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MATHILDE RENAUD

COÛTS ÉNERGÉTIQUES DE LA THERMORÉGULATION CHEZ LES JEUNES DE LA GRANDE OIE DES NEIGES EN MILIEU NATUREL

Mémoire
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RÉSUMÉ

La présente étude nous a permis de mesurer les coûts énergétiques associés à la thermorégulation chez les oisons de la Grande Oie des neiges en croissance à l'île Bylot. Dans un premier temps, nous avons calibré en laboratoire des mannequins taxidermiques de quatre âges différents avec des oisons vivants, dans des conditions de température, de vent et de rayonnement représentatives du milieu naturel. Ensuite, l'utilisation des mannequins taxidermiques sur le terrain nous a permis de décrire l'environnement thermique dans lequel croissent les oisons. La température opérante standard (T_{es}) moyenne pour la période s'étalant de l'éclosion jusqu'à l'âge de 40 jours a été de 5.3°C pour 1994-1997. Nous avons calculé que, pendant cette période, les oisons ont dépensé pour la thermorégulation environ 30 % de l'énergie allouée au métabolisme de maintien. Finalement, nous avons estimé que les oisons nés 6 jours après le pic d'éclosion doivent allouer environ 6 % plus d'énergie à la thermorégulation que ceux qui ont éclos 6 jours avant ce pic.

Auteur: Mathilde Renaud (Mathilde Renaud)

Directeur de recherche: Gilles Gauthier (Gilles Gauthier)

Codirecteur de recherche: (Jacques Larochelle)

ABSTRACT

In this study, we evaluated the energetic cost of thermoregulation for Greater Snow Goose goslings during growth in the High Arctic. The study was divided in two sections. In the first one, we calibrated in the laboratory taxidermic mounts of four different ages against live goslings using an array of thermal conditions representative of what is found in nature. In the second section, by using the taxidermic mounts in the field, we described the thermal environment within which goslings grow. Between 0 and 40 d of age, the mean (1994-1997) standard operative temperature (T_{es}) experienced by goslings was 5.3°C. For this period, we evaluated that goslings must allocate to thermoregulation about 30 % of the energy required for maintenance metabolism. We also estimated that goslings hatched 6 d after the peak day of hatch spent about 6 % more energy to thermoregulation than those hatched 6 d before peak hatching.

AVANT-PROPOS

Ce mémoire comporte quatre chapitres. Le chapitre I est une introduction générale et on y présente une synthèse des connaissances ayant trait à la thermorégulation chez les oiseaux, les Ansérinés en particulier, ainsi qu'à l'utilisation de mannequins taxidermiques dans la description de l'environnement thermique d'un animal. De plus, les objectifs de l'étude y sont présentés. Les chapitres II et III constituent le corps du mémoire et sont rédigés en anglais sous forme d'articles scientifiques. L'objectif principal du chapitre II est de valider nos instruments de mesure, les mannequins taxidermiques, en les calibrant en laboratoire avec des oisons vivants. Ces mannequins taxidermiques sont utilisés au chapitre III pour évaluer les coûts énergétiques associés à la thermorégulation en milieu naturel chez les jeunes de la Grande Oie des neiges. Finalement, le chapitre IV est une conclusion générale qui fait la synthèse de l'ensemble des résultats obtenus.

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INTRODUCTION GÉNÉRALE

LA THERMORÉGULATION

Les mammifères et les oiseaux sont des homéothermes puisqu'ils maintiennent une température corporelle (T_b) élevée, relativement constante et indépendante de celle de l'environnement. On peut les définir aussi comme des endothermes parce qu'ils sont capables de maintenir leur T_b bien au-dessus de la température ambiante par des processus internes de génération de chaleur (Whittow, 1986; Schmidt-Nielsen, 1990). De telles caractéristiques ont permis à ces deux groupes d'envahir des milieux dont les conditions thermiques sont des plus extrêmes, des régions polaires aux déserts les plus chauds. Dans tout système homéotherme, il doit y avoir un équilibre entre les gains et les pertes de chaleur. Chez les endothermes, le maintien d'une température corporelle stable implique donc que la production métabolique de chaleur compense les pertes à l'environnement. La plupart des oiseaux conservent une T_b d'environ 40 ± 2°C tandis que, chez les mammifères euthériens typiques, elle est d'environ 38 ± 2°C (Schmidt-Nielsen, 1990). Puisque les oiseaux sont les vertébrés endothermes possédant la température corporelle la plus élevée, le gradient entre leur température corporelle et celle de l'environnement est le plus prononcé, ce qui peut provoquer des pertes de chaleur plus rapides (Welty et Baptista, 1988).

