UNIVERSITÉ DU QUÉBEC

Étude à long terme du comportement et de l'énergétique du vol chez l'Eider à duvet (*Somateria mollissima*) en milieu naturel

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Par

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À Soleil-Anne, ma fille qui préfère pour l'instant

les petits canards jaunes en plastique

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Contributions des auteurs

La contribution de chacun des auteurs est présentée en fonction de leur ordre d'apparition dans la liste d'auteurs des articles.

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RÉSUMÉ

Le vol est un moyen de locomotion pratiqué par de nombreuses espèces du règne animal, mais il constitue l'adaptation majeure de la classe avienne. Il permet aux oiseaux de remplir diverses fonctions, dont fuir d'éventuels prédateurs, augmenter le repérage et l'accessibilité à des sites d'alimentation, ainsi que migrer sur de longues distances. Le vol est par contre difficile à étudier du point de vue comportemental et énergétique chez des oiseaux libres en milieu naturel car peu de techniques permettent de suivre en continu les individus pratiquant ce moyen de locomotion; celui-ci les rend hautement mobiles. Une nouvelle technologie basée sur l'enregistrement de données physiologiques a cependant servi à identifier les paramètres permettant d'observer indirectement les vols courts et migratoires chez une espèce pratiquant le vol battu. Nous publions donc, pour la première fois dans la littérature, la compilation exhaustive de tous les vols effectués quotidiennement chez une espèce d'oiseaux en liberté pendant plusieurs mois. Cette technique a également été utile pour estimer la dépense énergétique de ce mode de locomotion et pour associer le temps de vol journalier à la dépense énergétique quotidienne.

Pour ce faire, des consignateurs de données qui enregistrent la fréquence cardiaque, la pression hydrostatique (la profondeur de plongée) et l'angle postural ont été implantés chez 20 femelles Eider à duvet (*Somateria mollissima*) en 2003, et 10 en 2004, nichant sur l'île Christiansø, dans la mer Baltique.

La première partie de cette étude (chapitre 2) a consisté à comparer la fréquence cardiaque enregistrée pendant le vol à celle enregistrée pendant 10 comportements effectués par l'Eider à duvet. Des séances d'observations comportementales ont été réalisées pour 14 femelles expérimentales durant la période post-éclosion. Tous les comportements observés se sont avérés avoir une fréquence cardiaque plus basse que lors des vols ($p < 0{,}02$ et $p < 0{,}001$) à l'exception du comportement de baignade (durant lequel les oiseaux battent rapidement des ailes sur l'eau en submergeant fréquemment leur tête) et des pauses entre les plongées successives d'une séance d'alimentation. Le second comportement a été facilement discriminé avec l'utilisation de la pression hydrostatique qui indiquait que la fréquence cardiaque élevée résultait de la tachycardie produite après une plongée. La baignade a pu être isolée des vols par le tracé de sa fréquence cardiaque en forme de cloche qui se distinguait de celui des vols. Ce tracé, ou la *signature cardiaque du vol*, se différenciait quant à lui par des pentes ascendantes et descendantes abruptes ($\geq$ 10 battements min^{-1} s^{-1}) et un plateau possédant un seuil supérieur à 300 battements min^{-1}.

La seconde partie de cette étude a consisté à décrire l'aspect temporel (chapitre 2 et 3), à l'échelle quotidienne, du vol chez l'Eider à duvet en utilisant la *signature cardiaque du vol*. Il a été observé que cette espèce consacre peu de temps à la locomotion aérienne. Il effectue en moyenne 4,1 vols par jour (95% *CI* = 3,6 – 4,8), ceux-ci durant en moyenne 2,3 min (95% *CI* = 2,2 – 2,5 min), ce qui fait un temps total passé en vol par jour de 9,4 min (95% *CI* = 8,3 – 11,0 min). Jusqu'à preuve du contraire, il a été démontré que l'Eider à

duvet est l'une des espèces qui vole le moins parmi toutes les espèces étudiées. Or, ce mode de locomotion est employé préférentiellement durant l'aube, le matin et l'après-midi (en ordre décroissant) et l'utilisation de ce moyen de locomotion est fortement corrélée aux activités d'alimentation en plongée (r de Pearson = 0,88; test de permutation $p < 0{,}001$).

La troisième et dernière partie de cette étude (chapitre 3) a été consacrée à l'étude des coûts associés au vol chez l'Eider à duvet et à la relation qui existe entre le temps de vol journalier et la dépense énergétique quotidienne. Pour estimer le coût du vol, trois différents types de modèles ont été utilisés : deux modèles basés sur l'équation de Fick (Bishop 1997), un modèle basé sur la théorie aérodynamique (avec le logiciel *Flight 1.11* de Pennycuick 1989) et deux modèles allométriques basés sur la masse corporelle et des mesures alaires (Masman et Klaassen 1987, Rayner 1995). La comparaison entre les modèles suggère que les modèles allométriques sont inappropriés pour estimer les coûts du vol pour cette espèce alors que les modèles basés sur la théorie aérodynamique et l'équation de Fick présentent des résultats réalistes. Les coûts de vol estimés se situent entre 123 et 149 W pour cette espèce (ou entre 17 et 20 fois le taux métabolique de base). Étonnamment, même si les coûts de vol sont élevés, il n'y a pas de corrélation entre la fréquence cardiaque journalière (*DHR – daily heart rate*) et le temps total passé en vol par jour (r de Pearson = 0,08; test de permutation p = 0,785) ainsi qu'entre le *DHR* et la fréquence quotidienne des vols (r de Pearson = 0,38; test de permutation p = 0,203). Toutefois, une tendance positive existe entre le nombre de vol courts par jour et le *DHR* (r de Pearson = 0,48; test de permutation p = 0,094). Les coûts énergétiques très élevés requis pour le décollage, causés par des faibles capacités de décollage, pourrait expliquer ce dernier résultat. Il est suggéré que l'utilisation de ce mode de locomotion chez cette espèce pourrait être le résultat d'un compromis entre la nécessité écologique de voler (pour l'alimentation et fuir les prédateurs) et la faible capacité aérobie (fréquence cardiaque et masse relative du coeur relativement basses, peu de marge disponible pour la puissance aérobie) combinée à une charge alaire excessive.

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LISTE DES ABRÉVIATIONS

Pour limiter le nombre d'abréviations utilisées dans le mémoire, il a été convenu d'utiliser seulement les abréviations anglophones. Les unités (lorsque présentes) sont indiquées entre parenthèses.

Abréviations	Description francophone (unités)	Description anglophone (unités)
AR	Rapport d'apparence	Aspect ratio
B	Envergure (cm)	Wing span (cm)
BA	Angle postural (°)	Body angle (°)
BMR	Taux métabolique de base (W)	Basal metabolic rate (W)
C_{aO_2}	Concentration en oxygène du sang artériel (ml 0_2 ml sang^{-1})	Oxygen content in arterial blood (ml 0_2 ml blood^{-1})
$C_{\bar{v}O_2}$	Concentration en oxygène du sang veineux mélangé (ml 0_2 ml sang^{-1})	Oxygen content in mixed venous blood (ml 0_2 ml blood^{-1})
DHR	Fréquence cardiaque journalière (battements min^{-1})	Daily heart rate (beats min^{-1})
DL	Consignateur de données	Data logger
DMR	Taux métabolique journalier (W)	Daily metabolic rate (W)
E_{FM}	Efficacité des muscles du vol	Flight muscle efficiency
f_{H}	Fréquence cardiaque pendant le vol (battements min^{-1})	Heart rate during flight (beats min^{-1})
FMR	Ratio massique des muscles du vol	Flight muscle ratio
H_{sunrise}	Heure du lever du soleil	Sunrise time
H_{sunset}	Heure du coucher du soleil	Sunset time
M_{b}	Masse corporelle (g ou kg)	Body mass (g or kg)
M_{H}	Masse cardiaque (g)	Heart mass (g)
P_{ac}	Puissance mécanique disponible continuellement (W)	Mechanical power continuously available (W)
P_{i}	Puissance métabolique (W)	Metabolic power input (W)
P_{min}	Puissance métabolique à vitesse économique (W)	Metabolic power at the minimum power speed (W)
P_{mr}	Puissance métabolique d'autonomie ou de distance maximale (W)	Metabolic power at the maximum range speed (W)
P_{o}	Puissance mécanique (W)	Mechanical power output (W)
RHR	Fréquence cardiaque au repos (battements min^{-1})	Resting heart rate (beats min^{-1})
RMR	Taux métabolique au repos (W)	Resting metabolic rate (W)
RQ	Quotient respiratoire	Respiratory quotient
S	Superficie alaire (cm^2)	Wing area (cm^2)

Abréviations	Description francophone	Description anglophone
t_0	Heure du décollage	Take-off time
t_F	Nombre d'heures passées en vol par jour (h jour^{-1})	Hours spent flying per day (h day^{-1})
t_Fa	Pourcentage de la période active passé en vol (%)	Percentage of active period spent flying (%)
$\dot{V}_b$	Débit cardiaque (ml min^{-1})	Cardiac output (ml min^{-1})
$\dot{V}_{b,max}$	Débit cardiaque maximal (ml min^{-1})	Maximum cardiac output (ml min^{-1})
$\dot{V}O_2$	Taux de consommation d'oxygène (ml 0_2 min^{-1})	Rate of oxygen consumption (ml 0_2 min^{-1})
$\dot{V}O_{2,max}$	Taux maximal de consommation d'oxygène (ml 0_2 min^{-1})	Maximum rate of oxygen consumption (ml 0_2 min^{-1})
$s\dot{V}O_2$	Taux massique de consommation d'oxygène (ml 0_2 kg^{-1} min^{-1})	Body mass-scaling rate of oxygen consumption (ml 0_2 kg^{-1} min^{-1})
V_s	Volume éjectionnel du coeur (ml)	Cardiac stroke volume (ml)

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CHAPITRE I : INTRODUCTION GÉNÉRALE

État des connaissances et problématique

Le vol est un mode de locomotion qui apporte de nombreux bénéfices aux oiseaux. Il leur permet de fuir les prédateurs, d'augmenter le repérage et l'accessibilité à des sites d'alimentation imperceptibles au niveau du sol, de migrer entre les sites de reproduction et d'hivernage ainsi que de franchir des barrières géographiques et de se disperser sur de longues distances (Pennycuick, 1987; Rayner, 1988; Alerstarm, 1993; Lima, 1993; Hildebrand, 1995). Mais comparativement à la marche, à la nage et à la plongée, le vol battu est très coûteux d'un point de vue énergétique, par unité de temps (Berger et Hart, 1974; Masman et Klaassen, 1987; Butler, 1991). Le taux élevé de consommation d'énergie requis pour l'exécution de ce comportement, reposant en majeure partie sur le métabolisme aérobie, impose une forte demande aux systèmes respiratoire, cardiovasculaire et musculaire des oiseaux (Schmidt-Nielsen, 1997).

Selon Walsberg (1983), l'allocation de temps consacrée à divers comportements est l'un des éléments essentiels à l'analyse du budget énergétique des oiseaux. En d'autres termes, il affirme que la variation dans les budgets énergétiques ne peut être comprise sans analyse comportementale. Malheureusement, il existe très peu de méthodes qui permettent d'avoir à la fois des données sur le comportement et l'énergétique du vol chez des oiseaux en milieu naturel.

Cette étude permettra ainsi de faire le lien entre le comportement et l'énergétique liés au vol battu chez les oiseaux. Dans un premier temps, elle décrira la méthode utilisée pour identifier les vols à l'aide de consignateurs de données enregistrant la fréquence cardiaque (chapitre 2). Elle quantifiera ensuite l'aspect temporel du vol à l'échelle quotidienne chez l'Eider à duvet, *Somateria mollissima* (chapitres 2 et 3). Enfin, elle mettra en relation le temps de vol quotidien avec la dépense énergétique quotidienne et elle estimera les coûts énergétiques associés au vol chez cette espèce (chapitre 3).

L'originalité de cette étude repose sur le fait que, grâce à l'utilisation d'une technologie toute récente, il devient possible de réaliser la première description complète du budget de vol quotidien chez une espèce d'oiseau dans son milieu naturel et sans dérangement.

Facteurs contraignant la capacité de vol

Tout d'abord, pour comprendre le vol, il faut connaître ce qui limite ses deux principales phases : le décollage et le vol soutenu. Le décollage dépend principalement de la masse corporelle, de la charge alaire (Pennycuick, 1975) et de la masse des muscles pectoraux (Marden, 1987, 1994). La charge alaire, qui est le rapport de la masse corporelle sur la superficie alaire, augmente avec la masse corporelle. Les oiseaux de grande taille possèderaient donc généralement une charge alaire plus élevée. Meunier (1951) a proposé le seuil de 2,5 g cm^{-2} au-delà duquel les oiseaux n'ont plus la capacité de voler. Marden (1987, 1994) a quant à lui démontré qu'une masse réduite des muscles du vol nuit également au décollage. En fait, lorsque le rapport constitué de la masse des muscles pectoraux sur la masse corporelle (le *flight muscle ratio* - FMR) est inférieur à 0,160 chez un individu, cela signifie que celui-ci ne peut plus décoller sans l'aide du vent ou de la gravité. Guillemette et Ouellet (2005) ont cependant démontré que la capacité de décollage pourrait plutôt être expliquée par l'interaction qui existe entre la charge alaire et le FMR.

Une variation des facteurs mentionnés dans le paragraphe précédent peut donc entraîner des périodes dans les cycles quotidiens et annuels pendant lesquelles il y a une inaptitude temporaire au vol. De telles périodes se produisent lors de phases répétées et rapprochées d'alimentation qui favorisent l'accumulation de proies dans le système digestif (Guillemette, 1994); lors d'atrophie musculaire (Gaunt *et al.*, 1990) ou lors d'une augmentation de la charge alaire. Cette dernière peut être causée soit par une réduction de la superficie des ailes, comme au cours de la mue chez les canards, les oies et les grèbes (Gill, 1994), soit par une obésité pré-migratrice (Jehl, 1997) ou pendant la période pré-ponte lorsque les femelles sont gravides (Guillemette et Ouellet, 2005).

Le vol soutenu est quant à lui principalement dépendant des systèmes cardiovasculaire et respiratoire qui fournissent aux muscles en mouvement les métabolites nécessaires au métabolisme aérobie, ainsi que de l'efficacité des fibres musculaires à convertir cette énergie chimique en énergie mécanique (Pennycuick, 1989; Schmidt-Nielsen, 1997). Tout comme n'importe quelle forme d'exercice soutenu, le vol est par conséquent dépendant de l'apport en oxygène, des réserves énergétiques (lipides, glucides et protéines) et de l'évacuation des déchets métaboliques, mais à un rythme beaucoup plus élevé que toutes les autres formes. Il est également limité par le contrôle thermique et la perte hydrique (Withers, 1992).

L'influence du coût énergétique du vol sur le budget de temps

Le vol battu est, à masse égale, énergétiquement plus coûteux par unité de temps que la course ou la nage (Berger et Hart, 1974; Masman et Klaassen, 1987; Butler, 1991). Ce type de locomotion permet cependant aux oiseaux de minimiser les coûts de transport ($J\ kg^{-1}\ m^{-1}$) pour effectuer de longues distances parce que la vitesse atteinte est beaucoup plus grande que par la voie terrestre (Withers, 1992). Il reste que le coût métabolique du vol est plus élevé et c'est pourquoi les oiseaux sont parcimonieux dans l'utilisation qu'ils font de ce type de locomotion. Walsberg (1983) a démontré, en compilant les données de diverses études portant sur des espèces pratiquant le vol battu, que le temps passé en vol par période active quotidienne était approximativement de 11% chez des espèces de masse corporelle d'environ 10 g et de seulement 3% chez des espèces de plus de 100 g. Cependant, le temps passé en vol ne dépend pas uniquement de la masse corporelle. Selon Masman et Klaassen (1987), il faut aussi considérer la morphologie alaire. D'après ces auteurs, les espèces qui possèdent un rapport d'apparence (= envergure^2/superficie alaire) plutôt faible (qui est représenté par de courtes ailes pointues) passent moins de temps en vol parce que ce type de locomotion représente une dépense énergétique plus élevée en raison de la plus faible surface portante des ailes.

De plus, les études de budget temporel et énergétique ont démontré que la dépense énergétique quotidienne était directement reliée au temps passé en vol, principalement chez les espèces qui présentent une dépense énergétique plus élevée pendant le vol (Flint et Nagy, 1984; Tatner et Bryant, 1986; Carlson et Moreno, 1992; Nudds et Bryant, 2000). Par conséquent, toute étude qui veut quantifier l'impact des coûts énergétiques associés au vol sur le budget énergétique quotidien des oiseaux doit à la fois mesurer le temps de vol quotidien, la dépense énergétique qui lui est associée ainsi que la dépense énergétique quotidienne.

Les méthodes pour l'étude comportementale et énergétique du vol

Malgré la gamme des méthodes connues pour l'étude des oiseaux, il en existe très peu qui permettent à la fois d'étudier le comportement de vol des oiseaux en milieu naturel et de connaître la dépense énergétique qui lui est associée.

Traditionnellement, la méthode qui a été la plus utilisée pour étudier le comportement et pour déterminer la dépense énergétique quotidienne est celle du budget de temps. Malgré le fait que cette méthode a été employée dans plus de 40 études en ornithologie (revues par Weathers *et al.*, 1984, ainsi que par Nagy, 1989), un nombre limité d'entre elles a réussi à inclure la portion quotidienne de temps consacrée au vol dans le budget de temps quotidien, sauf dans des conditions contrôlées en laboratoire ou dans des environnements extérieurs modifiés (chapitre 3). Il s'avère que cette méthode soit inadéquate pour étudier le vol en milieu naturel : elle exige trop de temps d'observation et, en raison de la grande mobilité des oiseaux en vol, elle ne permet pas d'assurer un suivi continu et complet à partir d'un point fixe d'observation (Weathers *et al.*, 1984; Nagy, 1989).

Au niveau purement énergétique, quelques méthodes ont été développées depuis la fin des années 60 pour étudier le vol. Rares sont celles cependant qui ont permis d'étudier les oiseaux dans leur environnement naturel en raison de la difficulté à mesurer des paramètres physiologiques chez des individus en vol. C'est pourquoi des modèles théoriques et empiriques ont d'abord dû être élaborés. Ceux-ci se divisent en trois catégories :

- les modèles basés sur la théorie aérodynamique (Tucker, 1973; Greenewalt, 1975; Rayner, 1979; Pennycuick, 1989) ;
- les modèles empiriques développés à partir d'équations allométriques utilisant la masse corporelle (et parfois la masse du cœur pour certaines variables) (Berger et Hart, 1974; Bishop et Butler, 1995; Bishop, 1997) ;
- les modèles empiriques reposant sur la morphologie alaire et la masse corporelle (Masman et Klaassen, 1987; Rayner, 1995).

Bien que largement utilisés dans de nombreuses études pour estimer le coût du vol, ces modèles interspécifiques ne fournissent aucune donnée sur le comportement tandis que celles obtenues sur la dépense énergétique sont plutôt générales et ne permettent pas de décrire les variations temporelles du coût associé à une activité spécifique (Bishop *et al.*, 2002)

Certaines méthodes ont cependant été développées pour étudier le vol lors de périodes précises du cycle annuel en milieu naturel ou en laboratoire.

La plus ancienne est sans doute celle développée pour l'étude des vols migratoires. Cette méthode considère la perte pondérale, consécutive à un vol de longue durée, comme indicateur de la dépense énergétique. On simplifie encore plus en supposant que les lipides constituent la plus grande part de cette perte (Nisbet *et al.*, 1963). Cette méthode a été fortement critiquée: entre autres parce qu'elle ne permet pas de connaître le temps passé en vol par les oiseaux (Butler et Bishop, 2000) et parce que les oiseaux en migration catabolisent aussi des glucides et des protéines (ex. : intestins et muscles) en proportion plus ou moins importante selon le type et la durée des vols (Rothe *et al.*, 1987; Piersma et Jukema, 1990; Jenni-Eiermann et Jenni, 1991; Battley *et al.*, 2000).

La méthode la plus utilisée pour l'étude de l'énergétique avienne demeure celle de l'eau doublement marquée qui permet d'obtenir une approximation intéressante de la consommation d'oxygène en estimant la production de dioxyde de carbone (Hails, 1979; Weathers *et al.*, 1984; Nolet *et al.*, 1992; Hawkins *et al.*, 2000; Nudds et Bryant, 2000). Cette méthode a obtenu un certain succès en laboratoire et en milieu naturel, mais elle présente deux inconvénients majeurs pour l'étude du vol en milieu naturel : la durée de l'expérience (d'au moins quatre heures à quelques jours) est limitée par le taux de transfert des isotopes utilisés (Nagy, 1989) et l'estimation de la dépense énergétique est seulement une valeur moyenne entre deux moments de prélèvement (Speakman et Racey, 1988). Par conséquent, cette méthode utilisée seule ne permet pas d'isoler le coût énergétique relié au vol puisque qu'on ne connaît pas le temps passé à utiliser ce type de locomotion.

Enfin, les avancements technologiques récents ont permis le développement de la biotélémétrie et des consignateurs de données permettant l'étude du comportement et de la physiologie des oiseaux en milieu naturel (Hart et Roy, 1966; Butler et Woakes, 1980; Butler, 1989; Bevan *et al.*, 1995; Woakes *et al.*, 1995; Butler et Jones, 1997; Butler *et al.*, 1998; Weimerskirch *et al.*, 2001). Les consignateurs de données qui permettent d'enregistrer la fréquence cardiaque, la pression hydrostatique et la température corporelle semblent être les outils les plus prometteurs pour l'étude combinée du comportement et de la physiologie du vol chez des oiseaux en milieu naturel.

Ces dernières années, plusieurs études qui ont utilisé ces appareils se sont attardées à la relation existant entre la fréquence cardiaque (f_H) et la consommation d'oxygène ($\dot{V}O_2$) pour l'estimation du coût énergétique de différentes activités. Cette relation s'exprime par l'équation de Fick :

$$\dot{V}O_2 = f_H \times V_s \times (C_{aO_2} - C_{\bar{v}O_2})$$

où V_s est le volume éjectionnel du coeur, C_{aO_2} est la concentration en oxygène du sang artériel et $C_{\bar{v}O_2}$ est la concentration en oxygène du sang veineux mélangé (la différence correspond à l'extraction d'oxygène).

À partir de cette équation, deux méthodes ont été employées pour calculer la $\dot{V}O_2$ en vol : une première repose sur la mesure ou le calcul de chacune des variables de manière indépendante et une autre tente d'établir une relation idéalement linéaire entre la f_H et la $\dot{V}O_2$.

