50PC1 - 1.27	1.79 - 3.48	0.026	0.834
Predictor: Body mass								
Pectoralis	1.38Bm - 2.11	1.03 - 1.84	0.767	<0.001	1.25Bm - 1.57	0.94 – 1.65	0.548	<0.001
Supracoracoideus	1.32Bm - 2.82	0.94 - 1.85	0.653	0.001	1.10Bm - 2.01	0.82 - 1.48	0.462	0.006
Swim muscles[a]	1.19Bm - 1.76	0.83 - 1.72	0.563	0.005	1.26Bm - 1.88	0.94 - 1.70	0.503	0.002
Heart	1.85Bm - 4.98	1.37 - 2.49	0.740	<0.001	1.65Bm - 4.18	1.19 - 2.29	0.175	0.267

[a] in this case n=36 males

± 0.076, males: 0.982 ± 0.084; one-way ANOVA, P = 0.365; $F_{1,27}$ = 0.847). Protein concentrations per gram of muscle tissue do not differ between sexes neither in pectoralis nor in iliotibialis (Table 5).

TABLE 5. Comparison of enzyme activity (activity • g protein^{-1}) in locomotor (*pectoralis* and *iliotibialis*) and structural (*complexus*) muscles of female and male common eiders. Relative difference is calculated as the difference between means divided by the mean value of males.

	Females	Males	Δ (%)	One-way ANOVA	
				P	F (df)
		Pectoralis			
LDH	3496.7 ± 1627.9	2992.6± 644.5	16.8	0.284	1.19 (1, 31)
CS	403.7 ± 119.1	460.3 ± 149.7	-12.3	0.270	1.27 (1, 28)
PK	3186.8 ± 1277.6	3281.6± 966.9	-2.9	0.825	0.050 (1, 29)
Protein	143.3 ± 18.1	149.6 ± 17.4	-4.2	0.327	0.995 (1, 30)
		Iliotibialis			
LDH	3944.0 ± 1132.1	3722.9± 642.9	5.9	0.519	0.425 (1, 31)
CS	172.5 ± 43.6	181.4 ± 84.8	-4.9	0.709	0.142 (1, 29)
PK	2712.4 ± 776	3224.3± 893.6	-15.9	0.110	2.73 (1, 28)
Protein	118.7 ± 13.3	116.6 ± 29.7	-1.8	0.791	0.072 (1, 30)
		Complexus			
LDH	3239.7 ± 957.7	3520.3± 706.4	-8.0	0.366	0.843 (1, 31)
CS	213.1 ± 52.1	229.3 ± 92.9	-7.1	0.545	0.375 (1, 29)
PK	1716.3 ± 395.1	2151.5± 681.7	-20.2	0.045	4.42 (1, 27)

Interclass— Females of higher wing-loading showed an un-significant trend toward higher LDH activity in *pectoralis* (Table 6). Otherwise, all three enzyme activities are not affected by the wing-loading differences (Table 6). Protein concentrations do not differ between classes of wing-loading neither in pectoralis nor in iliotibialis (Table 6).

TABLE 6. Comparison of the enzyme activity (activity • g protein^{-1}) in locomotor (*pectoralis* and *iliotibialis*) and structural (*complexus*) muscles between females of low (LWL) and high (HWL) wing-loading. Relative difference is calculated as the difference between means divided by the mean value of LWL females.