L'entretien chimique, soit celui des structures biochimiques et des fonctions métaboliques, entraîne inévitablement chez tout organisme vivant une production de chaleur que l'on qualifie de thermogenèse de base. La gamme de températures ambiantes pour lesquelles cette thermogenèse est suffisante pour assurer le maintien de la température corporelle est connue comme la zone de thermoneutralité de l'animal. À l'intérieur de cette zone, limitée par les températures critiques inférieure (T_{lc}) et supérieure (T_{uc}), l'effort thermorégulateur est minimum (Monteith et Mount, 1974). Lorsque la température ambiante se situe au-dessous de la T_{lc} ou au-dessus de la T_{uc}, il y a apparition d'au moins une des réactions typiques d'un stress thermique. Au-dessus de la T_{uc}, les mécanismes de la thermolyse évaporative tels le léchage, la polypnée, le flutter gulaire, la sudation et l'urohidrose permettent de ralentir l'augmentation de la température corporelle (Monteith et Mount, 1974). À des températures ambiantes plus basses que la T_{lc}, l'augmentation de la production métabolique de chaleur est possible grâce aux divers mécanismes de la thermogenèse de régulation, tels que la thermogenèse sans frisson ainsi que l'activité musculaire liée au frissonnement ou à l'exercice (Schmidt-Nielsen, 1990). Cependant, l'animal ne pourra pas augmenter son métabolisme indéfiniment afin de maintenir son homéothermie puisqu'il existe un métabolisme maximum dit de sommet. Ce métabolisme de sommet, ainsi que la conductance thermique de l'animal, seront les facteurs qui détermineront la température ambiante la plus froide compatible avec le maintien d'une température corporelle stable (Schmidt-Nielsen, 1990).

De nombreux avantages découlent du maintien d'une température corporelle élevée. En particulier, la stabilité physiologique qui résulte de l'homéothermie permet à un animal de se libérer de restrictions environnementales telles que les limitations thermiques. Par contre, l'homéothermie comporte des coûts métaboliques très importants (Welty et Baptista, 1988). En effet, Walsberg (1983b) a estimé que chez les oiseaux adultes, les coûts énergétiques associés au métabolisme de maintien (entretien chimique et thermique) peuvent accaparer jusqu'à 40-60% du bilan énergétique total. L'énergie allouée au métabolisme de maintien est une dépense considérée obligatoire dans le bilan énergétique d'un animal. Lorsque l'accès à l'énergie devient un facteur limitant, plus la proportion des dépenses obligatoires est élevée et moins il y a d'énergie disponible pour les autres activités.

LA CROISSANCE EN MILIEU FROID

Une question fondamentale en écophysiologie concerne l'effet que peuvent avoir les relations thermiques d'un individu sur sa survie et sa contribution future aux prochaines générations (Walsberg, 1983a). L'étude de ces relations, chez des espèces vivant dans des milieux dont les conditions thermiques sont extrêmes, est particulièrement intéressante car ces animaux sont soumis à des stress thermiques considérables. De nombreuses espèces d'oiseaux nichent dans le Haut Arctique où ils profitent des longues journées d'ensoleillement estivales, d'une nourriture abondante et de qualité, ainsi que d'une faible pression de prédation (Owen, 1980). Par contre, l'environnement froid de l'Arctique impose des contraintes thermiques majeures, particulièrement chez les oiseaux de petite taille qui, par leur rapport surface/volume élevé, ont une faible capacité de conservation de chaleur. Les jeunes sont d'autant plus défavorisés parce que leurs muscles, spécialement ceux du vol, sont petits et peu développés, ce qui limite leur capacité de production de chaleur par frissonnement (Ricklefs, 1989). Quant à l'utilisation de la thermogenèse sans frisson par les jeunes oiseaux, elle n'a été mise en évidence que chez quelques espèces seulement, dont les jeunes canetons. Cette thermogenèse se situerait au niveau du tissu musculaire plutôt que du tissu adipeux brun, un tissu spécialisé dans la production de chaleur que l'on retrouve chez les mammifères (Barré *et al.*, 1990). Chez les oiseaux, le frissonnement demeure toutefois le principal facteur responsable de l'augmentation de la production métabolique de chaleur en réponse au froid (Dawson et Marsh, 1989).