La mesure de chacune des variables de l'équation de Fick (sauf une) a été réalisée une première fois par Butler *et al.* (1977), et une seconde fois par Peters *et al.* (2005), avec des pigeons (*Columba livia*) en vol dans une soufflerie (*wind tunnel*), mais jamais en milieu naturel (V_s a été déduit des autres mesures). Le problème repose essentiellement sur la difficulté technique à mesurer V_s et $C_{aO_2} - C_{\bar{v}O_2}$ chez des oiseaux en vol. Bishop et Butler (1995) affirment cependant qu'il est possible d'obtenir une estimation du $\dot{V}O_2$ minimal au vol en mesurant f_H avec les consignateurs de données conçus par Woakes *et al.* (1995), d'estimer V_s en utilisant la relation allométrique $V_s = 0{,}3\ M_h^{1{,}05}$ (où M_h est la masse du cœur) et en utilisant une valeur de $C_{aO_2} - C_{\bar{v}O_2}$ égale à 0,083 ml O_2 ml sang^{-1} obtenue avec des pigeons (Butler *et al.*, 1977). Jusqu'à tout récemment, cette dernière valeur était la seule à avoir été obtenue chez des oiseaux en vol. Peters *et al.* (2005), en reprenant sensiblement la même étude, ont toutefois obtenu des résultats beaucoup plus élevés pour le $\dot{V}O_2$. Puisque les valeurs de f_H et de V_s étaient similaires à celles obtenues par Butler *et al.* (1977), ils ont expliqué cette différence par une augmentation de l'extraction d'oxygène (0,138 ml O_2 ml sang^{-1}) due à un hématocrite plus élevé dans leurs oiseaux.

Bishop (1997) a par la suite proposé qu'il serait plus intéressant d'utiliser une valeur d'extraction d'oxygène qui permettrait d'estimer la valeur maximale de $\dot{V}O_2$. Il conseille d'utiliser une mesure (lorsque possible) ou une estimation de la concentration d'hémoglobine pour estimer C_{aO_2} ; cette estimation étant la valeur moyenne mesurée pour plusieurs espèces d'oiseaux, soit 0,151 g ml^{-1}. Ensuite, il multiplie cette valeur par 1,36 (pour calculer la capacité de transport de l'hémoglobine saturée) et par 0,94 (en supposant que le sang artériel est saturé à 94 % lors d'une activité maximale). Cette valeur est la moyenne qui a été obtenue pour sept espèces de mammifères courant à $\dot{V}O_{2,max}$ (Grubb, 1983). Peters *et al.* (2005) ont validé la méthode de Bishop (1997) chez des pigeons pour estimer C_{aO_2} puisque les résultats mesurés et estimés étaient très similaires. Finalement, pour estimer la $C_{aO_2} - C_{\bar{v}O_2}$ maximale chez des oiseaux volant à leur puissance aérobie maximale, Bishop (1997) suppose que la $C_{\bar{v}O_2}$ ne tombe pas en bas de 0,038 ml O_2 ml sang^{-1} (cette dernière valeur a également été mesurée chez sept espèces de mammifères courant à $\dot{V}O_{2,max}$ [Grubb, 1983]).

Ces dernières années, une autre méthode a été utilisée en laboratoire pour tenter d'estimer $\dot{V}O_2$. Cette méthode repose sur l'établissement d'une relation entre f_H et $\dot{V}O_2$ sans avoir à mesurer $C_{aO_2} - C_{\bar{v}O_2}$ et V_s. Quelques études ont permis de calibrer la relation $\dot{V}O_2 / f_H$ en laboratoire pour l'étude de la locomotion terrestre comme la marche et la nage (Nolet *et al.*, 1992; Bevan *et al.*, 1994; Hawkins *et al.*, 2000; Froget *et al.*, 2001), mais ce n'est que tout récemment que des chercheurs ont réussi à le faire pour l'étude du vol (Ward *et al.*, 2002). Ces résultats ont été obtenus en faisant voler des bernaches nonnettes (*Branta leucopsis*, 1,6 – 2,3 kg) et une Oie à tête barrée (*Anser indicus*, 2,9 kg) dans une soufflerie, en enregistrant simultanément les deux paramètres et en transposant la relation à des individus en milieu naturel pour lesquels f_H était enregistrée continuellement. Ils ont démontré qu'il existait une relation linéaire entre f_H et $\dot{V}O_2$ (chez la Bernache nonnette : $\dot{V}O_2 = 1{,}42\, f_H - 304{,}4$; $r^2 = 0{,}82$; $p < 0{,}001$; $N = 12$ vols et chez l'Oie à tête barrée : $\dot{V}O_2 = 1{,}97\, f_H - 467{,}5$; $r^2 = 0{,}90$; $p < 0{,}001$; $N = 11$ vols). C'est la seule étude à avoir calibré cette relation pendant le vol.

Même s'il existe des équations pour les autres types de locomotion, celles-ci ne peuvent pas être utilisées pour le vol. En comparant une même fréquence cardiaque obtenue pendant la pratique de la marche et du vol, Bishop *et al.* (2002) ont démontré que la consommation d'oxygène était le double lors du vol, ce qui pourrait être le résultat d'une augmentation substantielle du volume éjectionnel du coeur, due à une augmentation du retour veineux (loi de Frank-Starling) (Bishop et Butler, 1995), et par conséquent du débit cardiaque, associée à une augmentation de l'extraction d'oxygène du sang (Butler *et al.*, 1977). Bishop *et al.* (1996) ont expliqué ceci chez la Bernache nonnette par le fait que les muscles du vol sont approximativement le double de ceux associés à la locomotion terrestre et qu'ils ont une capacité aérobie plus élevée (Bishop *et al.*, 1995). Ce patron général est probablement le même pour la plupart des espèces (Hartman, 1961 cité par Bishop *et al.*, 2002) et ainsi, il semble vraisemblable que les relations $\dot{V}O_2$ / f_H durant des exercices nécessitant les muscles antérieurs ou postérieurs soient aussi différentes pour un grand nombre d'espèces d'oiseaux.

Au niveau comportemental, les consignateurs de données sont également prometteurs pour étudier le vol de manière continue en milieu naturel. En effet, lorsque les appareils ont la capacité d'enregistrer la fréquence cardiaque et la pression hydrostatique dans de courts intervalles de temps entre chacune des données, il est possible d'identifier certains comportements ou certaines périodes du cycle annuel. L'identification est effectuée en associant les profils de fréquence cardiaque avec des observations visuelles chronométrées. Les plongées sont, par exemple, caractérisées par une augmentation de la pression hydrostatique et par une bradycardie, suivies d'une tachycardie importante lors de la remontée et du retour à la surface (Stephenson *et al.*, 1986).

En ce qui concerne le vol, quelques chercheurs (Lord, 1962; Butler *et al.*, 1977; Kanwisher *et al.*, 1978; Bevan *et al.*, 1997; Butler *et al.*, 1998; Ely *et al.*, 1999; Butler *et al.*, 2000) ont noté que la fréquence cardiaque enregistrée pendant un vol présente un profil particulier. Celui-ci est caractérisé par une augmentation instantanée du rythme cardiaque jusqu'à l'atteinte d'un plateau et par le maintien de ce plateau pendant de longues séquences de temps (en fait, durant toute la durée du vol). Malgré que ces auteurs aient noté ces profils spécifiques, aucun d'entre eux ne les a utilisés pour identifier tous les vols (courts et migratoires) dans une longue série de données, principalement parce que les enregistrements étaient effectués sur des intervalles de temps allant de quelques minutes à quelques jours.

Par ailleurs, la moyenne de fréquence cardiaque enregistrée pendant le vol battu chez des oiseaux en liberté est significativement différente des valeurs enregistrées pour d'autres comportements (Bevan *et al.*, 1997), à l'exception d'un seul comportement qui a été observé une seule fois dans une seule étude (Ely *et al.*, 1999). En effet, Ely *et al.* (1999) ont observé qu'un comportement d'agression entre deux oies avait eu comme conséquence de faire monter très rapidement la fréquence cardiaque, en l'espace de quelques secondes, jusqu'à 400 battements min^{-1}. Or, d'après quelques études qui ont enregistré cette variable chez des oiseaux en milieu naturel, la fréquence cardiaque moyenne pour des bernaches nonnettes (*Branta leucopsis*) en migration est de 253 ± 10 battements min^{-1} (Butler *et al.*, 1998), 413 ± 6 battements min^{-1} pour des vols courts chez des oies rieuses (*Anser albifrons*, Ely *et al.*, 1999), 310 ± 18 battements min^{-1} pour des vols courts chez des cormorans géorgiens (*Phalacrocorax georgianus*, Bevan *et al.*, 1997) et 448 ± 9 battements min^{-1} pour des vols provoqués par un dérangement humain chez des Oies rieuses (*Anser albifrons,* Ackerman *et al.,* 2004). Par conséquent, l'identification des vols courts en utilisant les profils cardiaques pourrait poser plus de problèmes que l'identification des vols migratoires. C'est pourquoi il est essentiel d'effectuer une comparaison de la fréquence cardiaque mesurée dans différents comportements pour s'assurer que le profil cardiaque utilisé pour identifier les vols est spécifique à ce comportement (chapitre 2).

Espèce modèle

L'Eider à duvet (*Somateria mollissima*) est le plus gros anatidé (2 kg) de l'Hémisphère nord (Goudie *et al.*, 2000) et il possède une répartition circumboréale. C'est un canard plongeur qui se nourrit majoritairement de moules bleues (*Mytilus edulis,* Cottam 1939; Guillemette *et al.*, 1992). Cette espèce possède également des ailes de faible superficie, pointues et courtes. Ces caractéristiques font que l'eider est l'une des espèces qui possède la charge alaire (masse/superficie alaire) la plus élevée parmi tous les oiseaux volants (environ 2,0 g cm^{-2}; Rayner, 1988; Guillemette, 1994). Par conséquent, il se retrouve fréquemment à la limite de sa capacité de vol et subit des périodes d'incapacité temporaire de décollage (Guillemette, 1994; Guillemette et Ouellet, 2005). Cette espèce est aussi hautement philopatrique à son site de nidification (Anderson *et al.*, 1992). Ces deux dernières particularités sont les raisons principales qui font que cette espèce a été choisie comme espèce modèle pour l'étude du vol avec des consignateurs de données. La philopatrie élevée est essentielle pour récupérer les consignateurs l'année suivant l'implantation puisque ceux-ci ne transmettent pas la position géographique de l'oiseau. De plus, puisque cette espèce est à la limite de sa capacité de décollage, il est fort possible que le coût énergétique soit très élevé pour vaincre la gravité et se maintenir dans les airs. Par conséquent, on peut émettre l'hypothèse que cette espèce pourrait utiliser ce moyen de locomotion avec parcimonie tout au long de la journée et de l'année pour limiter sa dépense énergétique quotidienne.

À l'inverse, le type de technologie utilisé est également particulièrement adéquat pour l'étude de cette espèce de canards marins parce que ceux-ci passe la majeure partie du temps en mer et sont souvent inaccessibles avec les moyens traditionnels d'observation.

But général et objectifs

Le but général de cette étude consiste à effectuer la première analyse descriptive à long terme du budget de vol quotidien chez une espèce d'oiseau et d'estimer la dépense énergétique de ce type de locomotion en milieu naturel. Ceci a été possible grâce à l'utilisation des consignateurs de données qui ont permis d'assurer le suivi continu de la fréquence cardiaque. Les appareils ont été implantés dans la cavité abdominale de femelles Eider à duvet durant la période de reproduction. En plus d'enregistrer la fréquence cardiaque, ces appareils ont également consigné la température corporelle (celle-ci n'a pas été utilisée dans l'étude), la pression hydrostatique et, pour certains appareils utilisés dans le chapitre 2, un interrupteur permettant de distinguer la position horizontale et oblique du corps. Cette étude a comporté trois objectifs :

Objectif 1 : Calibrer les consignateurs de données en effectuant des observations visuelles chronométrées en continu des comportements de l'Eider à duvet en milieu naturel, durant la période post-éclosion. Cette calibration a eu pour but d'identifier et de quantifier les profils de fréquence cardiaque caractéristiques du vol et de les distinguer des autres comportements affichés par l'Eider à duvet (première partie du chapitre 2).

Objectif 2 : Partitionner le temps de vol en ses composantes migratoires et locales et analyser l'occurrence du vol en relation avec l'heure de la journée ainsi qu'avec le comportement alimentaire de l'Eider à duvet (seconde partie du chapitre 2).

Objectif 3 : Quantifier le temps de vol quotidien de l'Eider à duvet, estimer la dépense énergétique associée au vol chez cette espèce et tester la relation entre le temps de vol quotidien et la dépense énergétique quotidienne (chapitre 3).

CHAPITRE II : PREMIER ARTICLE

Manuscrit à être soumis à un journal scientifique

Veuillez prendre note que l'expression « Chapitre 3 », qui fait suite à « Pelletier et al. in prep. *» et qui réfère au deuxième article de ce mémoire, a été ajoutée pour nous assurer que le lecteur du mémoire comprenne bien la provenance de l'article cité. Celle-ci sera effacée lors de la soumission de l'article.*

It's time to move: a new technique to monitor flight behaviour of a free-living bird

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Résumé

Le vol est l'un des comportements les plus insaisissables chez les oiseaux. Les ornithologues sont par conséquent rarement capables d'étudier le vol sur de longues périodes de temps. Nous décrivons dans cette étude une nouvelle technique pour étudier la fréquence et la durée des vols sur plusieurs mois en implantant des consignateurs de données (DL – *data logger*) qui enregistrent la fréquence cardiaque (f_H), la pression hydrostatique (profondeur de plongée) et l'angle postural. Nous avons implanté les DLs dans 30 eiders à duvet (*Somateria mollissima*) femelles nichant sur l'île Christiansø (au Danemark), en 2003 et en 2004. Nous avons réalisé des observations focales pendant la période post-éclosion pour comparer la f_H associée à 10 comportements avec celle enregistrée pendant le vol. Bien que la f_H moyenne enregistrée durant le vol (374 ± 17 battements min^{-1}, moyenne ± *S.E.M.*) n'était pas significativement différente de celle enregistrée pendant la baignade (293 ± 50 battements min^{-1}) ou pendant la pause située entre deux plongées successives (332 ± 50 battements min^{-1}), il a tout de même été possible d'identifier le vol. La signature cardiaque du vol était caractérisée par une augmentation instantanée durant le décollage (seuil $\geq$ 250 battements min^{-1} et pente $\geq$ 10 battements min^{-1} s^{-1}), un plateau (seuil $\geq$ 300 battements min^{-1}) et une descente instantanée durant l'atterrissage (pente $\leq$ -10 battements min^{-1} s^{-1}). L'interrupteur de l'angle postural se mettait en fonction lors du décollage et s'arrêtait pendant l'atterrissage. Avec cette signature cardiaque du vol, nous avons cumulé le temps de vol durant huit mois et celui-ci a ensuite été divisé en temps de vol migratoire et en temps de vol local. Nous avons pu ainsi confirmer que les eiders sont des migrateurs de courte distance et que la plus grande part des coûts énergétiques associés au vol pendant le cycle annuel est allouée aux vols locaux. Toutefois, à l'extérieur des journées en migration, les eiders utilisent le vol avec parcimonie (0,16 ± 0,04 h jour^{-1}). Ils volent préférentiellement durant l'aube, le matin et l'après-midi (en ordre décroissant) et l'utilisation de ce moyen de locomotion est fortement corrélée aux activités d'alimentation en plongée (*r* de Pearson = 0,88; test de permutation $p < 0{,}001$). Nous proposons que la technique décrite dans cette étude présente un potentiel certain pour ouvrir de nouvelles avenues pour la recherche en ornithologie.

Mots-clés: comportement de plongée, comportement de vol, consignateur de données, Eider à duvet, fréquence cardiaque, individus en liberté, Somateria mollissima

Abstract

Flight is one of the most elusive behaviours of birds. Thus, ornithologists are rarely able to monitor flight behaviour over long periods of time. Here, we describe a new technique to monitor the frequency and duration of flights over several months by implanting a data logger (DL) which records heart rate (f_H), hydrostatic pressure (diving depth) and the body angle. We implanted DL in 30 female common eiders (*Somateria mollissima*) nesting on Christiansø Island (Denmark), in 2003 and 2004. We performed focal observations during the post-hatching period to compare f_H of 10 behaviours with f_H recorded during flight. Although the mean f_H recorded during flight (374 ± 17 beats min^{-1}; mean ± *S.E.M.*) was not significantly different than f_H recorded during bathing (293 ± 50 beats min^{-1}) or during the pause between two successive dives (332 ± 50 beats min^{-1}), it was still possible to identify flying behaviour. The f_H flight signature was characterized by instantaneous increase upon take-off (threshold $\geq$ 250 beats min^{-1} and slope $\geq$ 10 beats min^{-1} s^{-1}), plateau (threshold $\geq$ 300 beats min^{-1}) and instantaneous decrease upon landing (slope $\leq$ -10 beats min^{-1} s^{-1}). Body angle switch was turned on during take-off and turned off during landing. By using this flight signature, we cumulated flight time during eight months and we partitioned it into migratory flights and local flights. We concluded that eiders are short distance migrants and that the largest proportion of flight costs during the annual cycle was devoted to local flights. Outside migration days, we found that eiders use flight infrequently (0.16 ± 0.04 h day^{-1}), that activity occurs preferably during dawn, morning and afternoon (in decreasing order) and that flying activities are related to diving activities (Pearson $r = 0.88$, permutation test $p < 0.001$). We propose that the technique described here is sure to open new avenues of investigation in ornithological research.

Key words: Common Eider, data logger, diving behaviour, flying behaviour, free-living birds, heart rate, Somateria mollissima

Introduction

The long-term study of flight behaviour in free-living birds has not been previously possible because of technical and logistical difficulties. Although radars or satellite telemetry have been used to analyze orientation and duration of long migrating flights, they have not been able to provide information about flights of shorter duration (Casement 1966, Bruderer and Liechti 1995, 1998, Gudmunsson *et al.* 1995, Pennycuick *et al.* 1996, Butler *et al.* 1998, Desholm 2003). To quantify short local flights, researchers have used visual observations and time-budget methods, but they were limited to non-obstructed environments in daylight period, during a small period of the year and this elusive behaviour was often the reason for stopping an observation period (discussed by Walsberg 1983, Tatner and Bryant 1986, Pelletier *et al. in prep.* [Chapitre 3]).

New advances in data logging (DL) systems allow researchers to pass beyond the physical and environmental boundaries that have previously limited their investigations of flight (Boyd *et al.* 2004). DL that record heart rate (f_H) are now used to estimate energy expenditure during flight in the field (Butler *et al.* 1998). Knowing that forward flapping flight is the most energetically costly type of sustained activity per unit of time (Schmidt-Nielsen 1972, Norberg 1990) and knowing that f_H increases dramatically at take-off and decreases instantaneously upon landing (Lord 1962, Butler *et al.* 1977, Kanwisher *et al.* 1978, Bevan *et al.* 1997, Butler *et al.* 1998, Ely *et al.* 1999, Butler *et al.* 2000), the f_H

signature of flight (shape of trace in relation to time) could be described and thus, flight schedules (number and duration of flights) could be easily quantified with data from DL.

We used a DL (Woakes *et al.* 1995), which measures f_H, hydrostatic pressure (diving depth) and changes in body angle, to quantify the f_H flight signature in a seabird species.

The common eider (*Somateria mollissima*, hereafter eider), as many other large aquatic birds, needs to run across the water in order to take off and become airborne (Norberg 1990). This species is characterized by short pointed wings and high wing loading (Rayner 1988, Guillemette 1994) and the aerodynamic theory (Pennycuick 1969, 1975, Greenewalt 1975, Rayner 1988, Norberg 1990) predicts that for birds showing these characteristics, the energetic cost of flight is high. Thus, high and sustained f_H should be a good indicator of flight occurrence, easily distinguishable from other behaviours.

In the present paper, we report the characteristics of flight signature and we present data of observations during the post-hatching period in order to discriminate f_H recorded during flight from that recorded during other behaviours. Finally, to show the potential of this new technique, we analyze the occurrence of flight behaviour in relation to the time of day and foraging frequency. We also partition flight time into migratory flight and local flight categories to identify when the largest share of flight costs is expended during the annual cycle.

Methods

Study site. The field work was carried out on Christiansø island (55°19' N, 15°12' E), an old fortress located in the southern Baltic Sea, 18 km from the Danish island of Bornholm. The island is populated with 120 people and approximately 2 600 breeding pairs of eiders (Lyngs 2000). This colony was selected due to the abundance of prior information on general movement of individuals in the colony (Franzmann 1980, Lyngs 2000). Eiders are known to perform relatively short migrations (less than 1000 km along the longitudinal axis and 500 km along the latitudinal axis) from the breeding colony to a large wintering area (from southern Kattegat to the Dutch Wadden Sea; Franzmann 1980, Lyngs 1992).

Data loggers, selection and implantation procedure. In 2003 and 2004, 20 and 10 female eiders, respectively, were equipped with data logger (DL). All experimental females were captured in the second part of their incubation because they are more resistant to disturbance during this period (Bolduc and Guillemette 2003). Females were identified by a set of two colour bands on one tarsus and a numeric metallic band on the other tarsus. The 30 DL used in the present study recorded f_H (2 Hz) and hydrostatic pressure (diving depth) (2 Hz). DL of 2004 were also equipped with a body angle switch that turns on when the DL is at an angle of +45 ° or -45 °. This binary information (on or off) was recorded with a frequency of 1 Hz. DL were 36 mm long × 28 mm wide × 11 mm thick and had a mass of 21 g after encapsulation in paraffin wax to provide waterproofing and a silicone coating for biocompatibility. DL accounted for 1.2 % of the bird's body mass at implantation (2003:

1752 ± 144 g, $N = 20$; 2004: 1735 ± 176 g, $N = 10$). Previous studies have shown that implanting DL for one full year do not affect reproductive success when compared to a control group (Guillemette *et al.* 2002). All surgical procedures were conducted indoors by a veterinary surgeon under a licence from Dyreforsøgtilsynet (Royal Veterinarian Corporation) in Denmark and all birds were cared for in accordance to the principles and guidelines of the Canadian Council on Animal Care. Birds were under isoflurane anaesthesia while the sterilized DL was inserted into the abdominal cavity via midline incision in the skin and body wall. To prevent infection, a long-acting antibiotic (*LA Terramycin,* Pfizer, New York) was injected intramuscularly. The removal procedure, one year later, was similar. The implantation and removal times (from capture to release of the bird at the nest) were less than 45 min.

FLIGHT SIGNATURE AND CALIBRATION

Behavioural observations. To compare f_H recorded during flight to f_H recorded during different activities, we conducted focal observations (only one animal at a time) on 17 experimental females during the post-hatching period in 2003 and on 10 females during the post-hatching period in 2004 (total of 118 h of observation). However, data from only 10 of the 17 females were available for analysis in 2003: three females left the colony immediately after hatching and for four females it proved impossible to synchronise focal observation with the data recorded by the logger. For similar reasons, data from only four females were available for analysis in 2004. Behaviours were recorded using 7× binoculars and a 20-60× power spotting scope. Behaviours were assigned to one of 11 categories: (1)

aggression (between conspecifics, instigator or victim, instigator has head fully extended towards the victim, hitting or biting with bill, on water or land), (2) alarm (head up, neck fully extended, back horizontal to ground (or water) or chest higher than tail), (3) bathing (swimming on water with wing flapping and head submersion), (4) dabbling (head completely into water with body vertical to water or not), (5) diving (bird totally submerged), (6) flying (bird in the air), (7) pausing between dives (floating on water for several seconds between two successive dives throughout a foraging [diving] sequence), (8) resting (neck coiled on back or head and neck on back with bill pointing towards tail), (9) standing or preening (head up and not moving or manipulating feathers with bill, on water or land), (10) swimming (slow or fast movement on water) and (11) walking (slow or fast movement on land).