	LWL	HWL	Δ (%)	One-way ANOVA	
				P	F (df)
		Pectoralis			
LDH	2992.2 ± 1631.7	4127.2 ± 1481.3	37.9	0.146	2.33 (1, 17)
CS	396.1 ± 107.7	413.3 ± 139.0	4.3	0.771	0.874 (1, 17)
PK	3050.0 ± 555.5	3340.8 ± 1824.0	9.5	0.655	0.208 (1, 16)
Protein	145.9 ± 15.2	140.0 ± 21.8	-4.0	0.508	0.459 (1, 16)
		Iliotibialis			
LDH	4079.7 ± 1357.4	3774.2 ± 827.2	-7.5	0.585	0.310 (1, 17)
CS	174.9 ± 56.5	169.5 ± 22.2	-3.1	0.803	0.065 (1, 17)
PK	2834.7 ± 678.9	2555.0 ± 916.3	-9.9	0.494	0.494 (1, 15)
Protein	119.4 ± 13.5	117.8 ± 14.0	-1.3	0.807	0.062 (1, 16)
		Complexus			
LDH	3320.3 ± 1230.2	3138.9 ± 510.8	-5.5	0.702	0.151 (1, 17)
CS	203.2 ± 49.3	225.6 ± 56.0	11.0	0.380	0.816 (1, 17)
PK	1663.3 ± 416.1	1795.8 ± 384.0	8.0	0.545	0.387 (1, 14)

Digestive tract

Inter-sex— As shown in table 2, females had a significantly smaller corrected gizzard mass than males. Esophagus and intestine corrected masses were similar between sexes.

Interclass— Masses of digestive organs of females are similar between classes of wing-loading (Table 3).

Relative importance of flight apparatus

Wing-loading— The hypertrophied wings of females is yet not sufficient to maintain a low wing-loading as shown in figure 1, mean values for females and males are 2.42 ± 0.19 and 2.01 ± 0.18 $g \cdot cm^{-2}$, respectively. Indeed, this figure shows a sexual segregation along both axis, the females being heavier and the wings having similar area.

Flight muscle ratio— All females have a flight muscle ratio above 0.16 (Fig. 1). However, as evidenced by figure 1, their values remain low compared to males. Mean values are 0.195 ± 0.012 and 0.225 ± 0.014 for females and males, respectively (range 0.168 - 0.215 and 0.201 - 0.274). Mean FMR are similar between classes of females (LWL: 0.196 ± 0.014, HWL: 0.194 ± 0.010, one-way ANOVA, $P = 0.616$, $F_{1, 22} = 0.26$), despite significant difference in their uncorrected *pectoralis* mass (Fig. 1).