Chappell (1980) a suggéré, chez des espèces d'oiseaux de rivage en milieu naturel, que la chaleur dégagée par l'exercice ne se substituait pas à celle produite par la thermogenèse de régulation chez les jeunes oiseaux. Cette hypothèse est cependant controversée car elle implique que la conductance de l'oiseau augmenterait au même rythme que son métabolisme d'exercice, ce qui ne semble pas obligatoire en milieu aérien. De plus, Zerba et Walsberg (1992) ont observé chez le Colin à ventre noir (*Callipepla gambelii*) une substitution complète de la thermogenèse de régulation par la chaleur dégagée pendant l'exercice à des températures ambiantes entre 0 et 20°C sous la T_{lc}. En fait, l'exercice provoque une certaine augmentation de la conductance thermique de l'oiseau en modifiant sa posture, en accélérant le remplacement de la couche d'air isolante du plumage et en diminuant l'épaisseur de la couche limite (Withers, 1992). L'activité peut aussi empêcher le frissonnement. Ainsi, l'importante quantité de chaleur produite par l'exercice se substituerait probablement au moins partiellement à celle produite par la thermogenèse de régulation (Withers, 1992).

Chez les jeunes nidifuges croissant en régions polaires, les coûts énergétiques associés à la thermorégulation sont souvent considérés comme dominants dans la dépense quotidienne d'énergie (Klaassen *et al.*, 1989a). Par exemple, chez les jeunes de la Sterne Arctique (*Sterna paradisaea*), les coûts associés à la thermorégulation représentent environ 20% du bilan énergétique total de l'oiseau (Klaassen *et al.*, 1989a et b). Selon l'hypothèse dite "d'allocation de l'énergie", les coûts importants associés à la thermorégulation et à l'activité chez les jeunes nidifuges réduiraient d'autant la proportion d'énergie pouvant être allouée au développement et à la croissance (Chappell *et al.*, 1989; Chappell *et al.*, 1990; Olson, 1992), ceci en condition où l'assimilation d'énergie est limitante. D'un autre côté, la croissance optimale requiert la stabilité thermique. Puisque la croissance des jeunes est limitée par la quantité totale d'énergie disponible (Cooch *et al.*, 1991a; Lindholm *et al.*, 1994; Lepage *et al.*, 1998), la masse corporelle finale atteinte par les oiseaux sera grandement déterminée par les conditions environnementales rencontrées au cours de la croissance (Cooch *et al.*, 1991a).

Les Ansérinés

Les oies sont parmi les plus gros oiseaux migrateurs des régions arctiques. Elles doivent compléter leur cycle reproducteur durant le court été arctique. Les jeunes ne disposent que de quelques semaines pour croître et atteindre un niveau de développement compatible avec l'envol avant la migration automnale, ce qui constitue un défi de taille surtout pour des herbivores comme les oies (Hugues *et al.*, 1994; Lesage et Gauthier, 1997). En effet, les plantes constituent une nourriture de faible qualité par rapport à celle d'origine animale car elles contiennent peu de protéines et beaucoup de fibres indigestibles (Manseau et Gauthier, 1993). De plus, la saison de croissance des plantes est très courte. Puisque les distances à parcourir pour atteindre les haltes migratoires automnales peuvent être considérables, les oies doivent exploiter les ressources disponibles efficacement pour s'assurer que les jeunes atteignent une taille et une condition corporelle adéquates pour entreprendre la migration (Owen et Black, 1989).

On a observé, chez les jeunes de plusieurs espèces d'oies, des variations saisonnières considérables dans les taux de croissance et de survie. En particulier, les jeunes éclos tardivement ont souvent un taux de croissance plus faible que ceux qui ont éclos plus tôt en saison (Lindholm *et al.*, 1994; Lepage *et al.*, 1998). Le déclin saisonnier de la quantité et de la qualité de la nourriture a été suggéré comme facteur principal pouvant expliquer la diminution du taux de croissance des jeunes éclos plus tard en saison (Lindholm *et al.*, 1994; Lepage *et al.*, 1998). Toutefois, il est possible qu'un environnement thermique plus défavorable en fin d'été soit en partie responsable de cette baisse du taux de croissance, en augmentant la proportion d'énergie que les jeunes éclos tardivement doivent allouer à la thermorégulation (Lindholm *et al.*, 1994; Fortin, 1995). Lors d'années froides et humides, des réductions dans les taux annuels de croissance ont été effectivement observées, entre autres chez la Petite Oie des neiges, *Chen caerulescens caerulescens* (Cooch *et al.*, 1991b).