By using the signature of recorded flight activity performed during the post-hatching period, we found the set of parameters giving the best description of the shape of trace in relation to time. The parameters were programmed in a purpose-designed software for the extraction of all flights performed by each female. The set of parameters were then validated by visual analysis of traces in all recording days in each female to ensure that the parameters selected only the f_H signatures related to flight.

FLIGHT TIME

Data analysis. Only females implanted in 2003 were included in analysis of flight time. Eighteen females returned to the colony (90%) for laying, seventeen of which were recaptured one year later and their DL was removed. Only thirteen loggers had their memory full (220 days) or almost full (190 to 207 days) as four loggers failed because of power shortage or electronic problems. Thus, the number of recording days varied between females (range 45 to 221 days) spanning from May 2003 to the end of June 2003 until the middle of December 2003. Only data from DL with more than 190 recording days were included in analyses ($N = 13$).

Local vs. migration flights. Using the flight signature, we cumulated the total flight time of these 13 individuals. A frequency distribution of flight duration was used to discriminate local foraging flights from migration flights, taking into consideration that flights shorter than 30 min (99 % of total flights) were local flights. A complete description of migration strategies will be presented elsewhere (Guillemette *et al.*, *unpubl. data*). Briefly, migration periods are easily detected by both longer flight duration and higher flight frequency. Days with one flight longer than 30 min were considered migration days and we cumulated flight time recorded during these days (which included flights shorter or longer than 30 min) as migration flight time.

Daily time scale. Information from ringing recoveries (see *Study site*) and flight ground speed of this species (17.5 $m.s^{-1}$, Kahlert *et al.* 2003) was used to estimate geographical coordinates before, during and after each migration period with the ArcGIS software version 8.3. Then, with these estimated latitude and longitude, we calculated four distinct events of each day (nautical dawn, sunrise, sunset and nautical dusk) for each female via algorithms of the position of the sun (Schlyter 2005). This gave limits to four periods of the day : dawn, daytime, dusk and night.

Due to the extensive recording duration (about eight months), the duration of each period of the day varied along the sampling period: dawn lasted on average 1.8 h (range: 1.3 - 3.0 h), daytime lasted 6.9 h (range: 3.6 – 8.8 h), dusk lasted 2.0 h (range: 1.3 - 4.4 h) and night lasted 6.4 h (range: 0.0 – 13.7 h). Thus, we had to adjust take-off time of each flight to know which percentage of flights was performed according to time of day relative to sunrise and sunset. We used this equation with each flight:

$$Adjusted\ \ time = \frac{t_0 - H_{sunrise}}{H_{sunset} - H_{sunrise}}$$

where t_0 is the take-off time, H_{sunrise} is sunrise time and H_{sunset} sunset time. Flight was performed during daylight when the adjusted time was between 0 and 1 (where 0 is sunrise, 0.5 is midday and 1 is sunset); dawn, between -0.2 and 0.0 (exclusively); dusk, between 1.0 and 1.2 (exclusively). Flights occurring outside these boundaries were considered as nocturnal flights. Each class equals, on average, approximately 55 min. For the same reason, we adjusted time spent flying per period of the day (one of the four described earlier) by creating a new variable, the *preferential period index*, calculated by dividing time spent flying during a period of the day by the duration of this period at this moment and multiplying it by 100. One hundred percent means that an experimental bird was in constant flight for the entire period.

STATISTICAL ANALYSIS

Recordings from 2003 and 2004 were pooled for calibration of flight signature. Means were calculated from multiple recordings of the same individual to establish a mean f_H of each bird in a given activity. Due to the tachycardia following a dive (Stephenson *et al.* 1986), f_H of the first behaviour observed after a foraging sequence was not included in the calculation of mean f_H. Grand means were calculated for each activity by using means of each individual. Kolmogorov-Smirnov and Lilliefors tests were used to test data distribution. Analysis of variance (ANOVA) was used to test for differences between mean f_H. To detect differences among behaviours and females. ANOVA was followed by Tukey's test for multiple comparisons.

Diving data analysed by Bruneau *et al.* (*unpubl. data*) was used for comparison with flight frequency to investigate the relationship between flying activities and foraging activities. Correlation between these two series were tested using the Pearson correlation test. Pearson r was computed with the original series and then, the permutation distributions of Pearson r were derived for each couple of variables. The p-value was determined from the position of the original Pearson r among the 10 000 resampling values of Pearson r arranged in ascending order (Good 2001, 2005). The statistical significance (alpha) was recognized at $p < 0.05$.

Total flight time for the complete recording period was used to perform statistical analysis. For example, the total duration of all flights performed by one female per period of the day was calculated and divided by the number of flights per period to determine the mean duration of one flight per period of the day. The same analysis was performed with preferential period index by summing flight duration per period and dividing it by total duration of each period. Then, the difference between adjacent periods for each female was calculated and a mean difference (Δ) was calculated. The 95 % confidence intervals (*CI*) of means and average Δ were calculated using a bootstrap re-sampling analysis with 10 000 iterations (Quinn and Keough 2002). When the Δ 95 % *CI* was including the zero value, the two adjacent means were considered non-significantly different.

Systat version 10 for Windows and Resampling Stats add-in version 2 for Microsoft Excel were used for statistical analyses. Mean values are given ± 95% *CI* in the figures and ± *S.E.M.* in the text.

Results

FLIGHT SIGNATURE AND CALIBRATION

Overall, there was significant variation in f_H among behaviours ($F_{10,59} = 13.58$, $p < 0.001$; Figure 1). Mean f_H during flight (374 ± 17 beats min^{-1}), bathing (293 ± 50 beats min^{-1}) and between two successive dives (332 ± 50 beats min^{-1}) were not significantly different from each other. Nevertheless, the non-significant lower f_H of bathing was probably due to the small sample size ($N = 3$) and pausing between dives could be discriminated from flying behaviour with diving depth recordings. Moreover, values of f_H did not vary significantly among individuals ($F_{9,60} = 1.54$, $P > 0.150$). We could not perform statistical test for the interaction of behaviours*individuals due to missing values.

Parameters found to identify f_H flight signature during forward flapping flight was defined using focal observations. They are summarised in Figure 2. The almost instantaneous increase in f_H during take-off and the large decrease during landing are quantified with increasing and decreasing slopes $\geq$ 10 beats min^{-1} s^{-1} (in absolute values). The take-off ascending slope exceeded 250 beats min^{-1} and the f_H plateau reached after take-off and recorded during forward flapping flight exceeded a threshold of 300 beats min^{-1}. To eliminate some f_H events related to diving bouts or bathing behaviour with head submersion that are very similar to flights (Stephenson *et al.* 1986), we removed all f_H events with unstable hydrostatic pressure (standard deviation of diving depth $\geq$ 0.1 m). The body angle switch present in DL of 2004 turned on while birds were taking off from land, stayed on during the majority of plateau phase duration and turned off during the landing. We used this binary data to confirm the other parameters thresholds. With this set of parameters, we could identify flights longer than 18 s with a plateau phase longer than 8 s.

FLIGHT TIME

Mean total flight time (migration and local foraging combined) for females was 39.8 ± 10.7 h (range 20.6 to 54.5 h) over a period of eight months (Table 1). Females performed flights for, on average, 0.16 ± 0.04 h day^{-1} outside migration periods and 2.97 ± 0.81 h day^{-1} during migration periods. Local foraging flights accounted for 71 ± 10 % of total flight time while migratory flights accounted for the remaining 29 ± 10 %.

Local flights for each female were performed primarily between sunrise and sunset (morning = 39 ± 2 % and afternoon = 31 ± 6 %; Figure 3). However, a substantial number of flights were also performed during the night (14 ± 6 %), at dawn (12 ± 5 %) and at dusk (5 ± 2 %). Local flights began mainly 55 min either side of sunrise (20 ± 4 %), declined steadily throughout the day, and experienced a rapid decline at dusk.

Diving activities were performed more during the day (morning = 42 ± 5 % and afternoon = 40 ± 6 %) than during other periods (night = 10 ± 6 %, dusk = 5 ± 2 % and dawn = 3 ± 3 %). As a result, the average flight frequency and dive frequency were highly correlated (Pearson $r = 0.88$, permutation test $p < 0.001$; Figure 3), although diving frequency reached the maximum value about two hours after sunrise.

Females also performed longer flights during the first periods of the day (dawn and morning), from 2.6 ± 0.5 min during dawn and 2.4 ± 0.4 min compared to 1.9 ± 0.5 min during night (Figure 4a). Consequently, early morning flights by female eiders are longer than nocturnal flights by about 18-35 % (21-40 s longer on average or about 368-700 m longer in distance for each flight). The *preferential period index* (PPI) showed clearly that eiders preferred mornings (0.8 ± 0.2 %) and afternoons (0.6 ± 0.2 %) as opposed to nights (0.2 ± 0.1 %) for flying and even more dawns (1.0 ± 0.6 %) than mornings (0.8 ± 0.2 %, Figure 4b). Despite very different mean durations throughout the sampling period, dusk (mean 2.0 ± 0.9 h) and night (mean 6.4 ± 4.3 h) showed similar PPI for flying.

Discussion

That the fact that heart rate increases to high levels during forward flapping flight has been documented for almost four decades by physiologists studying both short flights (Lord 1962, Kanwisher 1978, Bevan *et al.* 1997) and migration flights (Butler *et al.* 1998, Butler *et al.* 2000). However, until now, f_H signature has never been used to identify and quantify flight events in a wild bird species. In the present study, we provide, to our knowledge, the first identification and quantification of flight events using f_H signature in a wild bird.

FLIGHT SIGNATURE AND CALIBRATION

It is easy to distinguish flights (duration > 18 s) from other activities using f_H data recorded in DL in a bird performing forward flapping flight. The only activity that could be similar to flight is bathing behaviour, during which the bird is flapping its wings continuously and rapidly over the water and frequently submerging its head underwater. However, bathing behaviour, in spite of high mean f_H, shows distinctive traces of f_H such as a bell shape (without abrupt ascending and descending slopes of f_H – Figure 2 [c]) with a lot of variation in f_H. This variation is caused by momentary bradychardia that occurs each time the bird submerges its head (Stephenson *et al.* 1986). Moreover, Ely *et al.* (1999) observed that antagonistic social interactions between geese could rapidly increase heart rate to 400 beats min^{-1} within a few seconds (1 - 2.5 s). However, since we only considered heart rate events > 18 s as a flight, we most probably excluded these types of behaviours.

The technique presented here permits the collection of extensive flight budget data for each experimental female. Based on approximately 300 h of visual observations in winter, 97 % of all flights by female common eider ducks lasted longer than 15 s (Pelletier and Guillemette, *unpubl. data*). Thus, we most likely did not underestimate flight frequency by recording only heart rate events > 18 s. However, this potential slight underestimation of flight frequency is probably counteracted by pre-flight increase of f_H. Ackerman *et al.* (2004) demonstrated that heart rate increases most rapidly at 5 s prior to flushing in disturbed Tule Greater White-fronted Goose (*Anser albifrons*). Since flights with our technique start with the dramatic increase of f_H (ascending slope ≥ 10 beats min^{-1} s^{-1}), we may overestimate the duration of each flight by about 5 s. Considering a mean flight frequency of 4.1 ± 1.3 flights per day (Pelletier *et al. in prep.* [Chapitre 3]), it is possible that we have overestimated daily flight time by 20 s. Also, Kanwisher *et al.* (1978) mentioned that a loud noise, like a shout, can produce a pre-flight acceleration in a startled bird. However, these pre-flight accelerations of f_H remain negligible in a bird species that use flight with such a low frequency. There is also the possibility that our technique fails to detect flights without accelerating and take-off phases (e.g. bird taking off from a small cliff), but eiders are rarely on high ground except during the breeding phase and, as other large aquatic birds, they need to paddle across the surface to take off (Norberg 1990).

FLIGHT TIME

Our results have demonstrated that eiders are short duration flyers (discussed by Pelletier *et al. in prep.* [Chapitre 3]) outside migration periods and that seasonal flight time is composed mostly of local flights (71 % of total flight time on average). The general belief among ornithologists is that the migratory period is the major achievement of birds in terms of flight time. It is clear from our data that the largest share of flight costs during the annual cycle stems from individuals commuting between suitable foraging and resting areas. Indeed, although there is considerable interest in the measurement of flight costs of wild birds, the actual time spent flying has always been largely estimated or assumed (but see Butler *et al.* 1998). With the new technique described here, realistic estimates of flight costs that can be related to the actual amount of time spent flying are now possible (Pelletier *et al. in prep.* [Chapitre 3]).

The DL record f_H continuously, thus permitting calculation of the total flight time during migration and on a daily basis. Therefore, our method can be considered an exhaustive flight monitoring tool. We showed short migration flights similar to those documented via ringing recovery studies (Franzmann 1980, Lyngs 2000) confirming that eiders in Baltic Sea are short distance migrants. Incorporating information on the flight ground speed of common eiders (17.5 m s^{-1}, Kahlert *et al.* 2003), we estimated that eiders flew short distances during migration days (mean = 188 ± 51 km day^{-1}, range 117 to 277 km day^{-1}). They covered a distance of 750 ± 397 km on average during moult and fall migrations.

Daily time scale. Our results illustrate that eiders are early flyers. Flight frequency is particularly high around sunrise, decreases during the day and drops markedly during the night (Figure 3). This pattern is matched by diving frequency which is highly correlated with flight frequency. Although a detailed analysis of this relationship is beyond the scope of the present study, we offer the following interpretation of this pattern. Common eiders are benthic predators, feeding mostly on blue mussels (*Mytilus edulis*), a sessile prey (Guillemette *et al.* 1992, Öst and Kilpi 1997, Guillemette 1998). As they feed little during the night (Figure 3), they are probably drifting on the sea surface, away from the food patches. As the starvation level increases throughout the night, hunger is at its highest level in the morning forcing eiders to move over the food patches again. The fact that morning flights are longer than afternoon flights (Figure 4a) could be also explained by this foraging movement.

Although this technique may be a major achievement in bird study, we must question whether or not this method affects the natural behaviour of experimental birds. Using a before-after design with a control group, it was impossible to detect any negative impact on laying date, clutch size and hatching success for individuals carrying a DL for one full year (Guillemette *et al.* 2002). Moreover, a total of 39 DL were deployed since 1998, of which 90 % (35 DL) returned to the breeding colony one year later. This return rate is similar to the survival rate of common eiders (about 90 %, Coulson 1984, Erikstad *et al.* 1994 cited by Bustnes *et al.* 2002). Furthermore, one salient feature of the DL used in this study is that they were implanted in the body cavity of the experimental bird, with no external protrusions, thus conserving aerodynamic and hydrodynamic properties of the study animals (Guillemette *et al.* 2002).

Here we have described a novel technique for monitoring flight behaviour using f_H signatures measured via internal DL. This technique is sure to open new avenues of investigation in ornithological research. For example, Guillemette *et al.* (*in prep.*) quantified flightless duration that occurred during wing moult in this species simply by counting days without flights. Moreover, this technique could be used with other species performing continuous forward flapping flight to (1) identify all flights performed during one year, (2) estimate flight costs, (3) describe migration strategies and (4) relate flight and foraging events (in diving species).

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Tables and figures

Table 1. Total migration and local flight time (percentage of total flight time) quantified by using heart rate flight signature over a period of eight months in 13 female common eiders.

Females	*MIGRATION FLIGHTS* Cumulated time (h)	*MIGRATION FLIGHTS* Time per day (h)	*LOCAL FLIGHTS* Cumulated time (h)	*LOCAL FLIGHTS* Time per day (h)	*TOTAL (h)*
BR	8.7 (20%)	2.18	34.9 (80%)	0.18	43.6
OO	8.1 (17%)	2.70	40.4 (83%)	0.23	48.5
OR	6.7 (20%)	3.34	26.4 (80%)	0.17	33.1
OY	4.2 (21%)	2.12	16.4 (79%)	0.11	20.6
RB	10.9 (35%)	3.64	20.0 (65%)	0.10	30.9
RR	23.1 (42%)	2.57	31.4 (58%)	0.17	54.5
RW	18.9 (38%)	3.16	30.4 (62%)	0.20	49.4
WB	20.8 (41%)	3.47	30.1 (59%)	0.14	51.0
WO	7.9 (18%)	3.96	37.0 (82%)	0.17	44.9
YB	7.4 (26%)	1.86	21.0 (74%)	0.12	28.4
YR	19.7 (40%)	3.28	29.4 (60%)	0.17	49.1
YW	8.8 (29%)	4.39	22.0 (71%)	0.14	30.8
YY	9.4 (28%)	1.89	23.8 (72%)	0.13	33.2
Mean ± S.E.M.	**11.9 ± 6.3 (29 ± 10%)**	**2.97 ± 0.81**	**27.9 ± 7.1 (71 ± 10%)**	**0.16 ± 0.04**	**39.8 ± 10.7**

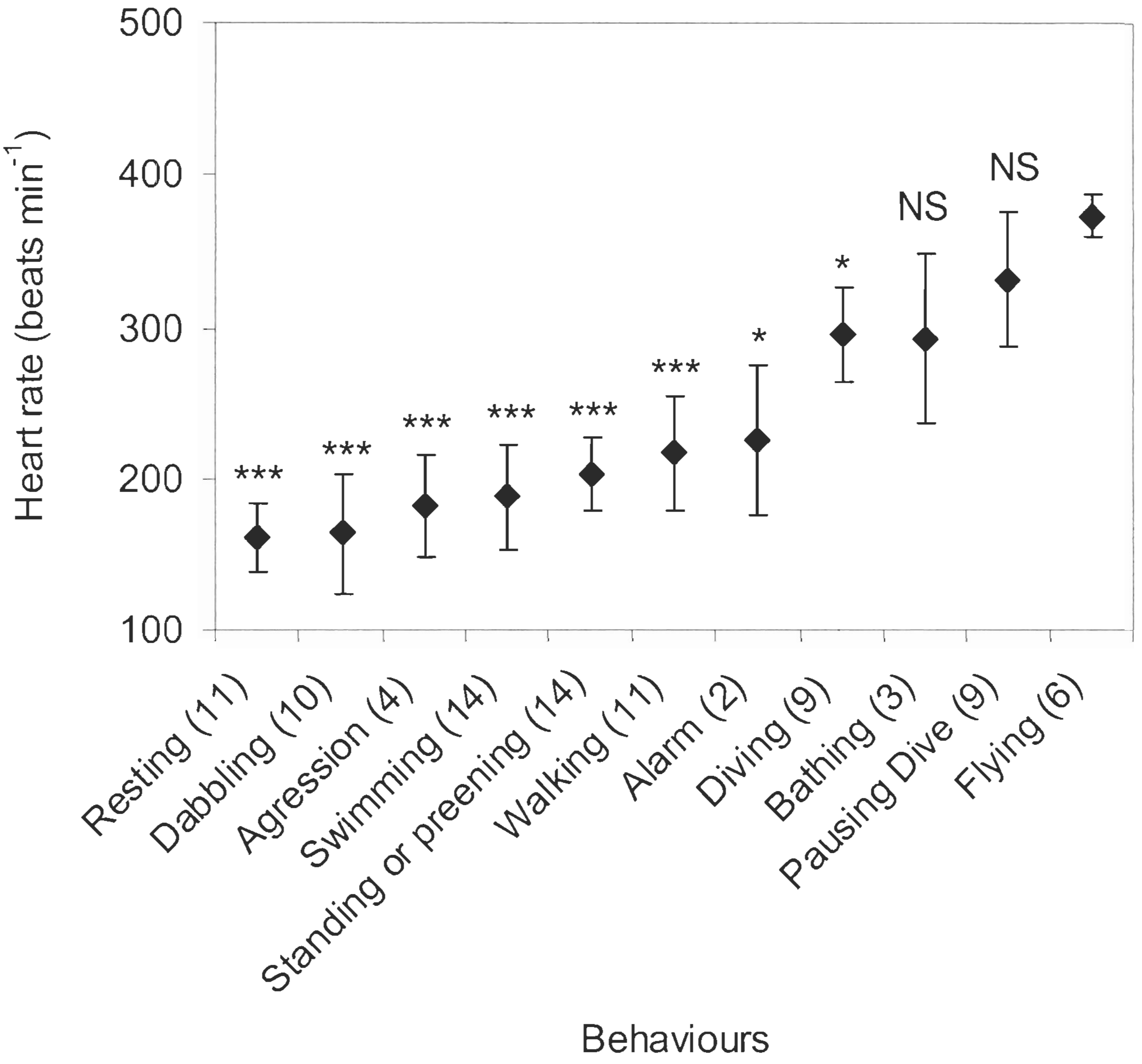

Figure 1. Mean heart rate (± 95% *CI*, beats min^{-1}) of common eiders engaged in 11 different behaviours (332 recordings, 4 to 86 recordings per behaviour). Asterisks indicate the statistical difference between flight and other activities (ANOVA - Tukey; * : $p < 0.02$, *** : $p < 0.001$ and NS : $p > 0.05$). Values in parentheses are number of individuals observed per behaviour.