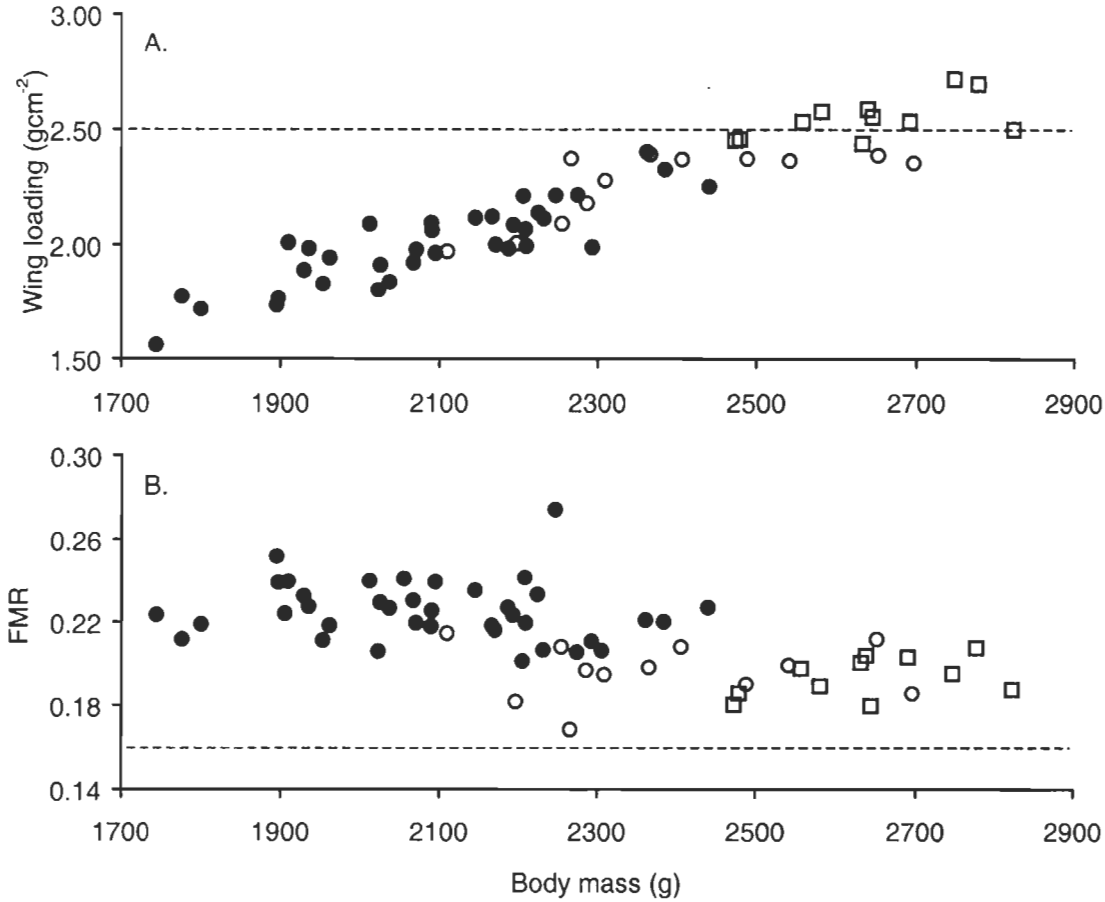

FIGURE 1. Sexual segregation in two parameters related to flight capability of pre-laying common eiders. Solid circles are for males, open circles and squares are for females of low (LWL) and high (HWL) wing-loading, respectively. A) wing-loading, horizontal line represents the upper threshold of flight capabilities after Meunier (1951) (23 females and 36 males); B) flight muscle ratio (FMR), horizontal line represents the lower threshold of takeoff capability after Marden (1987) (23 females and 38 males).

DISCUSSION

In order to become airborne, flighted animals must generate a mass-specific lift (lift force per unit body mass) higher than earth's gravity (9.8 $N \cdot kg^{-1}$ in average). Obviously, animals gaining surplus weight need extra work to achieve this. The means available to birds to generate more lift are 1) increasing absolute lift with larger wings, 2) enhancing mechanical power with larger muscles, 3) improving metabolic power with increased enzyme activity and 4) reducing body mass by the atrophy of organs. Our results indicate that pre-laying female eiders adopt a combination of all these strategies. Except for wings, the last three are outcomes of imbalance in the dynamic equilibrium of allocation/mobilization of resources and they can therefore be designed as physiological compensation. Physiological compensation is only possible in an individual provided it has sufficient phenotypic flexibility (Piersma and Lindström 1997) and is not resource-limited. In contrast, unless physiologists demonstrate post-molt growth of remiges or seasonal growth of appendicular bones in fully grown individuals, wings of anseriformes are considered as having fixed dimensions in post-molt period.

Flight morphology

Contrasting with their smaller skeleton, the wings of female eiders are hypertrophied relatively to males. We interpret this as a strategy to maintain a lower wing-loading in anticipation of the recurrent takeoff impairment inherent to the pre-laying period. However, this facilitating strategy is clearly insufficient as evidenced by the sexual segregation in wing-loading (Fig. 1). According to Guillemette (1994), wintering eiders have already

among the highest wing-loading found in volant birds, 1.96 and 2.03 $g \cdot cm^{-2}$ for wintering females and males, respectively. But during the pre-laying period, females reach much higher values (maximum observed 2.72 $g \cdot cm^{-2}$, Fig. 1). Although oversized relatively to males, the small wings obviously handicap flight in pre-laying females. It is noteworthy that the mass of the gut content (48 ± 18.9 g in average for females) was excluded in the computations. These high wing-loading values presented here are therefore slight underestimates of the actual wing-loading of the hyperphagic females. A heavy wing-loading has serious implications on flight performances for it raises the takeoff speed and thereby reduces the ability of heavy individuals to become airborne (Pennycuick 1975; Norberg 1995). The wing-loading values of our females indicate important impairment in absence of wind but the actual proportion of temporarily flightless individuals in the population of breeders remains to be quantified. Similar cases of sexual dimorphism in wing morphometry was reported in several instances. For example, much like the larger wings of female eiders allow them to carry extra weight, male black wheatears have wings larger than females' and their lower wing-loading facilitates their typical stone-carrying display (Møller et al. 1995). Wings of dark-eyed juncos are also sexually dimorphic in size and shape (Mulvihill and Chandler 1990; Chandler and Mulvihill 1992). Chandler and Mulvihill (1992) regarded the lower aspect ratio of females as partly counterbalancing the aerodynamic disadvantages of their high wing-loading. This interpretation of wing morphology of juncos is likely to pertain to female eiders who also have a lower aspect ratio than males (Table 1). Low aspect ratio indicates a rounded wing shape and is associated with poor energetic efficiency during sustained flight but facilitates takeoff.