Les conséquences écologiques d'une diminution du taux de croissance sont très importantes, la masse corporelle influençant la survie chez plusieurs espèces d'oiseaux dont les oies (Owen et Black, 1989; Francis *et al.*, 1992; Cooch *et al.*, 1993; Schmutz, 1993; Lindholm *et al.*, 1994). En particulier, Owen et Black (1989) ont observé que la masse corporelle et la survie des oisons de la Bernache Nonette (*Branta leucopsis*) étaient corrélées positivement durant la migration automnale. Chez la Petite Oie des neiges, le taux de survie des jeunes au cours de leur première année de vie a diminué significativement entre 1970 et 1987. Francis *et al.* (1992) attribuent ce déclin à un taux de croissance progressivement plus faible résultant en des juvéniles de plus petite taille. Il a été aussi suggéré que le taux de recrutement plus élevé des jeunes éclos tôt en saison dans la population refléterait un plus haut taux de survie attribuable à leur masse corporelle plus élevée (Cooke *et al.*, 1984). Chez les Anatidés, la taille corporelle peut aussi influencer la fécondité (Sedinger *et al.*, 1995). Ainsi, selon Alisauskas et Ankney (1990), la taille des femelles de la Petite Oie des neiges influence positivement leur fécondité, puisque les femelles de plus grande taille ont une capacité plus élevée d'emmagasiner des nutriments. Cependant, pour la même espèce, Cooch *et al.* (1991b) n'ont trouvé aucune évidence d'une différence de taille entre les femelles qui nichaient hâtivement (donc avec plus de succès) et celles qui le faisaient tardivement.

La Grande Oie des neiges

La Grande Oie des neiges (*Chen caerulescens atlantica*) constitue une population distincte qui niche dans le Haut Arctique canadien et passe l'hiver sur la côte est des États-Unis (Giroux *et al.*, 1984). Elle est l'espèce d'oie possédant l'aire de nidification la plus septentrionale en Amérique du Nord (Bellrose, 1980). Elle niche en colonies discrètes, du centre de l'île de Baffin (67 °N) jusqu'au nord de l'île d'Ellesmere (82 °N) ainsi qu'au nord-ouest du Groenland. C'est à l'île Bylot (73°08`N-80°00`W) dans le territoire du Nunavut que l'on retrouve la plus forte densité d'oiseaux nicheurs de cette espèce (Bellrose, 1980). Les conditions climatiques difficiles qui prévalent dans l'aire de nidification de la Grande Oie des neiges limitent la distribution de plusieurs plantes et la saison de croissance n'y dure qu'environ six semaines (Hugues *et al.*, 1994). De plus, les oisons de cette espèce étant nidifuges, ils vont suivre leurs parents dans la toundra dès les premières heures suivant leur éclosion. Pour survivre, ils doivent être en mesure de faire face aux rudes conditions climatiques du Haut Arctique au même titre que leurs parents. Ainsi, les oisons de la Grande Oie des neiges constituent un sujet idéal pour une étude sur les relations thermiques des jeunes en milieu naturel.

L'ENVIRONNEMENT THERMIQUE

La température de l'air est la mesure utilisée la plus fréquemment pour décrire thermiquement un environnement terrestre. Pourtant, l'échange de chaleur entre un corps biologique et son environnement peut se produire par quatre processus: la conduction, la convection, le rayonnement et l'évaporation. En milieu froid, la majeure partie de la chaleur produite par un animal est perdue par des mécanismes non-évaporatifs, la convection et le rayonnement étant les plus importantes avenues de transfert (Schmidt-Nielsen, 1990). Ainsi, l'environnement thermique tel que perçu par un animal peut différer grandement de ce qu'indique la température de l'air à cause de la présence de rayonnement solaire et de vent. Conséquemment, la manière la plus adéquate de décrire l'environnement thermique d'un animal est de le faire en termes de transferts de chaleur, de sorte que des milieux entraînant les mêmes échanges de chaleur soient considérés thermiquement équivalents (Bakken *et al.*, 1981; Bakken *et al.*, 1985).