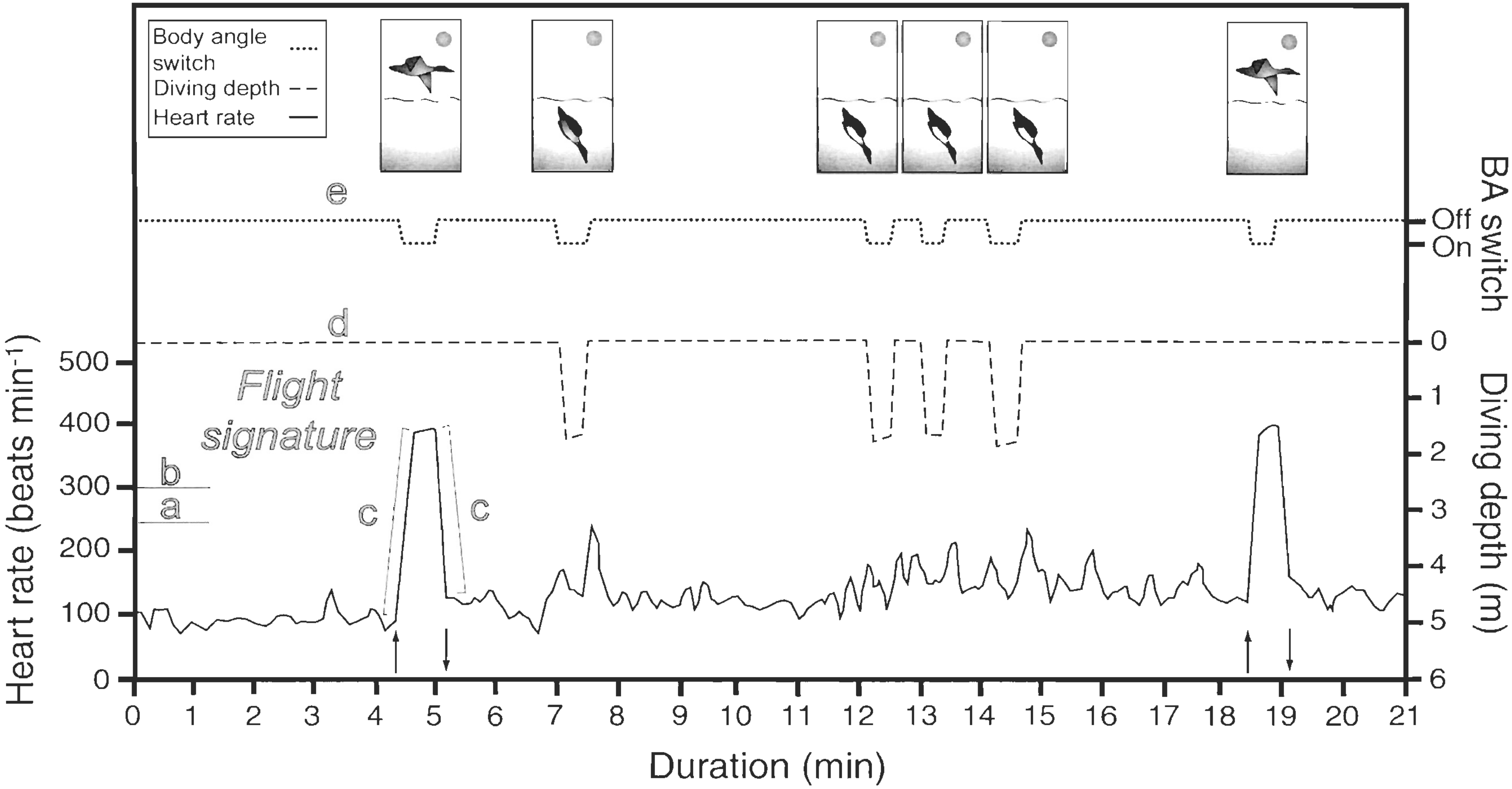

Figure 2. Traces of heart rate (f_H) and diving depth from a female common eider during dives and forward flapping flight. The flight signature is determined by these parameters: f_H threshold ≥ 250 beats min^{-1} (a), f_H plateau threshold ≥ 300 beats min^{-1} (b), f_H ascending and descending slopes ≥ 10 beats min^{-1} s^{-1} (absolute values) (c), standard deviation of diving depth ≤ 0.1 m (d) and body angle switch (BA switch) turned on (e). The upward and downward pointing arrows indicate the point of take-off and landing, respectively.

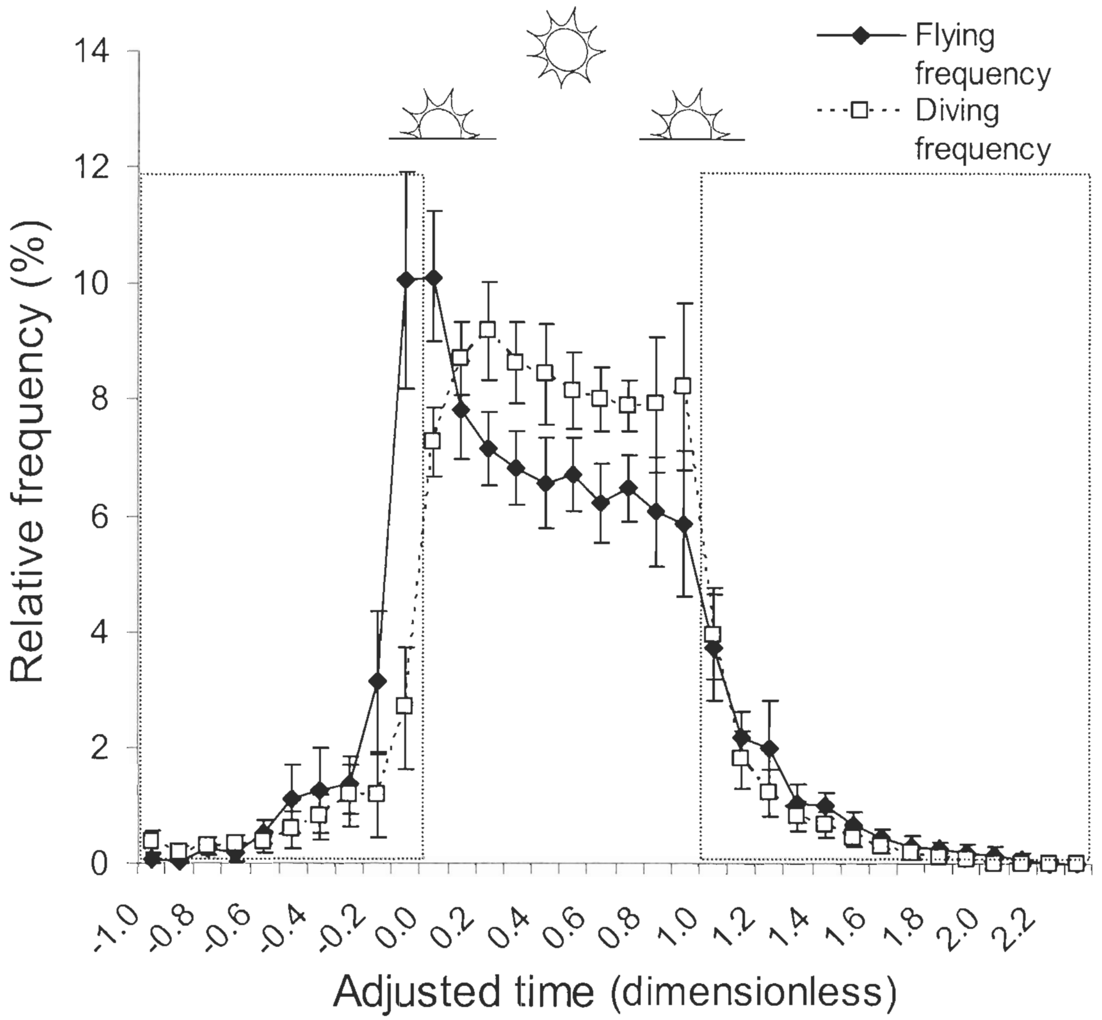

Figure 3. Mean relative flying and diving frequencies (± 95 % *CI*, %) recorded in 13 common eiders according to adjusted time of the day. These behaviours are performed outside migration and moult periods from May to December 2003. Adjusted time is calculated by the equation: $(t_0 - H_{\mathrm{sunrise}}) / (H_{\mathrm{sunset}} - H_{\mathrm{sunrise}})$ where t_0 is the take-off time of one flight, H_{sunrise} is sunrise and H_{sunset} is sunset. This adjusted time permits visualisation of flying and diving activities according to variable photoperiod during the year. Between 0 and 1, flights are performed during daylight (where 0 is sunrise, 0.5 is midday and 1 is sunset); between -0.2 and 0.0 (exclusively) it is the dawn; between 1.0 and 1.2 (exclusively) it is the dusk, and outside these boundaries it is the night. Each class equals, on average, 55 min.

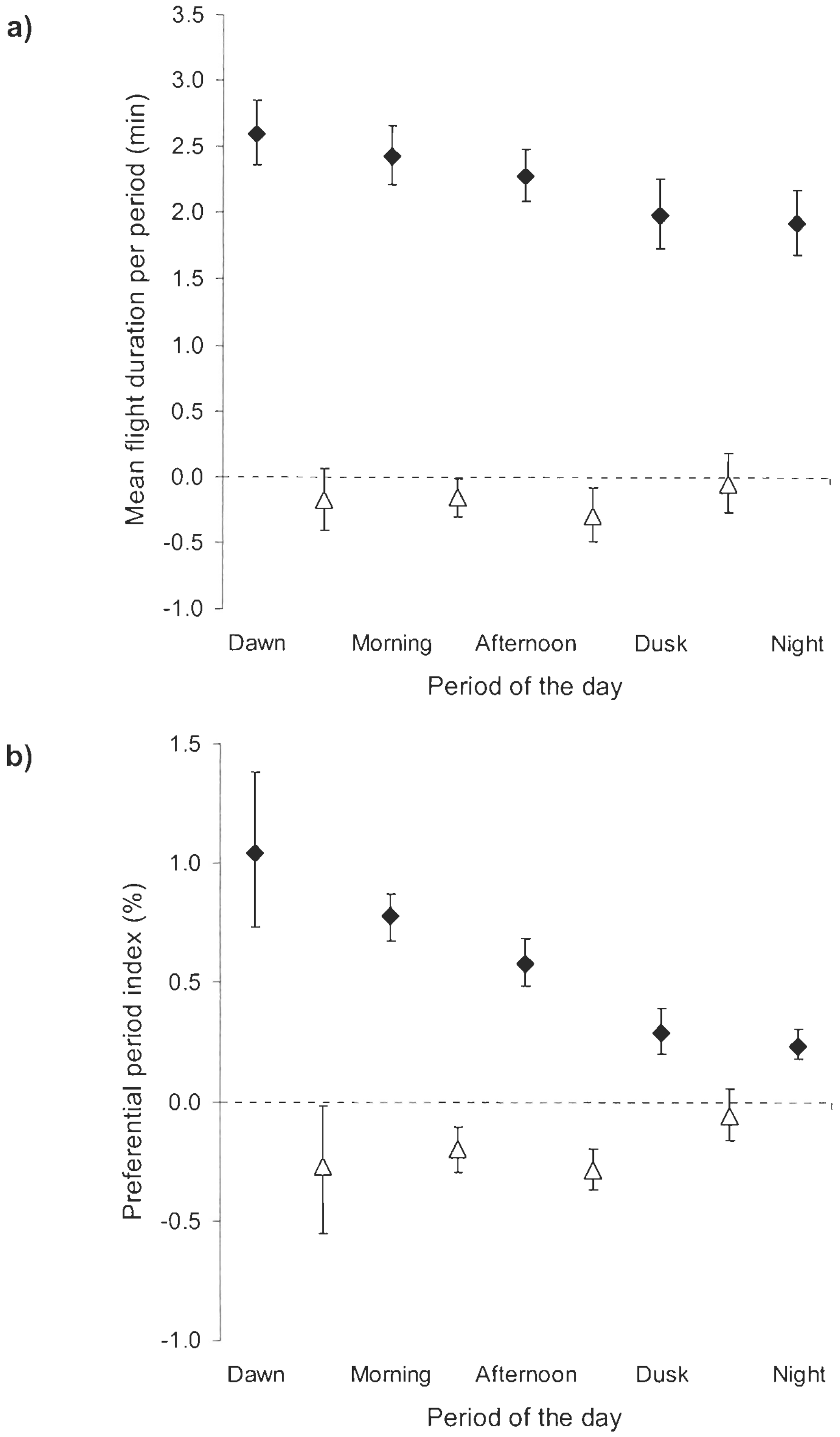

Figure 4. a) Mean flight duration (± 95 % *CI*, min) [filled diamonds] per period of the day and differences (± 95 % *CI*, min) [unfilled deltas] between each adjacent period of the day. **b)** Mean preferential period index (± 95 % *CI*, %) [filled diamonds] of all local flights performed by 13 common eiders and differences (± 95 % *CI*, %) [unfilled deltas] between each adjacent period of the day. The preferential period index is calculated with the equation: *cumulated time spent flying during one period of the day / cumulated duration of this period* × *100*. Means, differences and 95 % *CI* were calculated by bootstrap analysis with 10 000 iterations.

CHAPITRE III : DEUXIÈME ARTICLE

Manuscrit à être soumis à un journal scientifique

Veuillez prendre note que l'expression « Chapitre 2 », qui fait suite à « Pelletier et al. in prep. *» et qui réfère au premier article de ce mémoire, a été ajoutée pour nous assurer que le lecteur du mémoire comprenne bien la provenance de l'article cité. Celle-ci sera effacée lors de la soumission de l'article.*

To fly or not to fly: flight time and energy expenditure of a large diving bird

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Résumé

Cette étude présente la première quantification à long terme du temps de vol journalier chez une espèce d'oiseaux en liberté et des coûts de vol associés. Des consignateurs de données ont été implantés dans 13 femelles eiders à duvet (*Somateria mollissima*) nichant sur l'île Christiansø, dans la mer Baltique. La signature cardiaque du vol, décrite par Pelletier *et al.* (*en prép.* [Chapitre 2]), a été utilisée pour compiler tous les vols effectués durant une période continue de huit mois. Nos résultats indiquent que l'eider est l'une des espèces d'oiseaux les plus parcimonieuses en terme de temps de vol journalier. En effet, il vole en moyenne moins de 10 min par jour en exécutant environ 4 vols quotidiens de 2,3 min chacun. Trois types de modèles ont été utilisés pour estimer les coûts de vol de l'eider : deux modèles basés sur l'équation de Fick, un modèle basé sur la théorie aérodynamique et deux modèles allométriques basés sur la masse corporelle et la morphologie alaire. La comparaison réalisée entre les modèles suggère que les modèles allométriques sont inappropriés pour estimer les coûts du vol pour cette espèce alors que les ceux basés sur la théorie aérodynamique et l'équation de Fick présentent des résultats réalistes. Les coûts de vol estimés se situent entre 123 et 149 W pour cette espèce (ou entre 17 et 20 fois le taux métabolique de base). Étonnamment, même si les coûts de vol sont élevés, il n'y a pas de corrélation entre la fréquence cardiaque journalière (*DHR – daily heart rate*) et le temps total passé en vol par jour (r de Pearson = 0,08; test de permutation p = 0,785) ainsi qu'entre la *DHR* et la fréquence quotidienne des vols (r de Pearson = 0,38; test de permutation p = 0,203). Toutefois, une tendance positive existe entre le nombre de vol courts par jour et la *DHR* (r de Pearson = 0,48; test de permutation p = 0,094). Les coûts énergétiques très élevés requis pour le décollage, causés par des faibles capacités de décollage, pourrait expliquer ce dernier résultat. Nous suggérons que l'utilisation de ce mode de locomotion chez cette espèce pourrait être le résultat d'un compromis entre la nécessité écologique de voler (pour s'alimenter et pour fuir les prédateurs) et la faible capacité aérobie (fréquence cardiaque et masse relative du coeur relativement basses, peu de marge disponible pour la puissance aérobie) combinée à une charge alaire excessive.

Mots-clés: consignateur de données, coûts de vol, Eider à duvet, fréquence cardiaque, fréquence cardiaque journalière, temps de vol, Somateria mollissima

Abstract

This study reports the first long-term quantification of daily flight time in a free-living bird species and estimations of the associated flight costs. Data loggers were implanted in 13 female common eiders (*Somateria mollissima*) nesting on Christiansø Island, in the Baltic Sea. The *heart rate* (f_H) *flight signature* described by Pelletier *et al.* (*in prep.* [Chapitre 2]) was used to compile all flight events during a continuous period of eight months. Our results indicate that the eider is one of the thriftiest volant birds because they flew, on average, less than 10 min day^{-1} by performing about 4 daily flights of 2.3 min each. Three types of models were used to estimate their flight costs : two models based on the Fick equation, one model based on aerodynamic theory and two allometric models based on body mass and wing morphometrics. Between-model comparison suggests that allometric models are inappropriate to estimate flight costs for this species whereas those based on aerodynamic theory and the Fick equation provide realistic results. Flight costs are estimated between 123 and 149 W for this species (or between 17 and 20 multiples of basal metabolic rate). Surprisingly, even if flight costs are high, there is no correlation between the daily heart rate (*DHR*) and the total daily flight time (Pearson $r = 0.08$, permutation test $p = 0.785$), and between the *DHR* and the daily flight frequency (Pearson $r = 0.38$, permutation test $p = 0.203$). However, a positive trend exists between the number of short flights per day and the *DHR* (Pearson $r = 0.48$, permutation test $p = 0.094$). High energetic costs required for takeoff, due to eider's weak takeoff abilities, could explain this last result. We suggest that the use of flight in this species could be controlled by a trade-off between the ecological needs to fly (foraging, avoiding predation) and the poor aerobic capabilities (moderately low heart rate and relative heart mass, small aerobic power margin) combined with an excessive wing loadings.

Key words: Common Eider, daily heart rate, data logger, flight costs, flight time, heart rate, Somateria mollissima

Introduction

At the end of the 19th century, birds were described as flying machines (Marey 1890). Their many anatomical and physiological attributes were connected to the fact that flight was their predominant locomotion mode (Welty 1962). For example, one main adaptation is their compact multi-chambered respiratory system that enables unidirectional air flow in the lungs, thus avoiding mixing residual and fresh air as seen in mammals (Schmidt-Nielsen 1997). This system, coupled to a larger heart in comparison to mammals and thus providing a higher cardiac output (Grubb 1983) to deliver oxygen and remove waste from the exercising tissues, was thought to be the result of high energy demands imposed by flight (Smith *et al.* 2000). Bats also use flight and, although they fundamentally have a mammalian anatomy, they have been morphometrically and physiologically "refined" to achieve and sustain flight (Maina 2000). They possess the largest relative heart and lung sizes of all mammals (Canals *et al.* 2005). Moreover, one function of flight is to travel fast, for long distances, and therefore gain access to a wide range of ecological niches and ressources (Rayner 1995). However, in absolute terms, flight is the most energetically expensive form of sustained activity performed by animals (Schmidt-Nielsen 1972, Norberg 1990).

Although body mass predominantly influences flight costs (Berger and Hart 1974), aerodynamic theory predicts that wing morphology also plays a role in that respect (Tucker 1973; Greenewalt 1975; Rayner 1979a,b; Pennycuick 1989). For instance, birds with high wing-loading, *i.e.* the ratio of body mass to wing area, will mostly use flapping flight whereas birds characterised by high aspect ratio (wing span^2 / wing area) and low wing-loading will use mostly soaring flight (Rayner 1988, Norberg 1990). Because bird species using flapping flight mobilise their flight "apparatus" almost continuously, flight costs should be higher in these species (Butler 1991). This is specially true for diving birds characterised by short pointed wings enabling those species to move in two density-different media, *i.e.* air and water (Storer 1971, Lovvorn and Jones 1994, but see Rayner 1988).

Several approaches exist to calculate flight energy expenditure: those based on respirometry and doubly labelled water from which various allometric equations are derived (Masman and Klaassen 1987, Butler 1991, Rayner 1995), those using heart rate, heart mass and the Fick principle (Bishop 1997) and finally, the aerodynamic theory (Pennycuick 1989). Which of these methods better quantifies the total cost of flight is an open debate (see *Discussion*) but it seems so far that most studies estimate flight costs and then multiply them by any available approximation of the total time spent flying. However, any estimation of the total energy demand for flight is likely to be a questionable use without accurate quantification of flight time. For instance, Masman and Klaassen's (1987) review of flight costs and flight time revealed an interesting trend: birds with high flight costs seemed to fly much less than birds with low flight costs. Furthermore, studies of time-energy budgets have shown that when high-cost flyers increase their time spent flying per day they augment considerably their daily energy expenditure (Flint and Nagy 1984, Tatner and Bryant 1986, Carlson and Moreno 1992, Nudds and Bryant 2000). Therefore, any study aiming at quantifying the impact of total flight cost on the energy budget of birds ought to measure both, the flight time and the energy cost of flight for a single species. One problem is that one cannot follow a wild bird long enough to accurately and continuously quantify flight time 24 h per day throughout the annual cycle.

Another problem is that current estimates of flight costs are likely to be inaccurate because most measurements are made at cruising and sustainable flight speeds (*e.g.* Tucker 1973, Rothe *et al.* 1987, Ward *et al.* 2001). These estimates are conducted at speeds probably close to the lowest cost of flight speed (V_{mp}). Because many wind tunnel experiments are not able to reproduce the theoretical U-shape curve of mechanical power in relation to speed (Rayner 1994), it was suggested by some authors that experimental birds were reluctant to fly at slower or faster speeds, in order to minimise energy expenditure during the experimental trials (but see Tobalske *et al.* 2003). Recent studies using novel laboratory techniques to measure flight energy expenditure suggest that current measurements underestimate flight costs (Nudds and Bryant 2000, Hambly *et al.* 2002, 2004). These authors claim that many birds use both short and long flights during their daily routine and that short flights are more costly to perform per unit of time. Thus, current quantifications of flight costs would underestimate the daily flight budget. Two specific phases that would contribute to such an underestimation are takeoff and landings performed on a regular basis in wild birds.

Recent developments in data loggers (DLs) provide information on both flight behaviour and flight energetic costs in species performing flapping flight (Butler *et al.*

1998). Pelletier *et al.* (*in prep.* [Chapitre 2]) developed a new technique using heart rate (f_H) flight signature to detect every flight (migration and local) performed by common eiders during an extensive and continuous period of time, 24 h a day. Heart rate is also a good indicator of the metabolic rate in birds because of the relationship expressed by the Fick equation (Owen 1969, Bevan *et al.* 1992, 1994, Bishop & Butler 1995, Butler *et al.* 2000, Ward *et al.* 2002). One method proposed by Bishop (1997) allows the use of f_H to estimate the rate of oxygen consumption ($\dot{V}O_2$) from measured heart rate and estimates of stroke volume (V_s) and oxygen extraction (C_{aO_2} - $C_{\bar{v}O_2}$).

Species model. Common eider (*Somateria mollssima* hereafter eider) is a large sea duck (2 kg) with a circumpolar distribution, and which dives for food (Guillemette *et al.* 1992). In the Baltic Sea, eiders use flight to perform short migrations (about 1000 km) along the east-western axis (Franzmann 1980, Lyngs 1992). Throughout the year, they also fly regionally to search for blue mussel beds and probably perform short flights to escape from marine predators. Compared to other birds, the short pointed wings of eiders result in one of the highest wing loadings in volant birds (2.0 g cm^{-2}, Guillemette 1994) and, as do many other large aquatic birds, they need to run across the water to take off and become airborne (Norberg 1990). Since takeoff, acceleration and ascending components generate a high energy expenditure (Nudds & Bryant 2000), flight costs should be high for this species. Daily flight energy expenditure being the result of flight costs and flight time, we expect that high cost flyers like eiders may compensate using flight with parsimony.

Objectives. Our objectives were 1) to monitor and quantify daily flight budgets over an extensive period of time for a free-living bird species (outside migration periods), 2) to estimate flight costs for this species by using various models of estimation and 3) to test the relationship between daily flight time and daily energy expenditure.

Methods

Study site and population. Field work was carried out on Christiansø Island (55°19' N, 15°12' E) in the southern Baltic Sea, 18 km from the Danish island of Bornholm. The island is populated by approximately 2 600 breeding pairs of eiders (Lyngs 2000).

Selection and capture procedures. In 2003, 20 female eiders were equipped with DLs. All experimental females were captured in the second part of their incubation because they are more resistant to disturbance during this period (Bolduc and Guillemette 2003). Females were identified by a set of two colour bands on one tarsus and a numeric metallic band on the other tarsus.