If wing-loading is a handicap, why do females not grow larger wings? There are several hypothetical answers reviewed by Rayner (1988). 1) Developmental constraints: eiders are descendants of a long strain of ancestor species having small wings. If this phenotype shows little variability and/or if variations show little heritability, there is little possibility for the trait to evolve (Rayner 1988). In this sense, the phylogeny of the sea duck species by Livezey (1995b) reveals that the ancestor of the genus *Somateria* has undergone an important autapomorphic increase in body mass (Livezey 1995b). In respect to the scaling principles, wing area does not keep up with increments of body mass and the resulting wing-loading is high. 2) Hydrodynamic constraints: during dives, eiders assist their foot propulsion with wings partially outstretched. Perhaps their wing morphology faces selection toward small shape to reduce drag underwater (Rayner 1988). 3) Aerodynamic constraints: selection favors high wing-loading in eiders for it provides them a high flight speed in migration and thereby allows them to quickly escape adverse weather in high latitudes and maximize time spent on breeding grounds (Rayner 1988). In this point of view, selection favors migration efficiency rather than flight performances on the breeding grounds.

Flight musculature

Pre-laying females show an oversized flight musculature compared to males. In addition, the weak relationship linking flight muscle mass to body size and the strong relationship between the former and body mass show that flight musculature mass is not solely subject to developmental constraints. Instead, flight musculature closely keeps up

with the seasonal weight gain of females. We regard this as physiological compensation facilitating takeoff in addition to the hypertrophied wings. In addition to the enhanced power output, large *pectoralis* muscles could constitute an important depot of protein available to the fasting females (Cherel et al. 1988; Parker and Holm 1990; Cottam et al. 2002). *Pectoralis* growth has already been reported in similar cases of weight gain in different species such as wintering Cooper's hawks (Marsh and Storer 1981), incubating pied flycatcher (Kullberg et al. 2002) and pre-migratory gray catbirds (Marsh 1984). Nevertheless, the flight muscle ratio of females remains very low (observed range 0.168 - 0.215; Fig. 1) suggesting that an upper flight musculature mass relative to body mass cannot be exceeded. Some avian species maintain or even increase mass-specific lift by reducing their body mass and *pectoralis* mass (Swaddle and Biewener 2000; Veasey et al. 2001). This strongly suggests that a tradeoff exists between the benefits of enhanced power associated with a large musculature and the costs of maintaining and carrying extra muscular load. However, such a strategy of muscular mass minimization cannot be fully afforded by pre-laying female eiders who must build up large endogenous reserves and undergo an important increase in body mass. Marden (1987) determined experimentally that the FMR must exceed 0.16 for a bird to achieve takeoff in still air by the sole action of its wings (i.e. zero initial velocity). The scaling observed in the flight musculature enables pre-laying females to cope with the weight constraint. However, they seem to maintain their flight muscle ratio just above this value (Fig. 1). From this observation, it can be hypothesized that the strategy adopted by female eiders is a trade-off between muscular

compensation improving power output and body mass minimization reducing load and maintenance costs.