Dans le but d'estimer l'impact d'un environnement naturel complexe sur les échanges de chaleur d'un animal, on a défini des températures virtuelles qui décrivent l'environnement thermique en combinant les effets de la température de l'air, du rayonnement, du vent et de leurs interactions respectives en un seul nombre (Bakken *et al.*, 1981; Bakken *et al.*, 1985). Ces températures virtuelles, soit la température opérante (T_e) et la température opérante standard (T_{es}), sont dérivées de l'analyse des transferts de chaleur et reflètent effectivement les échanges de chaleur par modes non-évaporatifs entre un animal et son milieu (Bakken, 1976). La température opérante (T_e) d'un environnement complexe est définie comme la température d'un environnement de référence (une enceinte noire et uniforme) ayant les mêmes conditions de convection que l'environnement complexe et dans lequel les échanges de chaleur entre un animal et son milieu sont les mêmes (Bakken *et al.*, 1981; Bakken *et al.*, 1985; Bakken, 1992). La température opérante standard (T_{es}) se définit de la même manière que la T_e, à la différence que l'environnement de référence possède des conditions standards de convection normalement nulles (Bakken *et al.*, 1981; Bakken *et al.*, 1985; Bakken, 1990; Bakken, 1992). Mathématiquement, la T_e et T_{es} sont exprimées par les relations suivantes:

$$T_e = T_b - (M - E)/K_e \tag{1}$$

$$T_{es} = T_b - (M - E)/K_{es} \tag{2}$$

De sorte que l'on peut les définir l'une par rapport à l'autre selon:

$$T_{es} = T_b - (K_e/ K_{es})/(T_b - T_e) \tag{3}$$

où T_b (°C) est la température corporelle, M (W) est la production métabolique de chaleur, E (W) est la perte évaporative et finalement, K_e et K_{es} (W °C^{-1}) sont les conductances thermiques globales de l'animal dans l'environnement complexe et dans celui de référence respectivement (Bakken *et al.*, 1981; Bakken *et al.*, 1985; Bakken, 1990; Bakken, 1992).

L'utilisation de mannequins taxidermiques pour mesurer la T_{es}

Pour l'obtention d'une mesure directe de la T_{es} d'un animal dans un environnment donné, Bakken (1976) suggère l'utilisation d'un mannequin taxidermique chauffé de l'animal. Brièvement, un mannequin taxidermique est une réplique métallique du noyau corporel de l'animal à l'étude, chauffée électriquement et recouverte de la peau avec son isolant naturel. L'application principale de cette méthode de mesure est l'obtention de données descriptives de l'environnement thermique d'un animal et ce, à l'échelle de l'animal lui-même (Bakken, 1976). L'utilisation d'un mannequin taxidermique dans la détermination de la T_{es} requiert que le mannequin simule adéquatement les propriétés externes de l'animal affectant l'échange de chaleur, telles que sa taille et sa forme ainsi que la couleur et la structure de son isolant, fourrure ou plumage (Bakken *et al.*, 1981). Un mannequin taxidermique bien conçu reproduit alors efficacement l'ensemble des différents échanges de chaleur par modes non-évaporatifs entre un animal et son environnement, en incluant les effets de la distribution non-uniforme des échanges de chaleur (Bakken, 1976).

Il n'est pas nécessaire de mesurer indépendamment chacune des variables de l'équation 2 pour déterminer la T_{es} d'un mannequin taxidermique. Une méthode simple consiste à mesurer la puissance de chauffage (P) que l'on doit fournir au mannequin pour maintenir T_b constante dans un environnement complexe, et ensuite de placer le mannequin dans l'environnement de référence, où on peut varier la température ambiante jusqu'à ce que la puissance de chauffage soit égale à celle mesurée dans l'environnement complexe. La température de l'air de l'environnement de référence est alors égale à la T_{es} (Fortin, 1995). La principale incertitude quant à l'applicabilité aux animaux vivants des résultats obtenus à l'aide de mannequins taxidermiques concerne les conductances thermiques (Bakken, 1976).

En effet, on ne peut pas supposer que la conductance du mannequin (K_{es}) soit parfaitement égale à celle d'un animal vivant (G) car le mannequin ne peut reproduire les réponses posturales, pilo/ptilomotrices et vasomotrices communément observées chez les animaux vivants (Bakken *et al.*, 1981). De plus, les mannequins taxidermiques sont généralement dépourvus de pattes. Ainsi, la puissance de chauffage (P) requise par le mannequin pour maintenir T_b dans un environnement complexe n'est pas nécessairement égale au taux de dissipation de chaleur par modes non-évaporatifs (M - E) de l'animal vivant. Toutefois, P peut être utilisée pour estimer (M - E) après des validations appropriées. En effet, si on peut obtenir en laboratoire un facteur de correction permettant de relier la conductance des mannequins (K_{es}) à celle d'animaux vivants (G), l'utilisation de mannequins taxidermiques pour prédire les réponses thermiques d'animaux vivants peut être adéquate.