DLs and implantation procedures. We obtained a licence from Dyreforsøgtilsynet (Royal Veterinarian Corporation) in Denmark and all birds were cared for in accordance to the principles and guidelines of the Canadian Council on Animal Care. The 20 DLs used in the present study recorded heart rate (2 Hz) and hydrostatic pressure (diving depth, 2 Hz). They were 36 mm long × 28 mm wide × 11 mm thick and weighed 21 g after encapsulation in paraffin wax for waterproofing and silicone coating for biocompatibility. The loggers accounted for 1.2 % of the bird's body mass (1752 ± 144 g, *N* = 20) at implantation. All surgical procedures were conducted indoors by a veterinary surgeon. Birds were under isoflurane anaesthesia while the sterilized DL were inserted in the abdominal cavity via midline incision of the skin and body wall. To prevent infection, a long-acting antibiotic (*LA Terramycin,* Pfizer, New York) was injected intramuscularly. The removal procedure, a year later, was similar. The implantation time in 2003 (from capture to release of the bird at the nest) was 43 ± 8 min (S.D.) and the removal time in 2004 was 35 ± 6 min (S.D.).

DAILY FLIGHT TIME

Data analysis. Eighteen females returned to the colony (90 %) to breed the next year, and of these, seventeen were caught and their DLs removed. Only eleven loggers had their memory full (220-221 days), two were almost full (190 to 207 days) and four loggers failed completely. Thus, the number of recorded days varied between females and ranged from 45 to 221 days spanning from May-June 2003 to mid-December 2003. Data from DLs with more than 190 recorded days were analysed (*N* = 13). We used a purpose-designed software programme to identify all flight events from the recorded f_H flight signature described by Pelletier *et al.* (*in prep.* [Chapitre 2]).

Local flights. In this study, we concentrated on local foraging flights. Using a frequency distribution of flight duration, flights shorter than 30 min (99 % of total flights) were considered local flights. Knowing that flight speed (ground speed) of the eider is about 17.5 m s^{-1} (mean ground speed measured during headwind [15.3 m s^{-1}] and tailwind

[19.7 m s^{-1}], Kahlert *et al.* 2003), we assumed that local foraging flights were performed within a maximal radius of 31 km.

Flight time variables. Flight time was described using the following variables: daily flight frequency, flight duration (for each flight) and daily time spent flying. For each day, we calculated the number of flights and their duration (± 2 s). The time spent flying was determined by adding all flight events within a 24 h period. To calculate these parameters, migration and wing moulting days were excluded. Wing moult was described as consecutive days having 0 min of time spent flying per day.

Interspecific comparison. In order to compare with other species, literature on avian time-budget studies was reviewed. Only studies dealing with the time spent flying per day (24 h) or the percentage of time spent flying per active period (from dawn to dusk) were found. No information was found on flight frequency and local flight duration in free-living birds. Results of this review are presented in Figure 2 (detailed in *Appendix 1*). We present time spent flying per day (24 h) and percentage of time spent flying per active period when daylight duration was not given in studies. The potential biases of sampling only during the active period were discussed by including or excluding the flights performed from twilight to night's end.

FLIGHT COSTS

Specimen dissection. Twelve eiders (6 males and 6 females) were collected during winter to measure the parameters needed for the following calculations of flight costs, but only data for females were used. Wingspan (with the wing joints fully extended), body mass (with the digestive tract empty) and wing area (with wings separated from the body) were measured. We traced the outline of one fully extended wing on a sheet and measured the area using a digital planimeter (as described by Guillemette and Ouellet 2005). The body area between the wings was added to the wing area. This was done by subtracting both wing lengths from the wingspan and by multiplying the resulting value by the line between the two proximal ends of the wing (according to body). Then, the bird was dissected and the heart was emptied of its blood and weighed. We also removed and weighed pectoralis, supracoracoideus and wing muscles following Guillemette and Ouellet 2005.

Models. Normally, flight costs should take into account the energy expenditure related to each phase of a flight: takeoff, continuous forward flapping flight, landing and recovery (when the anaerobic takeoff portion is not recovered during flapping flight). But models estimating flight costs only predict the energy expenditure related to forward flapping flight. Three model types were used in our study: two models based on the Fick equation (Bishop 1997), one aerodynamic model using the software *Flight 1.11* (Pennycuick 1989, 2002) and two allometric models based on body mass and wing dimension (Masman and Klaassen 1987, Rayner 1995).

Model 1. The first model was based on the calculation of maximum oxygen uptake ($\dot{V}O_{2,\,max}$) during flight with the Fick equation ($\dot{V}O_2 = f_H \times V_s \times (C_{aO_2} - C_{\bar{v}O_2})$). This model is *Method 1* proposed by Bishop (1997). Heart rate (f_{H}) was measured directly by the implanted DL (f_H recorded during '*plateau*' phase of one flight, see Pelletier *et al. in prep.* [Chapitre 2]). The mean f_H was calculated during flights performed in winter (females with DL) because the morphological measurements were obtained from eiders collected in winter (from November until the end of the recordings). Stroke volume (V_s) was then estimated from heart mass (M_H) using an equation of heart mass-specific scaling of V_s during flight (with M_H measured for the six females without DL collected on their wintering site, Table 1). The following equation proposed by Bishop and Butler (1995) was used:

$$V_{s,\,\mathrm{flight}} = 0.3\ M_H^{\ 1.05} \qquad (1)$$

Unfortunately, it was impossible to take blood samples at the moment of collection. Difference in arteriovenous oxygen content $(C_{aO_2} - C_{\bar{v}O_2})$ was estimated from haemoglobin concentration by considering an average value for all birds of 0.1513 g ml blood^{-1} (as prescribed by Bishop 1997, *pers. comm.*). C_{aO_2} was estimated by using this average value × 1.36 (to estimate saturated oxygen carrying capacity) and then by 0.94 (assuming 94 % saturation during maximal activity as measured in seven species of mammals running at $\dot{V}O_{2,\,max}$, Bishop 1997). This author assumed that the value of $C_{\bar{v}O_2}$ does not fall below 0.038 ml 0_2 ml blood^{-1} (it is again the mean value of seven species of mammals running at $\dot{V}O_{2,\,max}$ [Bishop 1997]).

Model 2. With the second model, another form of the Fick equation was used: $\dot{V}O_2 = \dot{V}_b \times (C_{aO_2} - C_{\bar{v}O_2})$, *Method 2* from Bishop (1997). He assumed that cardiac output ($\dot{V}_{b,max} = f_H \times V_s$) was a function of M_H and that there was no difference between birds and mammals during maximum cardiovascular performance (corroborated by Peters *et al.* 2005). Consequently, for both mammals and birds:

$$\dot{V}_{b,max} = 213\ M_H^{0.88} \qquad (2)$$

and $C_{aO_2} - C_{\bar{v}O_2}$ was estimated from haemoglobin concentration as in *Model 1*.

Model 3. Estimations with the third model were obtained using the software *Flight 1.11* (Pennycuick 1989, 2002), programmed with equations of the aerodynamic model of Pennycuick (1989) to estimate mechanical power output (P_o). To compare with other models, P_o was automatically converted into chemical power input (P_i), by using the equation $P_i = 1.1*[(P_o/E_{FM}) + BMR]$ where E_{FM} is flight muscle conversion efficiency, defined as the proportion of consumed fuel energy that is converted into mechanical work by the muscles, and *BMR* is the basal metabolic rate. *Flight 1.11* assumes a default value for E_{FM} of 0.23, but since recent literature showed that the E_{FM} of birds performing forward flapping flight appears to scale positively in respect to body mass (Bishop 2005), we used this equation to estimate E_{FM}:

$$E_{FM} = 0.3\ M_b^{0.137} \qquad (3)$$

Model 4. The fourth model allowed a direct estimate of the metabolic power input (P_i) in terms of body mass and wing morphology with this allometric equation:

$$P_i = 17.36 M_b^{1.013} B^{-4.236} S^{1.926} \qquad (4)$$

where M_b is body mass (g), B is wingspan (cm) and S is wing area (cm^2). Values of P_i were obtained by using mass loss and doubly labelled water techniques from 14 species with body masses ranging from 3.8 to 1000 g (Masman and Klaassen 1987).

Model 5. The last method is similar to *Model 4* consisting of an allometric equation derived from 95 species (Rayner *et al.* 1995, cited in Rayner 1995). The equation is the following:

$$P_i = 417.1 M_b^{1.371} B^{-3.384} S^{0.917} \qquad (5)$$

Since for models 1 and 2, the watt (W) is the SI unit for power and is equivalent to joules per second (J s^{-1}), we had to convert $\dot{V}O_{2,max}$ (ml O_2 min^{-1}) in an estimate of P_i following values for fuel energy equivalents (Schmidt-Nielsen 1997): 1 ml O_2 s^{-1} = 21.1 W during pure carbohydrate oxidation (with a respiratory quotient [RQ] of 1; dominates in exercise of short duration) and 1 ml O_2 s^{-1} = 19.6 W during pure fat oxidation (with a RQ of 0.71; dominates in exercise of long duration). Since the RQ is unknown, a compromise RQ of 0.8 (where 1 ml O_2 s^{-1} = 20.1 W) has been used to calculate P_i during aerobic activity.

Flight energy expenditure was expressed by relating energetic costs to basal metabolic rate (*BMR*) in order to compare results across species (Drent and Daan 1980). Since Bryant & Tatner (1991) suggested that it was more appropriate to use *BMR* derived from a specific species, we only used values obtained from empirical studies. Jenssen *et al.* (1989) determined the *BMR* of winter-acclimatized eiders in air and water respecting all *BMR* criteria: 3.83 W kg^{-1} or 7.39 W with eiders of 1.93 kg (Table 1). In another study, authors measured the metabolic rate of eiders under post-absorption state but it was not mentioned if it was within the thermoneutral zone (Hawkins *et al.* 2000). Nevertheless, the resting metabolic rate (*RMR*) of eiders measured by Hawkins *et al.* (2000) was 12.8 ml kg^{-1} min^{-1} or 7.56 W (using the body mass of 1.79 kg and a respiratory quotient of 0.70 where 1 ml O_2 s^{-1} = 19.8 W). As an indicator of maintenance cost in this species, Guillemette (*in prep.*) used the smallest 5-min mean of heart rate per day (resting heart rate, *RHR*). With a regression obtained from the results of Hawkins *et al.* (*Table 1,* 2000) between heart rate and oxygen consumption, we obtained a *RMR* of 7.90 W with a *RHR* of 86 beats min^{-1} (95% *CI* = 77 – 94 beats min^{-1}).

DAILY FLIGHT TIME VS. DAILY METABOLIC RATE

For testing the relationship between the daily flight time and the daily energy expenditure, we used the daily heart rate (*DHR*) as an equivalent of the daily metabolic rate (*DMR*) because it has been shown in many species that there is a close relationship between rate of oxygen consumption and heart rate (Owen 1969, Lund *et al.* 1976, Pauls 1980, Butler 1993, Boyd *et al.* 1999, Froget *et al.* 2001). We calculated the *DHR* for each day (excluding moult and migration periods) by summing the number of heartbeats per day and dividing by 1440 min.

STATISTICAL ANALYSIS

According to the flight time variables and heart rate data, our data resulted more from a census in each individual than a typical sampling. In other words, the variables were not estimated for the 13 eiders in our study, but they were measured exhaustively and continuously during eight months. Thus, to illustrate raw data of flight variables (flight frequency per day, flight duration, time spent flying per day, daily heart rate and heart rate during flight – see Figures 1, 4 and 5), we cumulated all values and divided by the number of recording days (excluding moult and migration periods). However, because the sample size was moderately low ($N = 13$), because the sampling distribution was unknown and in order to transfer our results to the population level, we calculated a bootstrap estimate for the mean (± 95% confidence interval, *CI*) of each flight variable, based on 10 000 bootstrap samples with replacement from the original sample of 13 individuals. The bootstrap estimate was the mean of 10 000 bootstrap sample means and the 95% *CI* was determined from the 250th and 9 750th values of the bootstrap means arranged in ascending order (Good 2001, 2005; Quinn and Keough 2002). To test the effect of different sampling periods (24 h, daylight with and without twilight) on the quantification of daily flight time, we calculated the difference between adjacent sampling periods for each female and the mean difference (Δ). The 95 % *CI* of means and mean Δ were calculated using a bootstrap resampling analysis with 10 000 iterations (Quinn and Keough 2002). When the Δ 95 % *CI* included the zero value, the two adjacent means were considered non-significantly different.

To analyse the relationships between flight time variables and the daily heart rate, the summed values of each variable were used to perform statistical analyses. The null hypothesis was that there was no relationship between each flight time variable and the daily heart rate. First, Pearson correlation tests were computed with the original observations between flight time variables and daily heart rates. Then, the permutation distributions of Pearson r were derived for each couple of variables. The p-value was determined from the position of the original Pearson r among the 10 000 resampling values of Pearson r arranged in ascending order (Good 2001, 2005). The statistical significance (alpha) was set at $p < 0.05$.

Systat version 10 for Windows and Resampling Stats add-in version 2 for Microsoft Excel were used for statistical analyses.

Results

DAILY FLIGHT TIME

The four parameters measured in this long-term study of flight behaviour are provided in Figure 1. We recorded a total of 9 527 flights for these 13 females, ranging from 498 to 1 252 flights per female.

Flight duration. Flights were of short duration for all individuals (Figure 1a). For female eiders, local flights lasted, on average, 2.3 min (95% $CI = 2.2 - 2.5$ min). Using the mean flight speed measured for eiders (17.5 m s^{-1}, Kahlert *et al.* 2003), we estimated that they flew over relatively short distances most of the time, on average, 2.4 km. The distribution of all local flights showed that 95 % of them lasted less than 6.0 min (equivalent to a distance of 6.3 km).

Flight frequency and time spent flying per day. The number of flights per day was very low since female eiders flew, on average, only 4.1 times day^{-1} (95% *CI* = 3.6 – 4.8 flights day^{-1}) for a total of 9.4 min day^{-1} (95% *CI* = 8.3 – 11.0 min day^{-1}; Figure 1b and 1c). With the same flight speed presented above, we estimated that they covered a mean distance of about 10 km day^{-1}.

Interspecific comparison. We compared the time spent flying with values for other species in absolute and percentage (of active period) terms, and found that other species flew on average 4.1 ± 5.1 (S.D.) h day^{-1} (Figure 2a) or during 15.6 ± 17.1 % (S.D.) of their active period (Figure 2b). In comparison, eiders in our study spent 0.66% (9.4 min day^{-1}) of their time flying per 24 h (or 0.16 h day^{-1}). However, because almost all studies presented time spent flying during the active period, we recalculated the time spent flying according to the active period with or without twilights, by removing flights recorded during twilight and/or the night (Figure 3). Pelletier *et al.* (*in prep.* [Chapitre 2]) showed that eiders performed 17 % of their flights during twilight (dawn and dusk) and 14 % at night. Thus, by excluding these flights, eiders would have flown during 0.95% (8.5 min) of their active period including twilights (95% *CI* = 7.1 – 9.5 min) and during 0.96% (6.7 min) of their active period without twilights (95% *CI* = 6.0 – 7.5 min; figure 4). There was a significant difference between sampling periods because zero was not included in the Δ 95 % *CI*.

According to the interspecific comparison, 86 % of species spent a higher percentage of time flying than the eiders (Figures 2a and 2b). However, some species did have similar or even lower flight times than eiders: *Cygnus buccinator* (0.02 h day^{-1}, Lamontagne *et al.*

2004), *Charadrius wilsonia* (0.04 h day^{-1}, Morrier & McNeil 1991), *Lanius ludovicianus* (0.11 h day^{-1}, Weathers *et al.* 1984), *Bubo scandiacus* (0.13 h day^{-1}, Boxall and Lein 1989), *Parus montanus* (0.40 h day^{-1}, Carlson and Moreno 1992), *Auriparus flaviceps* (0.48 h day^{-1}, Austin 1978), *Melanitta fusca* (0.08 % active period, Brown and Fredrickson 1987) and *Toxostoma rufum* (0.37 % active period, Fischer 1981).

FLIGHT COSTS

We found a dimorphism for most of the measurements between males and females collected during winter (Table 1). Males were significantly heavier than females ($p = 0.004$), had longer wings ($p = 0.036$) and had larger wing areas ($p = 0.037$). Moreover, males had the largest pectoralis ($p = 0.006$), the largest supracoracoideus ($p = 0.011$), the heaviest flight muscles ($p = 0.004$) and the heaviest heart mass ($p = 0.037$). Because of this dissimilarity between sexes and because flight time was only recorded for females, only the values for females were used in the calculation of flight costs.

Table 2 lists the estimates of metabolic power input (P_i) during flight in wintering eiders according to the five different models of estimation. In order to estimate $\dot{V}O_{2,max}$ with the first model, f_H data during winter was obtained from 13 females with DL. The mean f_H recorded during the plateau phase of flight was 359 beats min^{-1} (95% CI = 342 – 376 beats min^{-1}, Figure 4), 4.0-fold higher than the resting heart rate recorded with the smallest 5-min mean of heart rate per day (89 beats min^{-1}, 95% CI = 84 – 94 beats min^{-1}). As seen above, the mean heart mass measured for six female eiders, without DL, was

17.9 ± 1.2 g (*S.D.*) (Table 1). Using the heart mass-specific scaling (equation 1), we obtained a V_s value of 6.20 ml. Consequently, assuming that $C_{aO_2} - C_{\bar{v}O_2}$ was 0.155 ml O_2.ml blood^{-1} and by incorporating these three variables into the Fick equation, the first model rendered a $\dot{V}O_{2,\,max}$ of 346 ml O_2 min^{-1} and a P_i of 116 W for flying female eiders during winter. With the second model, we obtained a maximal cardiac output ($\dot{V}_{b,\,max}$) of 2 692 ml min^{-1} with the heart mass-specific scaling (equation 2). Multiplying it with the same estimate of $C_{aO_2} - C_{\bar{v}O_2}$ as in model 1, we obtained a 21 % higher result : $\dot{V}O_{2,\,max}$ = 418 ml O_2 min^{-1} and P_i = 140 W.

With the aerodynamic model (model 3), two values were obtained for P_i. The minimum power input (P_{min}) was 129 W while chemical power at the maximum range speed (P_{mr}) it was 160 W when we used a E_{FM} of 0.33 (estimated with the equation 3). However, by using the default value of 0.23 for E_{FM} in *Flight 1.11*, we obtained 43% higher results: 185 W and 229 W.

We obtained two different results with both allometric models. They provided one of the lowest and the highest results of our P_i estimations. We estimated the second lowest cost of flight (117 W) in our study for this species with equation 4 (Masman and Klaassen 1987) and the highest cost (160 W) with equation 5 (Rayner 1995).

Table 2 also provides detailed information on basal or resting metabolic rate (*BMR* or *RMR*) in eiders and flight costs in multiple of *BMR* or *RMR*. Empirical measurements for *BMR* (Jenssen *et al.* 1989) and *RMR* (Hawkins *et al.* 2000 and the present study) were similar, from 7.39 W to 7.90 W. We estimated flight costs in eiders from 15 to 22 × *BMR* (or *RMR*) according to the five different models. In fact, we kept mainly the *BMR* value (7.39 W) of Jennsen *et al.* (1989) for further analyses of flight costs. We used the other results of *BMR* for later discussion about flight cost and multiple of *BMR* in literature.

DAILY FLIGHT TIME VS. DAILY METABOLIC RATE

The daily heart rate (*DHR*) was used as an equivalent of daily metabolic rate (*DMR*) in the present study, the mean value for 13 eiders being 149 beats min^{-1} (95% *CI* = 140 – 158 beats min^{-1}) (Figure 5). We found no relationship between time spent flying per day and *DHR* (Pearson $r = 0.08$, permutation test $p = 0.785$, Figure 6a) and between flight frequency per day and *DHR* (Pearson $r = 0.38$, permutation test $p = 0.203$, Figure 6b). These results suggest that the total daily flight time did not affect the daily energy expenditure of eiders. However, we found a trend for a negative correlation between flight duration and *DHR* (Pearson $r = -0.53$, permutation test $p = 0.069$, Figure 7a) and another trend for a positive correlation between number of short flights (< 2 min) per day and *DHR* (Pearson $r = 0.48$, permutation test $p = 0.094$, Figure 7b). Moreover, there was also a tendency for a positive correlation between the number of flights lasting less than 1 min and *DHR* (Pearson $r = 0.49$, permutation test $p = 0.091$ or Pearson $r = 0.71$, permutation test $p = 0.007$ if we removed an outlier).

Using flight costs and the daily flight time, we evaluated the fraction related to flight into the eider's daily energy budget. Eiders in the present study flew for a total of 9.4 min day^{-1} and flight costs were about 129 W (P_{min}, see *Discussion*). Thus, daily energy costs related to flight are 73 kJ. To estimate the daily energy expenditure (*DEE*), we took the equation 3 from Hawkins *et al.* (2000) in which a relationship between f_H and $\dot{V}O_2$ was $s\dot{V}O_2 = 10.1 + 0.15 f_H$ ($r^2 = 0.46$, $N = 272$, $p < 0.0001$) where $s\dot{V}O_2$ is in ml O_2 kg^{-1} min^{-1}. We used the mean *DHR* measured for eiders (149 beats min^{-1}, Figure 5) and the result was 62 ml O_2 min^{-1} or 1 812 kJ per day. The proportion of the daily energy budget associated with flight was therefore 4.0 % or 6.1 times the portion of daily flight time budget (0.66 % time spent flying per day).

Discussion

The data from the present study are the first measurements of flight time budget to be obtained for a very long period of time (eight months) in a free-living bird. By quantifying exhaustively all flights performed by the 13 eiders, results indicate that this species uses flight with quite infrequently throughout the annual cycle (excluding migration periods) since flights are of short length and performed at a low daily frequency. Moreover, in spite of flight being energetically costly, eider's daily metabolic rate is not correlated with the daily flight time but it seems to be more correlated with the number of takeoffs per day.

DAILY FLIGHT TIME

Common eider is one of the thriftiest volant birds with less than 10 min spent flying per day. Most time-budget studies found in other species (44 species in 36 studies) were conducted during a single phase of the annual cycle (mainly breeding, 48 %, or wintering, 30 %), during a few days of the annual cycle (1 study) or was unspecified (18 %). Moreover, most studies were conducted during daylight (98 %) and/or in semi-artificial environments like large aviaries (39 %). All these potential biases most probably illustrate the logistical difficulty in following flying birds. Therefore, we need to keep in mind that these results may be different from reality.

For obvious reasons, in most studies, it was not possible to follow flight behaviour at night and we illustrate here with eiders the possible biases by using only the daylight period (or active period) to sample the daily flight time. We found that if we had monitored flight only during the daylight period, we would have introduced a significant error of -12 % (8.5 min, including twilight) or -30 % (6.7 min, excluding twilight) for the estimation of time spent flying per day. Thus relates to the fact that eiders prefer to fly around dawn (Pelletier *et al. in prep.* [Chapitre 2]).