The strong relationship relating *pectoralis* to body mass reflects the high constraints put on its wing-depressor action by gravity. In contrast, the *supracoracoideus* does not act directly against gravity and is thereby less strongly correlated with body mass (Table 4). Marsh (1981) observed a similarly asymmetric response to fattening between *pectoralis* and *supracoracoideus* in pre-migratory gray catbirds. The *supracoracoideus* is the main wing elevator muscle and its action pays an important contribution in the wing beat frequency which is a major factor limiting power output at takeoff (Ellington 1991). Our results show that the protein allocations to flight musculature in pre-laying period are partitioned between the wing depressor unit transmitting lift to the wing and the wing elevator unit ensuring a rapid wing beat frequency.

Heart

Physiological compensation is also observed in heart mass of females where is found the steepest allometric scaling (Table 4) and the largest sexual dimorphism (Table 2). We interpret this improvement in the female cardiovascular system as a response to a higher energy demand caused by pre-laying hyperphagy (Guillemette 2001). Guillemette (2001) showed that, in average, pre-laying female eiders spend one more hour diving than males each day. This intense apnoeic activity and the inherent post-prandial activity undoubtedly require adjustments in cardiovascular system.

Energy metabolism for flight

Despite our strong sampling design, we did not detect any significant dimorphism in *pectoralis* energy metabolism, neither between sexes nor between classes of wing-loading (Table 5). We therefore conclude that no physiological compensation facilitating takeoff occurs in female *pectoralis*. Interestingly, the metabolic power of female *pectoralis* does not undergo any deterioration either. This lack of dimorphism has several implications. First, it indicates that, in this case, it is appropriate to compare mass of *pectoralis* muscle between sexes for they have similar protein content and metabolic power per unit muscle tissue (Table 5). Second, it shows that the metabolic machinery in female *pectoralis* is not altered by follicular growth in contrast with what Cottam et al. reported (2002). Finally, it indicates that pre-laying female eiders protect their metabolic pathway in flight musculature and do not abdicate flight. However, this protection does not compensate for their weight increase, otherwise they would take off with the same ease as males. Muscle mass-specific LDH activity in *pectoralis* is similar between sexes, but owing to the increasing body mass of females and since no physiological compensation occurs, the body mass-specific LDH activity is also lower in females (females: 59.1 ± 19.5 U•kg body mass^{-1}, males: 77.2 ± 14.6 U•kg body mass^{-1}; one-way ANOVA, $P = 0.007$; $F_{1,30} = 8.39$). As females fatten up, LDH activity becomes insufficient and there comes a point where they cannot develop enough mechanical power output to produce lift. This results in the takeoff impairment we observed near the breeding colonies. There is a cost associated with the maintenance of the metabolic machinery. The proteins must be replaced as they wear out so even a neutral

equilibrium necessitates important allocations of nutrients. This further supports the idea that female eiders do not abdicate flight in pre-laying period.

Muscle mass-specific activity of LDH in female *pectoralis* never exceeded 7196.9 U•g protein^{-1} and averaged 4426.9 ± 1481.3 U•g protein^{-1} in females having wing-loading values high enough to be safely presumed flightless (i.e., WL > 2.45 g•cm^{-2}). Apparently, female *pectoralis* cannot afford higher metabolic activity, suggesting that, at the time of collection (April and May), females had reached the upper limit of their metabolic power and then protect their metabolic pathway against deterioration in order to recover their takeoff aptitude as soon as their body mass has decreased sufficiently after laying (Guillemette and Ouellet in press, b).

We can then speculate that the body mass-specific LDH activity measured in the heavy females corresponds to the minimum metabolic power required by these large-sized birds to take off. This threshold of body mass-specific activity could roughly be placed somewhere between 50 and 65 U•kg body mass^{-1}. It is apparent in figure 2 that most males (all flighted) have values higher than 65 U•kg body mass^{-1}, with two eccentric individuals as the only exceptions (males minima: 52.7 and 57.0 U•kg body mass^{-1}). On the other hand, 14 females have lower values than 65 U•kg body mass^{-1} of which six are lower than 50 U•kg body mass^{-1}. We are not aware of any mention in the literature of such a critical limit to takeoff capability in birds. An experimental design using specimens of known takeoff capability could allow investigators to determine more precisely this critical value. It is

noteworthy that the exceptional breeding strategy of female eiders makes this species a proper model for such investigations.

A case where physiological compensation does occur in order to facilitate takeoff was reported by Lundgren and Kiessling (1985) in breeding passerines when they perform mostly short foraging flights and frequent takeoffs as opposed to the migratory period. These authors observed an increase in LDH activity and a decrease in CS activity in *pectoralis*. Oppositely, Marsh (1981) reported that muscle mass-specific activity of CS in catbird *pectoralis* is maintained at its maximum value during the pre-migratory fattening period when birds prepare for a long sustained flight. Furthermore, Saunders and Klemm (1994) did not detect any significant deterioration in *pectoralis* LDH activity in blue-winged teal at the onset of wing molt when the anseriformes are rendered flightless by the simultaneous loss of their flight feathers. These authors, however, observed a significant decrease in CS activity in *pectoralis*, which we did not detect in our study.

Our mean value for tissue-specific LDH activity (activity × g tissue^{-1}) in *pectoralis* is more than five times lower than in the pheasant which has probably the highest value reported in avian *pectoralis* [eider, sex pooled: 482.3 U•g tissue^{-1}; pheasant: 2523 U•g tissue^{-1}, Davis and Guderley (1990)]. Also, Marsh (1981) regarded tissue-specific CS activity in pre-migratory catbird *pectoralis* as the highest value reported in vertebrate skeletal muscles (201 U•g tissue^{-1}). This is more than three times higher than our mean value for tissue-specific CS activity in eider *pectoralis* (mean 63.1 U•g tissue^{-1}, maximum : 98.2 U•g tissue^{-1}; sexes pooled).

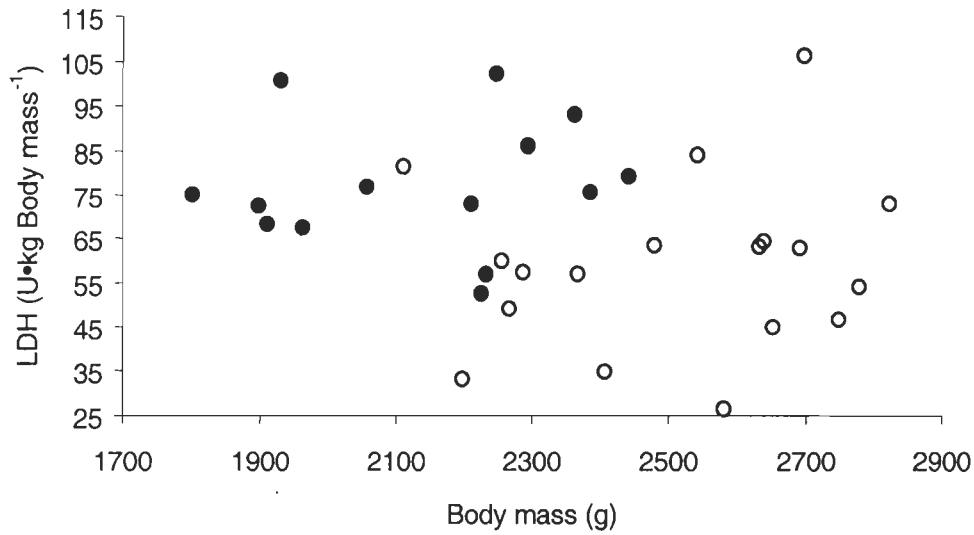

FIGURE 2. Relationship between body mass-specific total LDH activity and body mass of pre-laying common eiders. Solid and open circles are for males and females, respectively. N = 18 females and 14 males.