Consequently, and for the following reasons, we believe that the time spent flying was underestimated in other studies, for species that fly less than the eider. For example, *L. ludovicianus* (Weathers *et al.* 1984) and *P. montanus* (Carlson and Moreno 1992) were restricted by limited space in the aviary and they had unlimited food supplies. Apparently, *C. wilsonia* (Morrier and McNeil 1991) and *B. scandiacus* (Boxall and Lein 1989) needed to forage at night to counterbalance their daily energy expenditure; thus, we could expect that the flight time increases with night foraging. Concerning *A. flaviceps* (Austin 1978), the time spent searching for food was included in the foraging activities and not in flight, but it is known that this insectivorous bird needs to fly to capture its prey. Time-budget for

M. fusca (Brown and Fredrickson 1987) was conducted during the breeding period when females stay most of the time (80 %) on the nest. We also believe that flight, in the study of *T. rufum* (Fisher 1981), was the main reason to stop the focal observations because this species lives in a forest environment. *C. buccinator* (Lamontagne *et al.* 2004) were observed during stopover, when recovering during migration, and since flight costs are high (14 × *BMR*) we suppose that these individuals limited their daily energy expenditure by avoiding flight locomotion. Consequently, our comparison suggests that the eider is one of the thriftiest volant birds and has one of the smallest known daily flight times.

FLIGHT COSTS

Heart rate during flight. This is the first study to measure heart rate (f_H) of eiders during flight. However, other recordings of f_H do exist. Hawkins *et al.* (2000) investigated the relationship between f_H and $\dot{V}O_2$ for eiders swimming on a water flume and running on a treadmill at various speeds. In comparison to our results for flight, the f_H measured during aquatic or terrestrial locomotion were much lower: 163 beats min^{-1} when swimming at 1 m s^{-1} (-2.2-fold), 182 beats min^{-1} when swimming at 1.3 m s^{-1} (-2.0-fold) and 195 beats min^{-1} when running at 0.7 – 0.8 m s^{-1} (-1.9-fold). Although Hawkins *et al.* (2000) quantified the linear relationship between f_H and $\dot{V}O_2$ for these modes of locomotion, we cannot use their calibration curves to estimate flight costs (as suggested by Nolet *et al.* 1992, and confirmed by Ward *et al.* 2002). This is because V_s (Bishop and Butler 1995) and oxygen extraction from the blood (Butler *et al.* 1977) both increase during flight more than they do during terrestrial locomotion. Bishop and Butler (1995) plotted the data for heart rate during intense activity against body mass for 42 different species and the relationship scales as $f_H = 480\ M_b^{-0.187\pm0.022}$ ($r^2 = 0.855$). This equation predicts a f_H of 425 beats min^{-1} for eiders, an 18 % overestimation. Peters *et al.* (2005) revised this equation with results obtained with pigeons and adjusted it for 'highly athletic' birds flying at $\dot{V}O_{2max}$ with the equation: maximum $f_H = 545.7\ M_b^{-0.187}$. With this equation, the predicted f_H should be 483 beats min^{-1} (a 35 % overestimation). Because Bishop and Butler (1995) used data from minimal metabolic requirements in flying birds and because our results of f_H are much lower than the two predicted values, we suggest that eiders may be a species with a low maximum f_H, perhaps lacking the ability to fly near its predicted $\dot{V}O_{2max}$, being in other words, a 'modestly athletic' bird.

Heart mass. We could suppose that this relatively low heart rate should be balanced by a higher V_s to increase cardiac output and reach the high aerobic demands of flight and $\dot{V}O_{2max}$. However, our eiders do not seem to have a heart proportionally larger than birds of equivalent size. As the M_H decreases with M_b in birds, and scales as $9.63\ M_b^{0.93}$ (Bishop 1997), our mean M_H (17.9 g, Table 1) is similar to the value predicted by the allometric equation (17.7 g). However, Peters *et al.* (2005) stipulated that Bishop's equation tends to underestimate the M_H of 'highly athletic' birds and M_H should scale as $11.80\ M_b^{0.93}$. With this equation, the M_H is rather higher than our measurement (21.7 g, 21 % higher). The higher predicted value obtained with the equation of heart mass for 'highly athletic' birds also suggests that eiders may have a cardiovascular system similar to that of 'modestly athletic' birds.

Comparison of estimation models. Concerning the 5 models used to predict flight costs, it is difficult to say which model gives the most suitable prediction of P_i for three reasons (Figure 8 illustrates a visual comparison of estimates provided by the five models). First of all, we did not measure energetic expenditure empirically during flight in our study. Therefore, we can suggest which model predicts the more realistic values but cannot state on which is best. Secondly, results predicted by different models depend on measurement errors and natural variability of each measurement (for example, with annual variation in body mass and heart mass, we could get different results for the same species during different times of the year). Thirdly, predictions of P_i by different equations may be inaccurate since the used models have different sensitivity to various parameters.

In model 1 and 2, Bishop (1997) predicted that $\dot{V}O_2$ was sensitive to errors in M_H and haemoglobin concentration. A 1.00 % increase in M_H (+0.18 g) will raise V_s by 1.05 % (0.07 ml) and P_i by 1.05 % (1.3 W) and a 1.00 % increment in haemoglobin concentration (0.0015 g ml blood^{-1}) will raise C_{aO_2} by 1.00 % (0.02 ml O_2 ml blood^{-1}) and P_i by 1.24 % (1.5 W). In model 2, Bishop (1997) predicted that $\dot{V}O_2$ was also sensitive to errors in M_H and haemoglobin concentrations: a 1.00 % increase (0.18 g) will raise $\dot{V}_b$ by 0.88 % (24.5 ml blood min^{-1}) and P_i by 0.88 % (1.3 W). With Pennycuick's aerodynamic model (1989), the predicted P_i is sensitive to errors in P_o (a 1.00 % increase in P_o will raise P_i by

0.90 %) but it is most sensitive to the value of E_{FM}: a 0.01 raise in the assumed E_{FM} will decrease the predicted P_i by 4.01 % (7.2 W decrease). With the Masman & Klaassen model (1987), P_i is very sensitive to wing span and wing area : a 1.00 % increase of wingspan (0.01 m) will lower predicted P_i by 4.13 % (4.8 W decrease) and a 1.00 % increase of wing area (0.001 m^2) will raise P_i by 1.93 % (2.3 W). With Rayner's allometric model (1995), P_i is sensitive to every variable : a change of +1.00 % in body mass (+0.02 kg), wing area (+0.001 m^2) and wing span (+0.01 m) will modify P_i by +1.37 % (+2.2 W), +0.91 % (+1.5 W) and -3.31 % (-5.3 W), respectively. As we can see, models 3, 4 and 5 are the most sensitive, since errors or variability in measurements of wing morphology and E_{FM} provide the highest modifications in P_i.

Moreover, estimates obtained with the allometric models (4 and 5) also depend on the experimental conditions in which they were developed, the range of body masses and the type of flight performed by the birds used to compute the equations. For example, model 4 was developed with 14 bird species (body mass 3.8 – 1000 g) performing flapping and gliding flight, four of which were extremely aerial species (Masman and Klaassen 1987). It would then be inappropriate to use this model with eiders because they are low aerial species and their body mass surpasses the maximal range limit. With Rayner's model (1995), no information is provided concerning the source of the extra 40 data used to compute the equation 5 (71 additional data to those of Masman and Klaassen 1987). Nevertheless, as we know that 51 % of the studies used by Masman and Klaassen (1987) were conducted in wind tunnels, we can suppose that at least the same proportion of studies in Rayner's unknown data were carried out in wind tunnels. Masman and Klaassen (1987) and Rayner (1990) have suggested that data on flight energy costs obtained from birds flying in wind tunnels were high (30-50 % higher than natural conditions, but they did some errors in the evaluation of wind tunnel data, as reported by Butler and Bishop 2000). Other factors (reported by Bishop *et al.* 2002) can also cause an overestimation of flight costs in wind tunnels if they are not taken into account: effects of wearing a respiratory mask; encumbered flight; turbulence; stress associated with the laboratory environment and trainer; primary feathers abraded in confined aviaries and by the birds tending to peck at each other; and heat stress related to warm ambient temperatures in wind tunnels. For these reasons, we suggest that it would be improper to use these models to estimate flight cost in eiders, as in other large and low aerial species.

Moreover, results of P_i predicted by models 4 and 5 can vary largely whether the section of body between the wings (hereafter the back) is included or not in wing morphology measurements. Masman and Klaassen (1987) and Rayner (1995) did not specify whether they included the back in wing area and wingspan or not. We supposed that it was included, as for the calculations using the model 3 (aerodynamic theory, Pennycuick 1989). However, if we exclude the back, flight costs increase by 1.7-fold for models 4 and 5 (Figure 8). For example, the estimate from Masman and Klaassen's model with the back (4) is 117 W and without it (4') is 200 W and the estimate from Rayner's model with the back is 160 W (5) and without it (5') is 270 W. This specification concerning measurement of the back is therefore very important and should be mentioned in the literature as these models are very sensitive to these parameters.

In the light of these considerations, models 1, 2 and 3 would the best to estimate flight costs for eiders, but which?

The only difference between models 1 and 2 is that in the first model, f_H is measured in free-living birds and that in the second model, f_H is included in the estimates of cardiac output. Bishop (1997) compared measured and estimated values of $\dot{V}O_{2,\ max}$ according to models 1 and 2 for five bird species and concluded that model 2 appeared to be the 'method of choice' because it had a smaller overall error and the advantage of simplicity. Peters *et al.* (2005) did the same comparison between estimated and measured values with homing pigeons (*Columbia livia*) flying in wind tunnel and also suggested that model 2 was the preferred way to estimate a flying bird's $\dot{V}O_{2,\ max}$. From these comparisons, it has been shown that model 1 overestimated $\dot{V}O_{2,\ max}$ by 8.0 % and model 2 by 5.8 %. However, as discussed above, the f_H measured in eiders was lower than the estimated maximal value calculated with the allometric relationship $f_{H,\ flight} = 480\ M_b^{-0.187}$ (Bishop and Butler 1995). In other words, eiders do not seem to have the ability to fly near their theoretical $\dot{V}O_{2,\ max}$ value. In this context, the result from model 1 should be considered more as an estimate of minimal power input (P_{min}) required during flight and model 2 as an estimate of maximal power input (P_{max}) during flight.

However, a correction could be made to models 1 and 2 by measuring the concentration of haemoglobin in eiders or at least in diving ducks. As suggested by Lovvorn and Jones (1994), ducks adapted to shallow diving increase their blood volume and blood oxygen levels, and decrease their respiratory volume to counteract the upward buoyancy while feeding at the bottom. Therefore, diving species may have higher haemoglobin concentrations to increase their oxygen-carrying capacity. Lovvorn and Jones (1994) reviewed some studies with haemoglobin measurements in diving birds. By averaging the values found for three species of diving ducks (*Aythya sp.*) [Hb] = 0.1593 g ml blood^{-1}). By using this value with models 1 and 2, we obtain 123 W (1', Figure 8) and 149 W (2', Figure 8), respectively.

With this correction, model 1 provides results similar to the results obtained with the aerodynamic model for P_{min} with $E_{\mathrm{FM}} = 0.33$ (129 W, a difference of only 5 % with model 1 corrected with Hb of diving ducks). Moreover, the predicted minimum power speed estimated with *Flight 1.11* is similar to the average flight speed measured for eiders with radar (17.9 m s^{-1} for P_{min} and 17.5 m s^{-1}measured by Khalert *et al.* 2003). It has also been shown that larger species fly with power close to P_{min} and that power exceeding P_{min} represents a surplus that can be allocated for extra effort such as increase speed and gaining altitude (Hedenström and Alerstam 1992).

Model 3 (Pennycuick 1989) better fits the results of other models when using $E_{\mathrm{FM}} = 0.33$ (value from allometric equation of Bishop 2005) rather than $E_{\mathrm{FM}} = 0.23$ (default value). We cannot confirm the assumption of Bishop (2005) that E_{FM} scales with body mass since we did not measure $\dot{V}O_{2,\ max}$ directly. Nevertheless, with the similarity obtained between models 1, 2 and 3 when using $E_{\mathrm{FM}} = 0.33$, we suppose that mass-scaling E_{FM} could give more realistic values for P_{i}. As a consequence, estimates of flight costs found in the literature and those calculated with the aerodynamic model for larger birds should be lower when assuming that E_{FM} scales with body mass.

Finally, we suggest that the models 1' and 3' could be efficient to estimate P_{min} (123-129 W) and model 2' to estimate P_{max} (149 W). If it is true that model 2 estimates P_{max}, the P_{mr} estimated with the aerodynamic theory could be impossible to reach naturally for eiders. It is then possible to broaden some conclusions regarding the aerobic flight performance of eiders with the ratio "*available* P_{max} */ required* P_{min}" = 1.2 (Bishop 2005). This weak aerobic power margin shows that eiders have little aerobic capacity above their minimum requirement. For example, an additional 0.17 kg (9 %) of M_{b} would bring eiders to the brink of their aerobic abilities and force them to use supplementary anaerobic metabolism to sustain flight.

Flight costs (× BMR). For a long time, providing flight cost as multiples of *BMR* has been used in studies of time-energy budget to evaluate the total *DEE* and the proportion devoted to flight locomotion (Weathers and Nagy 1980, Weathers *et al.* 1984). It has also been used in some studies to compare flight cost between species (Drent and Daan 1980, Masman and Klaassen 1987, Nudds and Bryant 2000). This second method should not be used for literature comparisons between and within species because estimation models provide erroneous results of *BMR* and hence, estimates of flight costs are incorrect (Pelletier, *unpubl. data*). It is preferable to use actual flight costs in watts or in ml O_2 min^{-1} to reduce biases caused by transformations. Although it is useful to measure flight costs as multiples of *BMR* when computing *DEE*, empirical data must be preferred because *BMR* is not a single value for a species and it could be underestimated (Aschoff and Pohl 1970, Reynolds and Lee 1996, McKechnie and Wolf 2004) or overestimated (Prinzinger and Hanssler 1980) for eiders when yielded by models in the literature (*pers. obs.*). This is true whether comparing with *BMR* values measured by Jenssen *et al.* (1989), *RMR* values measured by Hawkins *et al.* (2000) or with the *RMR* values calculated in this study (Table 2). Consequently, by using the value of Jenssen *et al.* (1989) and estimates of P_{min} (models 1' and 3') and estimates of P_{max} (model 2'), energetic costs for foraging flights performed by wintering eiders should range between 17 and 20 × *BMR*. In comparison, these energetic costs were substantially higher than those obtained for other modes of locomotion in eiders: 3.2 × *BMR* (39.0 ml O_2 kg^{-1} min^{-1}) while running on a treadmill at speeds between 0.7 and 0.8 m s^{-1}; 4.5 × *BMR* (55.5 ml O_2 kg^{-1} min^{-1}) while swimming at maximum sustainable surface speeds; and 4.0 × *BMR* (49.0 ml O_2 kg^{-1} min^{-1}) while performing a whole dive cycle (Hawkins *et al.* 2000).

DAILY FLIGHT TIME VS. DAILY METABOLIC RATE

Even if flight costs estimated for eiders are very high, a notable result of our study is the absence of correlation between daily heart rate (*DHR*) and daily flight time (Figures 6a and b). This contrasts with many reports stating that time spent in high-cost activities like flight is positively related to daily energy expenditure (Flint and Nagy 1984, Tatner and Bryant 1986, Carlson and Moreno 1992, Nudds and Bryant 2000), *i.e.* the more a high-cost flyer spends time in flight per day, the higher its daily metabolic rate (*DMR*) will be. However, these authors mentioned that inaccurate predictions of flight times could yield errors in correlation tests and that it should be a priority in future studies to ensure that the flight component be accurately sampled. Thus, since we exhaustively quantified all flights performed during eight months, we can exclude this error source in our study.

So, why is *DHR* not correlated with daily flight time? There are at least three possible hypothesis that could explain this result. (1) Despite the high flight costs, the estimated proportion of flight within the energy budget is low (4 %) because eiders do not spend a large percentage of time in flight per day (0.66 %). Thus, it is possible that we did not detect increases in *DHR* at the interindividual level for the days outside migrations. However, we could expect a strong positive correlation during migration days.

(2) The *DHR* does not give a realistic estimate of *DMR*. For example, flying eiders increase their heart rate during flight by 4.2-fold (comparatively to resting heart rate = 86 beats min^{-1}) but they increase their P_i by 16-fold (comparatively to resting metabolic rate = 7.90 W). In this context, V_s and $C_{aO_2} - C_{\bar{v}O_2}$ should increase together by 3.8-fold. As a consequence, it is possible that a positive correlation exists between daily flight time and *DMR* when taking into account all possible variables that influence daily energy expenditure and not only the heart rate.

(3) Since there was a trend for a negative correlation between mean flight duration and *DHR* (Figure 7a) and a trend for a positive correlation between daily frequency of flights shorter than 2 min and *DHR* (figure 7b), we suggest that the *DMR* of a species having a very low daily flight time depends more on the number of takeoffs per day than on the number of flights per day. Takeoffs, ascents, descents and landings make up a large part

of every short flight and are more costly than cruising flights (Nudds and Bryant 2000, Hambly *et al.* 2002, 2004). For short flights performed by passerines (duration of few seconds), high costs can be explained in part as a result of the large induced power requirement to generate lift, work against gravity and fly at speeds below minimum power speed (Pennycuick 1989). However, birds with pointed and low-area wings and with consequent high wing-loading, cannot generate lift and will not function at low speeds (Lovvorn and Jones 1994). These birds must run, as other diving ducks, along the surface of the water or take off into a headwind to achieve minimum air speeds at which their wings can provide sufficient lift (Rayner 1988, Norberg 1990). In addition, with their weak takeoff ability, eiders would be observed to be temporary flightless all over the year when the interaction between their high wing-loadings and their flight muscle ratio is not sufficient to produce a lift, *e.g.* during pre-laying period (Guillemette and Ouellet 2005).

Moreover, the short-burst flight performance required for takeoff is dominated mainly by the anaerobic metabolism in large birds (Marden 1994). Larger birds must generate more power to achieve the same lift and, as a consequence, they increase their flight muscle power output over the typical aerobic limit (100 W kg^{-1}, Marden 1994). Therefore, the cost for takeoff can be calculated using the muscle mass-specific maximal anaerobic power output value of 225 W kg^{-1} as suggested by Marden (1994) and used by Guillemette and Ouellet (2005), when eiders were temporary flightless. With the flight muscle mass measured in this study (406.8 g, Table 1) and assuming a 33% muscle efficiency (estimated with Bishop 2005), the maximum power consumption of flight muscles is 277 W (37 × BMR or 2.1 × P_{min}) for takeoff. With the average sustained ascension rate of eiders

(0.41 m s^{-1}, Hedenström and Alerstam 1992), we know the time required to reach a given altitude. For example, if birds are flying at an altitude of 2 m above the sea level, it took them 5 s and they spent 1 353 J to attain this level (each 1 m elevation increases the daily energy expenditure by 676 J). In the same way, if eiders performed each flight at an altitude of only 10 m, they would increase their flight energy budget by +38%. This estimation could be higher whether we take into account the estimation of energy expenditure associated with the contraction of leg muscles during the running component for takeoff.

Masman and Klaassen (1987) proposed that an inverse relationship existed between flight costs and time spent flying. Our study confirms this trend and we suggest three different avenues for future research. First, comparisons of our data with allometric models of f_H and M_H suggest that eiders have relatively weak aerobic capabilities when they are not migrating: they have moderately low heart rate during flight, small heart mass and it appears that they fly with high energetic costs but close to their minimum power input (with low power margin). These relatively poor aerobic capabilities could be compensated by a higher oxygen carrying and extracting capacity, as in other diving birds. In order to evaluate the aerobic capability of this species throughout the year, we propose to collect data in various annual phases (body mass, heart mass, haemoglobin concentration, enzymatic activity, etc). Second, the correlation between the daily metabolic rate and the frequency of short flights suggests that takeoff cost is the major determinant of total flight cost. A method should be developed to properly measure takeoff costs of large birds in the field and/or in laboratory. Third, the low flight time of the eider could be the result of their abundant and low depleting food resources composed of sessile prey (Guillemette, Reed and Himmelman 1996). In another paper, we showed a strong correlation between the flight frequency and the dive frequency on a hourly basis (Pelletier *et al. in prep.* [Chapitre 2]). Thus, the low flight time observed in this study may result from low requirements of foraging movements. In that respect, we believe that a detailed analysis of their migration strategies will give some cues to discriminate between the ecological hypothesis and the suggestion that flight time of eiders is constrained by their physiology.

List of symbols

B	Wingspan
BMR	Basal metabolic rate
C_{aO_2}	Oxygen content in arterial blood
$C_{\bar{v}O_2}$	Oxygen content in mixed venous blood
DHR	Daily heart rate
DL	Data logger
DMR	Daily metabolic rate
E_{FM}	Flight muscle efficiency
f_{H}	Heart rate
M_{b}	Body mass
M_{H}	Heart mass

P_{i}	Metabolic power input
P_{max}	Maximum metabolic power input
P_{min}	Metabolic power at the minimum power speed
P_{mr}	Metabolic power at the maximum range speed
P_{o}	Mechanical power output
RHR	Resting heart rate
RMR	Resting metabolic rate
RQ	Respiratory quotient
S	Wing area
$s\dot{V}O_2$	Body mass-scaling rate of oxygen consumption
$\dot{V}_{b,max}$	Maximum cardiac output
V_{mp}	Minimum power speed
$\dot{V}O_2$	Rate of oxygen consumption
$\dot{V}O_{2,\,max}$	Maximum rate of oxygen consumption
V_s	Cardiac stroke volume

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Tables and figures

Table 1. Mean (± *S.D.*) body mass (M_b), heart mass (M_H), wing morphology and flight muscles of 12 common eiders (6 males and 6 females) collected during winter (without DL). The *p*-value is associated with the results of two-sample *t*-test testing for any significant difference between sexes.

Parameter	**Males (6)**	**Females (6)**	***t***	***p*-value**
M_b (g)	2333 ± 207	1929 ± 74	-4.50	0.004
M_H (g)	20.6 ± 2.1	17.9 ± 1.2	-2.49	0.037
M_H / M_b (%)	0.91 ± 0.06	0.92 ± 0.04	0.12	0.909
Wingspan (cm)[a]	101.1 ± 3.3	97.1 ± 2.4	-2.45	0.036
Wing area (cm^2)[a]	1241 ± 40	1185 ± 40	-2.41	0.037
Pectoralis (g)	317.2 ± 11.1	266.4 ± 28.6	-4.05	0.006
Supracoracoideus (g)	42.9 ± 3.1	36.7 ± 3.7	-3.13	0.011
Flight muscles (g)	482.6 ± 14.5	406.8 ± 40.1	-4.35	0.004

[a] Including the area between the wings

Table 2. Estimates of basal metabolic rate (BMR) or resting metabolic rate (RMR) and estimates of power input (P_i, in *W* or as multiples of *BMR* or *RMR*) during flight in wintering eiders ($N = 13$) according to five different models of estimation (see *Methods* for details).