Swimming apparatus

Females do not develop better aptitudes in swimming than males. Female paddle area is not oversized relatively to males, which is counterintuitive with the marked propensity of females toward escape-dives. Females go on land only for nesting and their takeoff aptitudes are then at the lowest point of the non-molting period (Guillemette and Ouellet in press, a). They are then extremely vulnerable to mammalian predators and their only way to elude attack is to outrun their pursuer. Indeed, female eiders show aptitudes in terrestrial locomotion comparable to that of most dabbling ducks (personal obs.) and this specific

ability was attributed by Raikow (1973) to the small paddle area of the species. Only tarsus length is significantly oversized in females compared to males (Table 2), contrasting with the smaller skeleton of females (Table 1). This partly validates our hypothesis since longer tarsi permit longer strides and thereby improve gait and swimming speed (Hildebrand 1995). In a phylogenetic study of locomotor morphology in avian flightless species, Cubo and Arthur (2001) observed a significant correlation between the occurrence of flightlessness and peramorphosis of the pelvic apparatus. There is a cost in having long tarsi, however. Foot propulsion acts as a lever arm system and longer tarsi elongate the load arm but reduce the out-force (Hildebrand 1995). Then, longer strides improve swimming performances as long as the bird has the appropriate musculature to power the strokes. Accordingly, swimming musculature is proportionally larger in females than in males (11.6% relative difference; Table 2) although the scalings with body mass are similar (Table 4). This muscular hypertrophy further validates our hypothesis and is likely a response to the longer strides. An evidence for this is the correlation between leg muscle mass and tarsus length in males ($R = 0.324$; $P = 0.054$). Cases of physiological compensation have been documented at the metabolic level in swimming musculature of blue-winged teal rendered temporarily flightless by wing molt. Leg muscle mass (Brown and Saunders 1998) and LDH activity (Saunders and Klemm 1994) increase drastically at the onset of the flightless period. However, we failed to detect any physiological compensation at the metabolic level in the swimming musculature. LDH and CS activities are nearly similar between sexes and PK activity is lower in females.

Mass minimization in non-locomotor organs

The smaller gizzard of females is surprising in regard to their hyperphagic behavior. Eiders are epibenthic feeders and their most common prey items are blue mussels, urchins and crabs that they swallow whole. The fact that these epibenthic feeders afford a reduction in gizzard mass during a period of hyperphagia suggests that pressures may be directed toward mass minimization, the females clearly dump ballast in order to diminish and retard their takeoff impairment. Piersma and Gill (1998) documented a similar case of body mass minimization at the expense of the digestive tract in migrating bar-tailed godwits. As suggested by Parker and Holm (1990), the reduction in gizzard mass reported here may be the result of a proximal cause other than the sole body mass minimization. However, the proximal cause is not an issue here and our point is that, unless physiological and/or behavioral compensation occurs, a gizzard mass reduction is likely to be highly detrimental to hyperphagic mussel eaters and the fact that they do afford this counterintuitive strategy reveals the importance for the females to lighten.

In conclusion, our results clearly indicate that female eiders do not abdicate flight during the pre-laying period despite the high power requirements for flight imposed by their obesity. Instead, by the means of phenotypic plasticity and physiological compensation, females adopt strategies enhancing lift production. Furthermore, the females of higher wing-loading supporting higher cost of flight allocate more nutrients and structures in musculature than the ones facing lower costs of flight. These results demonstrate that the maintenance of flight aptitudes is an issue of tremendous importance for pre-laying female eiders.

This study also reveals that compensation acts at different organizational levels but does not fully offset weight gain effects. For instances, at the first level, wings are oversized to maintain a low wing-loading. But this is truly insufficient as females become heavy. At the second level, flight musculature grows and remains slightly above a minimal body proportion. However, presumably for an issue of body mass minimization, it does not either compensate totally for the weight gain. For the same reason, digestive tract undergoes mass reduction. Finally at the third level, the female *pectoralis* maintain its mass-specific short burst capacities. However, females seem to reach the limit of their phenotypic flexibility in *pectoralis* and, at this level, physiological compensation fails to contribute in takeoff facilitation.

This study presents a first attempt to determine a critical body mass-specific LDH activity for takeoff capability in a large-sized bird. This hypothetic threshold could be refined with an experimental design similar to Marden's (1987). In addition, Marden's general model to takeoff capabilities (Marden 1994) could be updated by accounting for the seasonal and sex-specific fluctuations in anaerobic performances. Then, our conclusions could be extended further with a determination of the actual proportion of flightless females in the population of breeders of Île Bicquette. An inter-population comparison could be conducted along a latitudinal gradient. The eider population of the St. Lawrence River estuary (*S. m. dresseri*) does not winter on its breeding grounds as they migrate to suitable habitats when the estuary freezes over. This population, along with other obligate migratory populations, surely faces strong pressure toward maintenance of flight aptitude. But further south, in the Gulf of Maine, where suitable habitats are available year-round near the

breeding colonies, successful breeding by eiders sustaining wounds severe enough to preclude flight has already been reported (Mendall et al. 1984).

CONCLUSION GÉNÉRALE

Sans doute en raison de la fascination que les oiseaux exercent sur l'esprit humain, l'étude du vol est une préoccupation scientifique dont on trouve des traces à toutes les époques depuis l'Antiquité. Ce domaine de recherche a toutefois connu un essor remarquable à partir de la seconde moitié du XX^{e} siècle. Cet effort de recherche a fourni une compréhension approfondie des mécanismes qui permettent le vol des vertébrés et mis en évidence de nombreuses contraintes physiques, morphologiques et physiologiques qui lui sont imposées. De là s'est développé un intérêt marqué dans la communauté ornithologique pour l'étude des capacités de vol des oiseaux et des facteurs qui affectent les performances de vol et d'envol. La présente étude s'inscrit dans un vaste effort de recherche international consacré depuis plusieurs décennies à l'étude des capacités d'envol des oiseaux.

Afin d'examiner la réponse du système locomoteur des femelles eiders à duvet à leur handicap d'envol dû à leur alourdissement de pré-ponte, un échantillon de spécimens a été récolté dans l'estuaire du Saint-Laurent et soumis à des mesures morphométriques, à la pesée de la musculature locomotrice et à la mesure de l'activité d'enzymes-clés du métabolisme énergétique. Nos résultats démontrent que les femelles subissent des phénomènes de compensation morphologique et physiologique propres à réduire leur handicap locomoteur.

La principale contribution de cette étude a été de proposer un projet intégrateur. En démontrant que la compensation agit à plusieurs niveaux organisationnels, elle a mis en

évidence l'avantage d'avoir abordé notre question sous différentes perspectives qui, prises séparément, n'auraient fourni que des réponses partielles. En effet, la réponse du système locomoteur des femelles à leur alourdissement est le résultat d'une combinaison de phénomènes qui agissent en synergie entre les niveaux d'organisation. De façon similaire, cette étude a révélé que les espèces subissent aussi des contraintes à différents niveaux organisationnels. Un regard global sur ces contraintes permet de juger de la plasticité et flexibilité phénotypiques d'une espèce et donc de sa vulnérabilité puisque de celles-ci découle la capacité des organismes à s'adapter au changement (Meyers et Bull 2002).

En second lieu, cette étude a démontré à quel point il est important pour l'eider de maintenir ses capacités de vol. En effet, les femelles misent dans l'allocation de ressources dans leur système locomoteur jusqu'aux limites de leur flexibilité phénotypique alors qu'elles ont de grands besoins d'investir dans leurs réserves corporelles et dans leur système reproducteur.

Des efforts de recherche futurs devraient être consacrés à déterminer l'importance et la gravité réelles du handicap d'envol. Pour ce faire, il faudrait 1) quantifier la proportion de femelles qui souffrent de difficultés d'envol au cours de leur préparation à la ponte; 2) décrire la phénologie du handicap dans la population de nicheuses; 3) déterminer la contribution du vent dans le succès d'envol chez les femelles et 4) quantifier la proportion de temps où la vélocité du vent est insuffisante pour permettre l'envol des femelles. De plus, une étude des possibles stratégies comportementales facilitant l'envol complèterait avantageusement nos conclusions sur la compensation physiologique.

Une détermination fine du seuil minimal d'activité de la LDH pondérée à la masse corporelle nécessaire à l'envol des oiseaux serait une innovation importante en écophysiologie de la locomotion des vertébrés.

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