Models of estimation	**P_i *(W)***	**P_i (multiples of *BMR or RMR)***			***References***
		Jenssen *et al.* 1989[a]	**Hawkins *et al.* 2000**[b]	**This study**[c]	
BMR or *RMR* (W)		7.39	7.56	7.90	
1 Fick equation (f_H measured directly and estimations)	116	16	15	15	Bishop (method 1) 1997
2 Fick equation ($V_{b,\ max}$ scaling with M_h and estimations)	140	19	19	18	Bishop (method 2) 1997
3 Aerodynamic model	129^d-160^e	17^d-22^e	17^d-21^e	16^d-20^e	Pennycuick 1989 (*Flight 1.11*)
4 Allometry (scaling with M_b and wing dimensions)	117	16	16	15	Masman & Klaassen 1987
5 Allometry (scaling with M_b and wing dimensions)	160	22	21	20	Rayner 1995

[a] BMR measured in winter-acclimatized common eiders in air and water respecting all criteria of BMR

[b] RMR (W) measured in air in fasting eiders ($\dot{V}O_2$ at rest in ml kg^{-1} min^{-1} converted in W)

[c] RMR (W) measured as the smallest 5-min mean of heart rate per day and converted in energy by using the regression obtained from results of Hawkins *et al.* (2000) between heart rate and oxygen consumption

[d] Minimum power input (P_{min}) at the minimum power speed (V_{mp})

[e] Power input (P_{mr}) at the maximum range speed (V_{mr}) defined as the speed at which the effective lift:drag ratio has its maximum value (Pennycuick 1989)

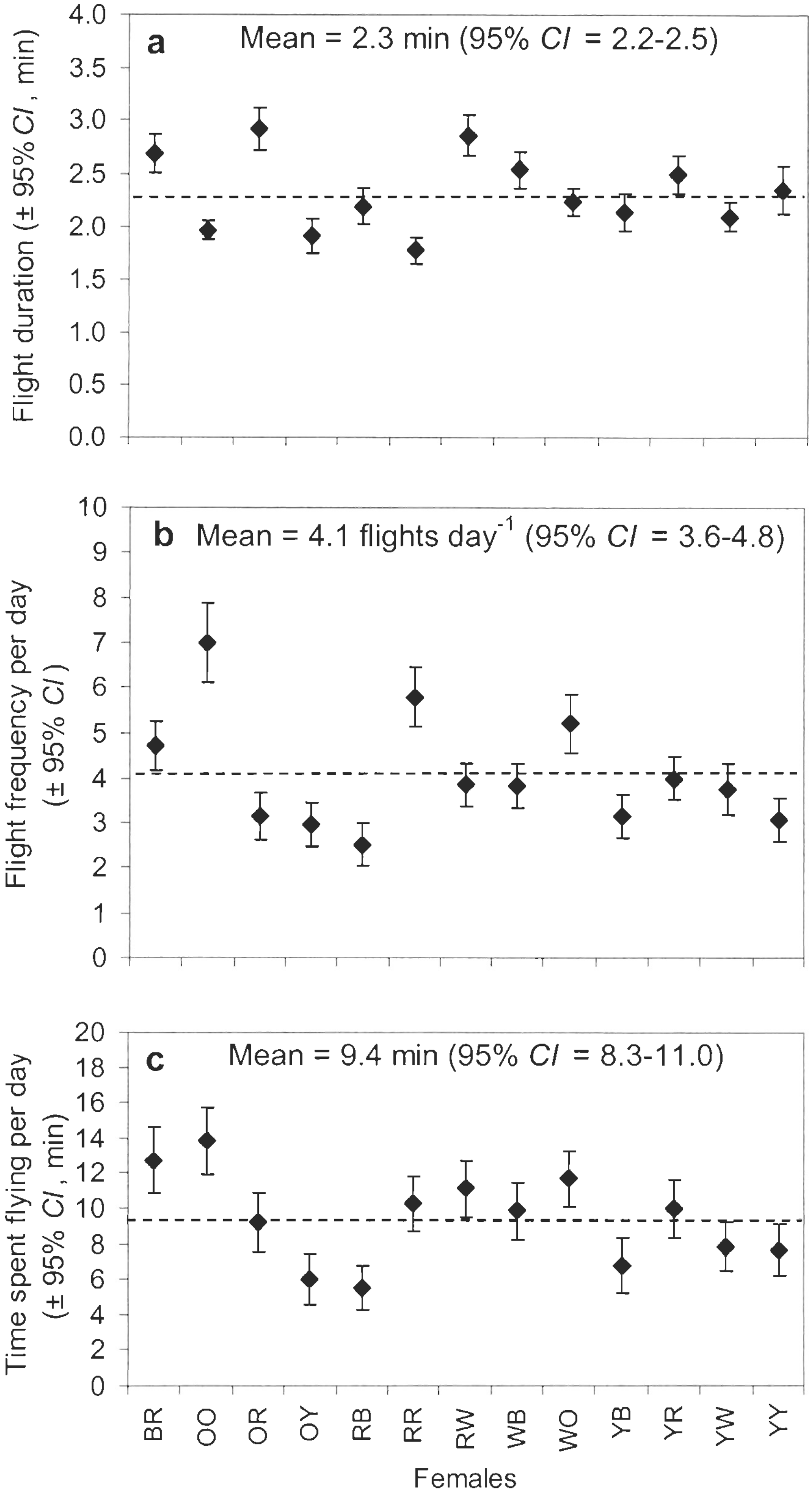

Figure 1. Mean local flight variables measured for 13 female common eiders during 178 ± 14 (*S.D.*) days from reproduction to winter period (excluding moult and migration periods): **a)** mean flight duration (min), **b)** mean flight frequency per day and **c)** mean time spent flying per day (min). Mean is represented by the dashed line in graphs. Values are means ± 95% *CI*.

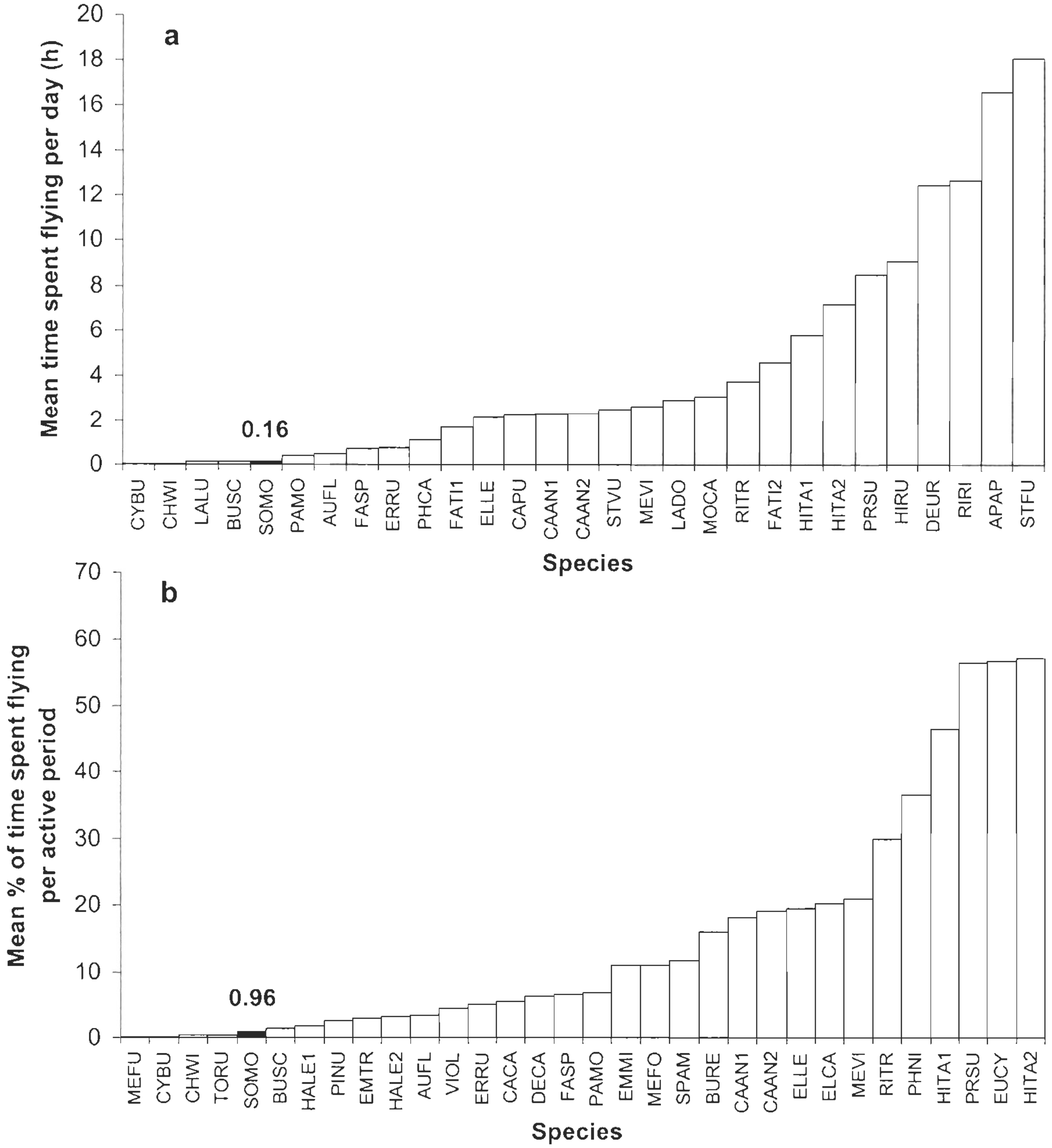

Figure 2. Interspecific comparison of **a)** mean time spent flying per day (h) and **b)** mean percentage (%) of time spent flying per active period (daylight) where black bars are the mean result for common eiders (SOMO, *Somateria mollissima*) in this study (APAP (*Apus apus*), AUFL (*Auriparus flaviceps*), BURE (*Buteo regalis*), BUSC (*Bubo scandiacus*), CAAN1 (*Calypte anna*), CAAN2 (*Calypte anna*), CAAN3 (*Calypte anna*), CACA (*Cardinalis cardinalis*), CAPU (*Calidris pusilla*), CHWI (*Charadrius wilsonia*), CYBU (*Cygnus buccinator*), DECA (*Dendroica caerulescens*), DEUR (*Delichon urbica*), ELCA (*Elanus caeruleus*), ELLE (*Elanus leucurus*), EMMI (*Empidonax minimus*), EMTR (*Empidonax traillii*), ERRU (*Erithacus rubecula*), EUCY (*Euphagus cyanocephalus*), FASP (*Falco sparverius*), FATI1 (*Falco tinnunculus*), FATI2 (*Falco tinnunculus*), HALE1 (*Haliaeetus leucocephalus*), HALE2 (*Haliaeetus leucocephalus*), HIRU (*Hirundo rustica*), HITA1 (*Hirundo tahitica*), HITA2 (*Hirundo tahitica*), LADO (*Larus dominicanus*), LALU (*Lanius ludovicianus*), MEFO (*Melanerpes formicivorus*), MEFU (*Melanitta fusca*), MEVI (*Merops viridi*), MOCA (*Morus capensis*), PAMO (*Parus montanus*), PHCA (*Phalacrocorax carbo*), PHNI (*Phainopepla nitens*), PINU (*Pica nuttalli*), PRSU (*Progne subis*), RIRI (*Riparia riparia*), RITR (*Rissa tridactyla*), SPAM (*Spiza americana*), STFU (*Sterna fuscata*), STVU (*Sturnus vulgaris*), TORU (*Toxostoma rufum*), VIOL (*Vireo olivaceus*) (see *APPENDIX I* for details)).

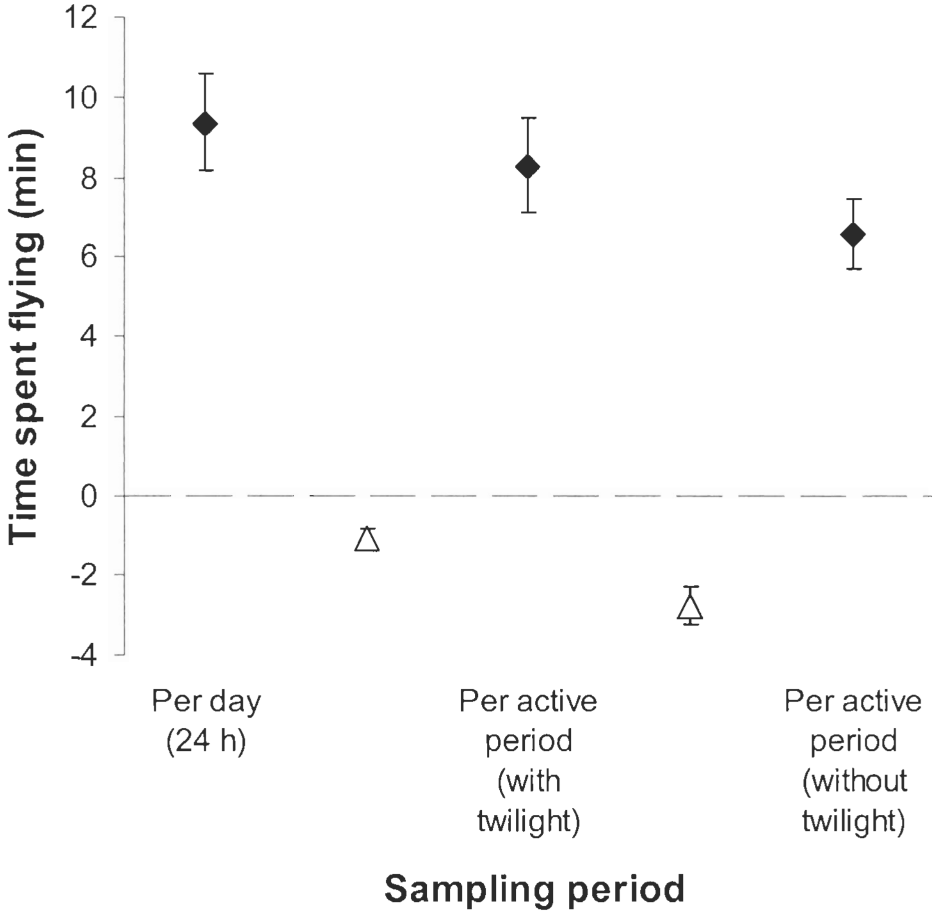

Figure 3. Mean time spent flying per day (± 95% *CI*, min) [filled diamonds] of common eiders ($N = 13$) according to duration of sampling period (24 h per day, active period with twilight and active period without twilight) and differences (± 95 % *CI*, min) [unfilled deltas] between 24 h sampling and active period sampling. Means, differences and 95 % *CI* were calculated using a bootstrap analysis with 10 000 iterations.

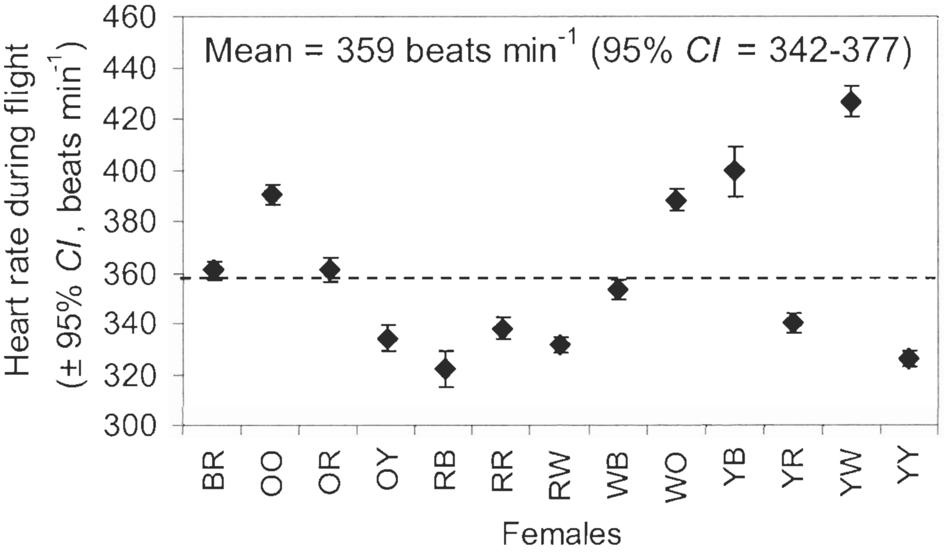

Figure 4. Mean heart rate (beats min^{-1}) recorded during flight in 13 female common eiders during winter. Mean is represented by the dashed line in graphs. Values are means ± 95% *CI*.

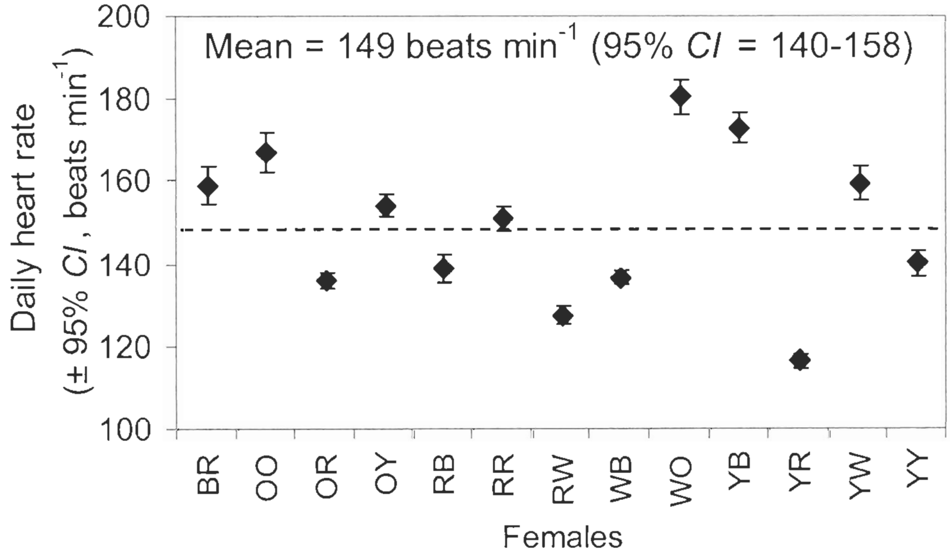

Figure 5. Mean daily heart rate (beats min^{-1}, see *Methods*) measured for 13 female common eiders during 178 ± 14 (S.D.) days from reproduction to winter period (excluding moult and migration periods). Mean is represented by the dashed line in graphs. Values are means ± 95% *CI*.

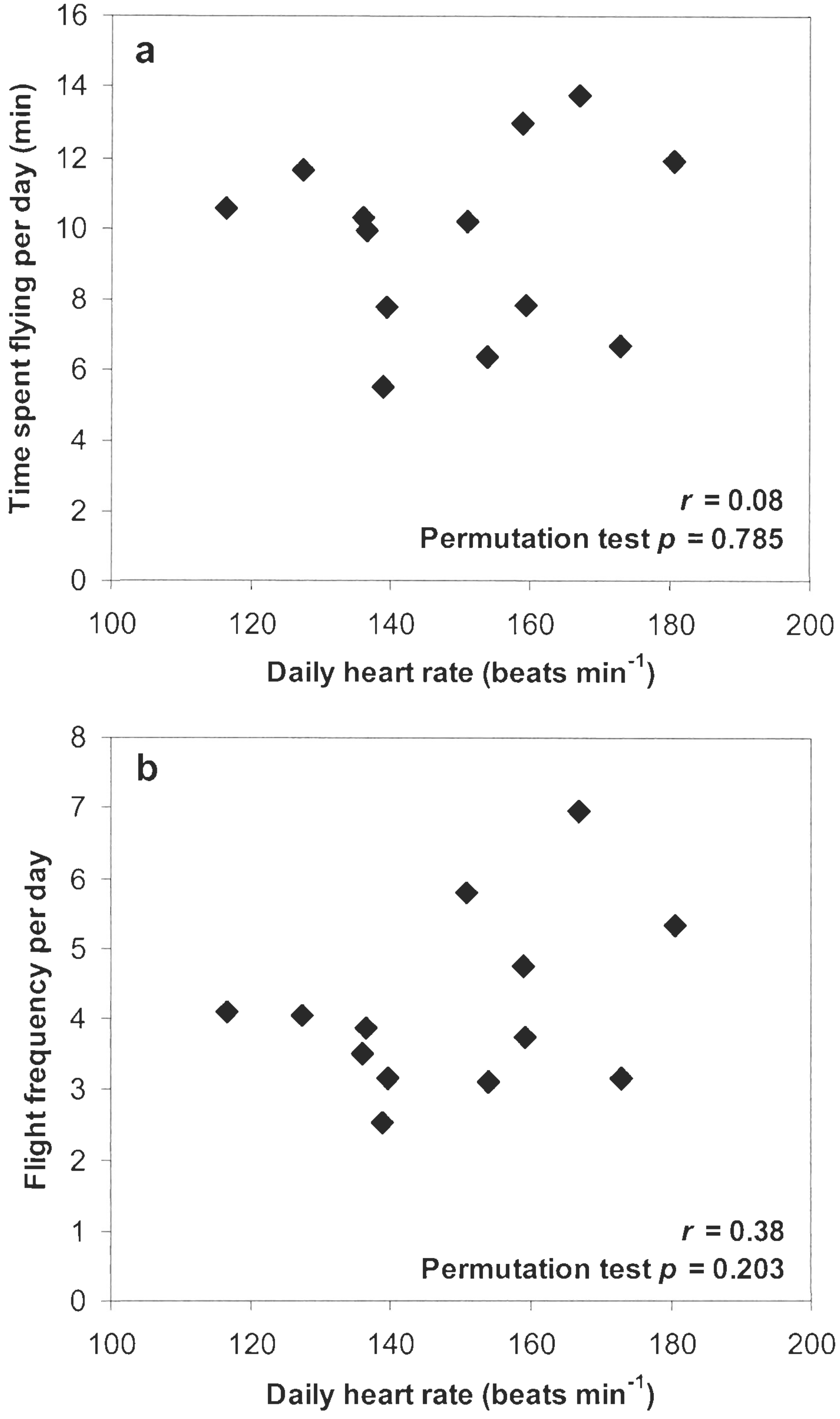

Figure 6. a) Mean time spent flying per day (min) plotted against daily heart rate (beats min^{-1}). **b)** Mean flight frequency per day plotted against daily heart rate (bmp) (N = 13). The p-value was determined from the position of the original Pearson r among the 10 000 permutations of Pearson r arranged in ascending order.

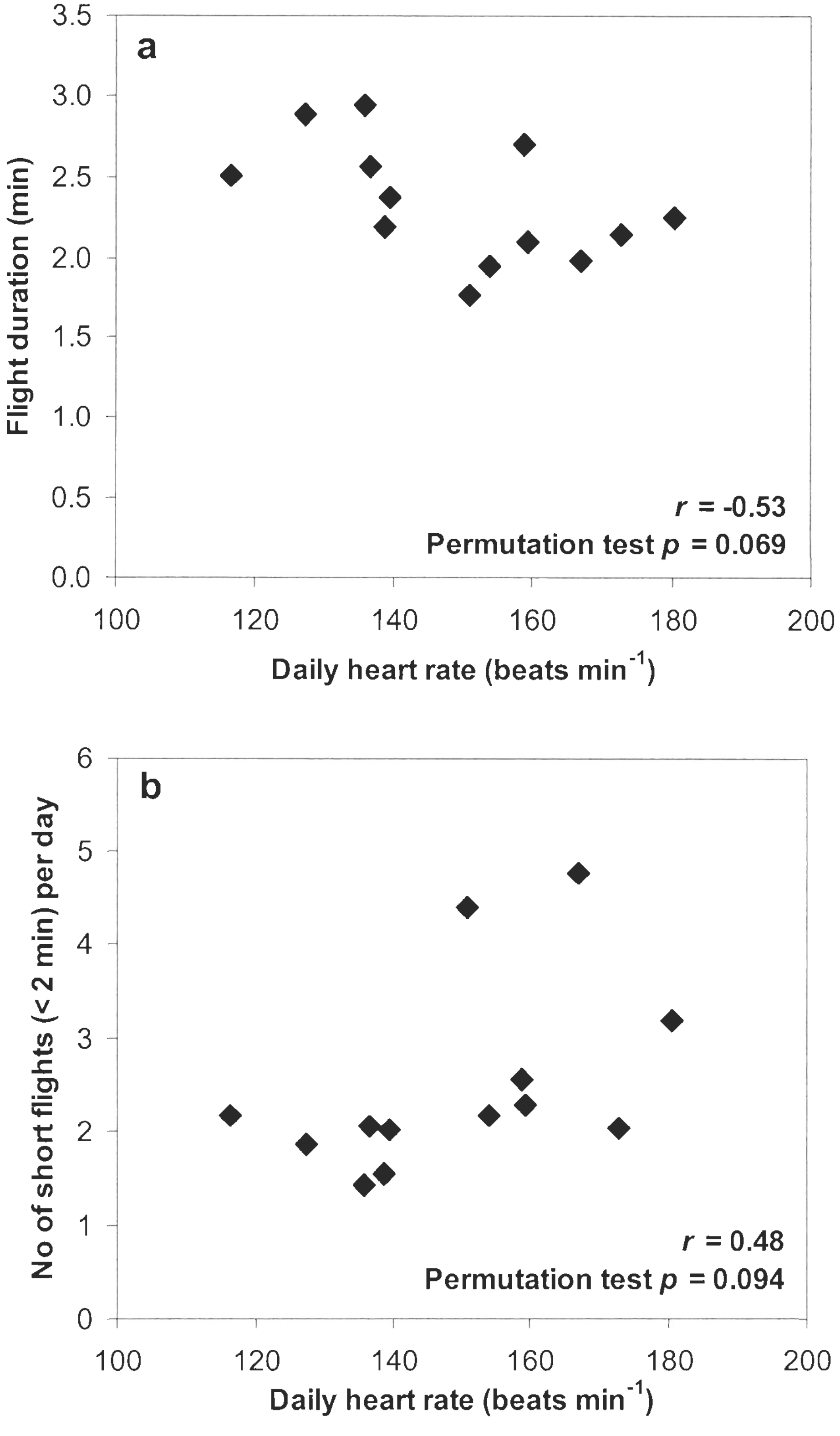

Figure 7. a) Mean flight duration (min) plotted against daily heart rate (beats min^{-1}). **b)** Mean number of short flights (less than 2 min) per day plotted against daily heart rate (beats min^{-1}) (N = 13). The p-value was determined from the position of the original Pearson r among the 10 000 permutations of Pearson r arranged in ascending order.

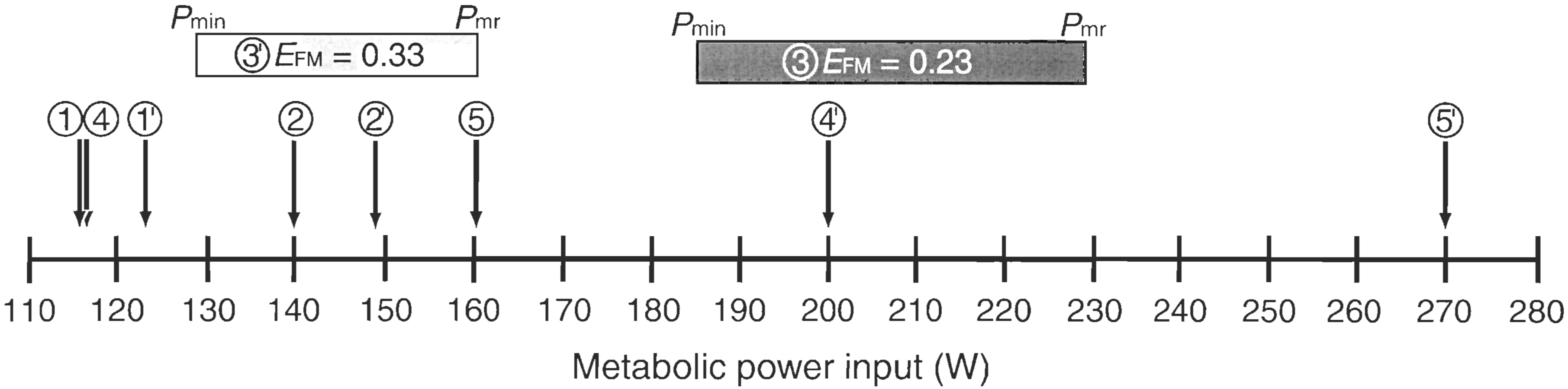

Figure 8. Comparison of values obtained with models used to predict power input (P_i) during flight of wintering common eiders. Grey bars represent range of P_i (from minimum power input [P_{min}] to power input at the maximum range speed [P_{mr}]) calculated with the Pennycuick model (1989) with E_{FM} = 0.23 (default value) and E_{FM} = 0.33 (estimated as suggested by Bishop 1997). See *Table 2* for references of models 1, 2, 3, 4 and 5. Numbers with apostrophe indicate a different estimation obtained by modifying a variable into the model (see *Discussion*).

Appendix 1. Measurements of time spent flying per day (h day^{-1}, % day^{-1} or % active period^{-1}) for 40 bird species.

Species	**Mass (g)**	**TSF (h day^{-1})**	**TSF (% day^{-1})**	**TSF (% active period^{-1})**	**Annual phase**	**Methods**	**Ref.**
Calypte anna	4.1	2.35	9.80	18.20	Post-repr.	Focal, botanical gardens, daylight	Pearson 1954
Auriparus flaviceps	6.8	0.48	1.98	3.42	Post-repr.	Daylight, free-living	Austin 1978
Dendroica caerulescens	9.4	-	-	6.25	Breeding	Daylight, free-living	Holmes *et al.* 1979
Empidonax minimus	10.0	-	-	10.96	Breeding	Daylight, free-living	Holmes *et al.* 1979
Parus montanus	11.5	0.40	1.66	6.80	-	Daylight, focal, large aviary	Carlson and Moreno 1992
Empidonax traillii	12.6	-	-	3.00	Breeding	Daylight (±30 min civil twilight), free-living	Ettinger and King 1980
Riparia riparia	12.9	12.70	52.92	-	?	?	Westerterp and Bryant 1984
Hirundo tahitica	14.1	7.19	29.97	57.26	Breeding	Daylight, free-living	Bryant el al. 1984
Hirundo tahitica	14.7	5.81	24.21	46.58	Breeding	Daylight (7h-19h), free-living	Hails 1984, Westerterp and Bryant 1984
Vireo olivaceus	17.0	-	-	4.47	Breeding	Daylight, free-living	Holmes *et al.* 1979
Delichon urbica	18.1	12.50	52.08	-	?	?	Westerterp and Bryant 1984
Erithacus rubecula	18.6	0.74	3.07	5.10	-	Large aviary, only daylight	Tatner and Bryant 1986
Hirundo rustica	19.1	9.10	37.92	-	?	?	Westerterp and Bryant 1984

Appendix 1. ... *SUITE*

Species	Mass (g)	TSF (h day^{-1})	TSF (% day^{-1})	TSF (% active period^{-1})	Annual phase	Methods	Ref.
Phainopepla nitens	24.0	-	-	36.52	Breeding	Daylight, free-living, focal	Walsberg 1978
Calidris pusilla	25.0	2.28	9.50	-	Breeding	Free-living, 24 h	Ashkenazie and Safriel 1979
Spiza americana	27.0	-	-	11.75	Breeding	Daylight, free-living	Schartz and Zimmerman 1971
Merops viridi	33.8	2.63	10.96	20.94	Breeding	Daylight, free-living	Bryant el al. 1984
Apus apus	40.4	16.60	69.17	-	?	?	Lyuleeva 1970, Dolnik 1982
Cardinalis cardinalis	45.0	-	-	5.52	-	Daylight, outdoor aviary, focal	Shuman *et al.* 1992
Lanius ludovicianus	45.5	0.11	0.46	-	-	Large aviary	Weathers *et al.* 1984
Progne subis	47.7	8.50	35.48	56.50	Breeding	Daylight, free-living	Utter and LeFebvre 1970, 1973
Charadrius wilsonia	60.0	0.04	0.18	0.37	Wintering	Daylight, free-living, focal	Morrier & McNeil 1991
Euphagus cyanocephalus	63.0	-	-	56.87	Wintering	Daylight, free-living, focals	Verbeek 1964
Toxostoma rufum	69.0	-	-	0.37	Wintering	Daylight (5h30-17h30), free-living	Fischer 1981
Sturnus vulgaris	75.0	2.50	10.42	-	?	?	Westerterp and Drent 1985
Melanerpes formicivorus	80.0	-	-	11.00	?	Daylight, free-living, focal	Hooge 1991
Falco sparverius	119.0	0.73	3.02	6.60	Wintering	Daylight (± 30 min), free-living	Koplin *et al.* 1980

Appendix 1. ... *SUITE*

Species	Mass (g)	TSF (h day^{-1})	TSF (% day^{-1})	TSF (% active $period^{-1}$)	Annual phase	Methods	Ref.
Pica nuttalli	155.0	-	-	2.60	Year	Daylight, free-living, 1-3 days per month	Verbeek 1972
Sterna fuscata	194.0	18.10	75.42	-	Breeding	Free-living	Flint and Nagy 1984
Falco tinnunculus	213.0	1.70	7.08	-	Wintering	Daylight, free-living, focal	Masman and Klaassen 1987
Falco tinnunculus	213.0	4.60	19.17	-	Breeding	Daylight, free-living, focal	Masman and Klaassen 1987
Elanus caeruleus	243.0	-	-	20.30	?	Daylight, free-living	Tarboton 1978
Calypte anna	298.0	2.29	9.56	19.10	Breeding	Daylight, free-living, focal	Stiles 1971
Elanus leucurus	331.0	2.14	8.94	19.50	Wintering	Daylight (± 30 min of twilight), free-living	Koplin *et al.* 1980
Rissa tridactyla	400.0	3.77	15.70	29.90	Breeding	Daylight, free-living, focal and radio-tagged	Jodice *et al.* 2002
Larus dominicanus	1 035.0	2.96	12.30	-	Breeding	Daylight, free-living, focal	Maxson and Bernstein 1984
Melanitta fusca	1 670.0	-	-	0.08	Breeding	Daylight, free-living	Brown and Fredrickson 1987
Bubo scandiacus	1 830.0	0.13	0.54	1.30	Wintering	Daylight (8h-18h), free-living	Boxall and Lein 1989
Buteo regalis	1 880.0	-	-	16.00	Wintering	Daylight, free-living, focal	Plumpton et Andersen 1997
Morus capensis	2 500.0	3.12	13.00	-	Breeding	Acceleration data-logger, free-living	Ropert-Coudert *et al.* 2004

Appendix 1. ... *SUITE*

Species	Mass (g)	TSF (h day^{-1})	TSF (% day^{-1})	TSF (% active period^{-1})	Annual phase	Methods	Ref.
Phalacrocorax carbo	3 335.0	1.13	4.72	-	Breeding	Daylight, free-living, focal	Kuntz 2004
Haliaeetus leucocephalus	4 325.0	-	-	3.20	Wintering	Daylight, free-living	Craig *et al.* 1989
Haliaeetus leucocephalus	4 325.0	-	-	1.80	Wintering	Daylight, free-living	Stalmaster and Gessaman 1984
Cygnus buccinator	10 800.0	0.02	0.10	0.10	Migration (stopover)	Daylight, free-living, focal	Lamontagne et al. 2004

CHAPITRE IV : CONCLUSIONS DU MÉMOIRE

Cette étude a démontré que le consignateur de données enregistrant la fréquence cardiaque est une nouvelle technologie tout à fait appropriée pour étudier le vol battu chez les oiseaux autant du point de vue comportemental qu'énergétique. La fréquence cardiaque élevée et le profil stéréotypé enregistrés lors des vols de courte et longue durées ont permis de discriminer ce moyen de locomotion des autres comportements quotidiens. Cette signature cardiaque du vol a ainsi pu permettre d'identifier, exhaustivement et pour la première fois, tous les vols effectués par une espèce animale au cours d'un cycle annuel presque complet.

Ces consignateurs de données et la technique développée pour identifier les vols ont été profitables pour l'étude de l'Eider à duvet qui est une espèce de canard marin vivant la plupart du temps sur l'eau, dans des environnements inaccessibles pour les observateurs et les chercheurs. Ils ont permis de mettre en lumière le fait que cet oiseau, doté d'une charge alaire souvent à la limite de sa capacité de décollage, utilise ce moyen de locomotion de façon parcimonieuse tout au long de l'année à l'exception des migrations. Malgré tout, près du trois quarts du temps de vol enregistré l'a été en dehors des migrations. En fait, l'Eider à duvet passe moins de 10 min en vol par jour en effectuant en moyenne 4 vols d'un peu moins de 2,5 min. Pendant les migrations, qui durent de 1 à 5 jours, le temps de vol monte à près de 3 h jour^{-1} en moyenne. De toutes les études qui ont tenté d'intégrer le temps passé à voler chez une espèce donnée, c'est l'Eider à duvet qui vole le moins parmi toutes les espèces étudiées capables de voler (chapitre 3). Au niveau des migrations, des études ultérieures devront être réalisées pour analyser les stratégies que cette espèce utilise avant, pendant et après les migrations.

Au niveau de l'échelle quotidienne, les vols sont effectués particulièrement au cours de la pénombre matinale et dans la matinée (chapitre 2). Cela pourrait correspondre avec le fait que l'Eider à duvet souffre d'incapacité temporaire au décollage après des séances d'alimentation et que la simple prise de poids journalière pourrait être suffisante pour diminuer ses capacités d'envol à mesure que la journée avance (Guillemette, 1994). Par conséquent, le jeûne nocturne pourrait être suffisant pour diminuer la masse corporelle et augmenter la probabilité de décoller. D'ailleurs, une corrélation très forte a été notée entre la fréquence relative des vols et la fréquence relative des plongée en fonction de l'heure (ajustée) de la journée (chapitre 2). Il a été démontré que la fréquence des plongées augmente juste après le lever de soleil et que la fréquence maximale de plongées est décalée d'environ deux heures après la fréquence maximale de vols. Des études complémentaires plus détaillées devraient cependant être réalisées pour mettre en relation le comportement d'alimentation en plongée avec le comportement de vol.

Au niveau de la fréquence cardiaque enregistrée en vol, il a été observé que celle-ci était relativement élevée pour l'Eider à duvet en milieu naturel (chapitre 3), environ le double de celle enregistrée lors de la nage et de la marche avec des eiders en captivité et quatre fois la fréquence cardiaque enregistrée au repos (Hawkins *et al.* 2000). Chez d'autres espèces de masse similaire à l'Eider à duvet, il y a peu de données sur la fréquence cardiaque enregistrée pendant le vol chez des individus en milieu naturel. Elle a été mesurée à 310 ± 18 battements min^{-1} pour des vols courts chez des Cormorans géorgiens (*Phalacrocorax georgianus*, Bevan *et al.*, 1997), 253 ± 10 battements min^{-1} chez des Bernaches nonnettes (*Branta leucopsis*) en migration (Butler *et al.*, 1998), 413 ± 6 battements min^{-1} pour des vols courts chez des Oies rieuses (*Anser albifrons*, Ely *et al.*, 1999) et 448 ± 9 battements min^{-1} pour des vols provoqués par un dérangement humain chez des Oies rieuses (*Anser albifrons,* Ackerman *et al.,* 2004). Étant donné le faible nombre d'espèces et le contexte de mesure particulier à chacune de ces études, il devient difficile de faire une comparaison interspécifique de la fréquence cardiaque enregistrée pendant le vol en milieu naturel. Toutefois, comme il l'a été démontré au chapitre 3 à l'aide de deux équations allométriques (Bishop et Butler, 1995; Peters *et al.*, 2005) obtenues à partir de fréquence cardiaque mesurée dans toutes sortes de conditions (ex. : oiseaux volant dans une soufflerie, derrière un camion en mouvement, etc.), l'Eider à duvet semble voler avec une fréquence cardiaque relativement plus basse que d'autres espèces de masse similaire.

Il en serait de même également en ce qui concerne la masse cardiaque. En effet, en comparant la masse du coeur obtenue à partir de deux équations allométriques (Bishop et Butler, 1995; Peters *et al.*, 2005) à celle mesurée dans le chapitre 3, il appert que l'Eider à duvet possède un coeur relativement petit pour une espèce de cette taille et que celui-ci devrait être plus gros pour une espèce qui doit voler à des vitesses très élevées. Par conséquent, le système cardiovasculaire pourrait être peu adapté au vol battu et énergique qu'utilise l'Eider à duvet pour se maintenir et se déplacer dans les airs.

Concernant maintenant la dépense énergétique liée au vol, les différents modèles utilisés dans le chapitre 3 ont montré de manière certaine qu'il est fort coûteux pour l'Eider à duvet de voler. La comparaison effectuée entre les modèles a suggéré que les modèles allométriques sont inappropriés pour estimer les coûts du vol pour cette espèce alors que les modèles basés sur la théorie aérodynamique et l'équation de Fick présentent des résultats réalistes. Les coûts de vol ont été estimés à environ 123 W pour la puissance minimale requise pour voler (P_{min}) et à 149 W pour la puissance maximale (P_{max}) pouvant être générée chez cette espèce en vol (ou entre 17 et 20 × *BMR*). Malgré le fait que ces estimations semblent réalistes, il faudrait dans de futures études récolter des données complémentaires pour pouvoir étudier l'énergétique du vol sur tout le cycle annuel et expliquer ses variations saisonnières. Par exemple, il faudrait soit prélever des données de masse pour le corps, le coeur et le muscle pectoral, ainsi que des concentrations d'hémoglobine chez des eiders tout au long de l'année ou soit établir la relation directe $\dot{V}O_2 / f_H$ avec des eiders à duvet volant en soufflerie. Il pourrait aussi être intéressant de jumeler un émetteur satellite chez les oiseaux possédant un consignateur de données pour connaître leur position géographique et ainsi acquérir des données météorologiques (ex. : orientation et vitesse des vents, température, etc.) qui peuvent influencer le coût du vol.

Malgré les estimations élevées de coût du vol pour l'Eider à duvet, il a été étonnant de découvrir qu'il n'existe pas de relation entre le temps de vol journalier et la dépense énergétique quotidienne chez cette espèce (chapitre 3). Trois hypothèses ont été proposées pour expliquer ce résultat : (1) la proportion quotidienne de temps passé en vol est trop faible pour influencer la dépense énergétique quotidienne, (2) la fréquence cardiaque journalière n'est pas un bon indicateur à elle seule du taux métabolique quotidien ou (3) le nombre quotidien de décollages est la variable qui influence le plus la dépense énergétique quotidienne chez cette espèce qui possède des capacités d'envol très faibles. Une combinaison des première et troisième hypothèses pourrait expliquer ce phénomène, mais il faudrait faire une étude plus poussée de la variation annuelle des deux autres variables composant l'équation de Fick (*i.e.* le volume éjectionnel du coeur et l'extraction d'oxygène) pour s'assurer que la fréquence cardiaque permet d'estimer avec justesse le taux métabolique quotidien.

Enfin, notre étude a permis de décrire l'aspect temporel du comportement qu'est le vol d'une façon plus exacte et exhaustive que dans toutes les études précédentes qui ont été effectuées en milieu naturel. Elle a également permis d'apporter des éléments de réponse pour expliquer la pratique parcimonieuse de ce comportement chez l'Eider à duvet en étudiant l'aspect énergétique. Toutefois, il reste que les raisons écologiques, physiologiques et évolutives justifiant la faible utilisation de ce comportement ne sont pas encore totalement comprises.

Si on résume, la pratique du vol chez l'Eider à duvet pourrait être la résultante de ses faibles capacités de vol (décollages limités par la charge alaire élevée, décollage et vol battu coûteux, fréquence cardiaque et masse cardiaque relativement faibles). Mais il reste également que l'Eider à duvet, qui utilise ce moyen de locomotion de façon corrélée à ses activités d'alimentation en plongée (chapitre 2), pourrait ne pas avoir besoin de se déplacer puisqu'il passe la majeure partie de son temps sur l'eau au courant de l'année, le jour comme la nuit, juste au-dessus de ses sites d'alimentation (principalement des bancs de moules bleues). Or, ces derniers subissent peu de variations temporelles d'abondance et présentent de grandes densités de proies fixées au substrat rocheux (ce qui diminue les déplacements reliés à la quête alimentaire). Et comme les eiders vivent presque en permanence sur l'eau en dehors de la reproduction, les courts déplacements entre chacune des parcelles d'alimentation peut s'effectuer à la nage. Par conséquent, il se peut que la faible pratique du vol découle d'une faible nécessité à l'utiliser en dehors des migrations.

Pour être capable de déterminer si ce sont les faibles capacités ou les faibles nécessités qui gouvernent la pratique du vol chez l'Eider à duvet, il faudrait étudier plus en profondeur les migrations. Par exemple, au cours de ces périodes, les faibles capacités au vol devraient être illustrées par une série de vols de durée courte à moyenne (de quelques minutes à deux-trois heures) lors des migrations, ponctués de séances d'alimentation. En effet, étant donné que cette espèce présente une charge alaire élevée, il est fort à parier que celle-ci ne puisse pas transporter une masse supplémentaire importante en réserves lipidiques puisqu'elle ne pourrait tout simplement plus voler. La stratégie serait donc plutôt de s'alimenter tout au long de ses migrations pour ne pas nuire à ses capacités d'envol. Par ailleurs, il est possible aussi que pour diminuer ses coûts de vol, l'eider développe des stratégies comportementales pour être capable de voler sur de plus longues périodes (en volant en formation en V, en attendant l'orientation et l'intensité optimale du vent), ce qui se traduirait par une fréquence cardiaque plus faible. De plus, pour surpasser la contrainte que ce comportement impose au niveau du budget énergétique, il est à supposer que la fréquence cardiaque au repos serait plus faible lors de ces journées pour limiter les coûts métaboliques autres.

Pour investiguer du côté de l'hypothèse de la faible nécessité, il pourrait être intéressant de connaître le positionnement géographique des eiders au courant de la journée de manière combinée à la disponibilité des bancs de moules. Des localisations rapprochées au courant de la journée nous indiqueraient que les eiders ne se déplacent que sur de faibles distances à l'échelle quotidienne (soit par la nage ou par le vol). Par conséquent, on pourrait supposer que la quête alimentaire exige un temps de recherche relativement court et par conséquent, une faible nécessité à voler. Une étude de la densité et de l'étendue des bancs de moules dans les secteurs fréquentés par les eiders à duvet permettraient de confirmer la faible nécessité des déplacements quotidiens.

Finalement, cette étude a permis de décrire le vol chez une espèce d'oiseau vivant dans un milieu peu accessible aux chercheurs et aux ornithologues. Elle ouvre donc la voie à d'autres investigations qui permettront peut-être de comprendre pourquoi ce comportement est peu utilisé chez cette espèce et quels sont les facteurs qui l'influencent.

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