Un article récent de Walsberg et Wolf (1996) soulève certaines critiques quant à la validité des mesures obtenues à l'aide de mannequins taxidermiques. Les auteurs soutiennent que l'utilisation de mannequins taxidermiques entraîne la violation de deux principes fondamentaux de l'échantillonnage biologique. Le premier est une conséquence de la variation inhérente à tout système biologique. Cette variation rend nécessaire l'obtention de larges tailles d'échantillons (*i.e.* l'utilisation de plusieurs mannequins taxidermiques). Le deuxième principe concerne la calibration des instruments de mesure qui devrait couvrir l'étendue des conditions sous lesquelles les données expérimentales sont obtenues. Dans leur article, Walsberg et Wolf (1996) citent plusieurs études qui ont été réalisées à partir d'un seul mannequin taxidermique, vraisemblablement en raison des difficultés et des coûts associés à leur construction. Les auteurs font aussi état du fait que peu d'études ont comparé la réponse thermique des mannequins à celle d'animaux vivants exposés à des conditions représentatives du milieu naturel.

Dans leur étude, Walsberg et Wolf (1996) ont comparé les réponses de mannequins taxidermiques avec celles d'animaux vivants exposés aux mêmes conditions de vent et de rayonnement. De plus, afin d'explorer la variabilité qui peut exister entre différents mannequins taxidermiques, ils ont effectué des mesures à l'aide de plusieurs répliques des mannequins. Les résultats obtenus démontrent une variabilité très importante entre les réponses des différentes répliques (C.V. = 149 %) ainsi qu'une performance peu reluisante des mannequins dans la prédiction de réponses d'animaux vivants, alors que l'écart entre les T_{es} estimées à partir des mannequins et les "vraies" valeurs peut atteindre 28.5°C. Ces résultats ont amené Walsberg et Wolf à déconseiller l'utilisation de mannequins taxidermiques. Pourtant, cette conclusion découle d'une étude qui comporte elle-même de nombreuses failles. Larochelle (1998) décrit certains problèmes majeurs de l'étude de Walsberg et Wolf (1996).

Un premier concerne la construction des mannequins taxidermiques utilisés par Walsberg et Wolf. En effet, des tests effectués au laboratoire de Jacques Larochelle à l'Université Laval mettent en évidence des lacunes importantes dans la construction de leurs mannequins taxidermiques. Celles-ci pourraient être responsables de variations au moins aussi grandes que celles mesurées dans leurs expériences. Par exemple, les mannequins de Wasberg et Wolf offrant les plus piètres performances sont ceux dont le corps métallique est constitué d'aluminium plutôt que de cuivre, un métal dont la conductivité thermique est de 70 % plus faible que celle du cuivre. De plus, au lieu d'utiliser un ensemble de fils chauffants distribués uniformément sur la surface intérieure de l'enveloppe métallique, Walsberg et Wolf ont utilisé quelques résistances chauffantes disposées seulement dans la partie inférieure du corps du mannequin. Cette disposition des éléments chauffants nuit beaucoup à l'uniformité de la température interne du mannequin. Ainsi, la variabilité dans la réponse des mannequins rapportée par ces auteurs pourrait être considérablement réduite par l'utilisation de mannequins taxidermiques mieux construits.

Une deuxième préocupation est celle du choix des deux espèces de mammifères utilisées dans l'étude de Walsberg et Wolf pour comparer les réponses des mannequins taxidermiques avec celles d'animaux vivants. Les réactions thermiques particulières de ces deux espèces (*Spermophilus variegatus et lateralis*) sont difficiles à expliquer en termes théoriques et ne sont surtout pas représentatives de celles communément observées chez les homéothermes. Ainsi, selon Larochelle (1998), l'incapacité des mannequins taxidermiques à reproduire de telles réponses n'est pas une raison valable pour discréditer la technique. Il est important d'attirer l'attention sur l'erreur la plus extrême de 28,5°C rapportée par Walsberg et Wolf et citée comme étant un argument majeur contre l'utilisation de mannequins taxidermiques. Cette valeur provient de mesures effectuées à partir de mannequins non-chauffés exposés au vent en absence de rayonnement solaire. Pourtant, un mannequin taxidermique non-chauffé, en l'absence de rayonnement, est insensible au vent puisque qu'il se comporte alors comme un thermomètre inerte. Dans cette situation, il ne peut pas produire d'autre signal que celui de la température de l'air, et il n'est donc pas approprié d'extrapoler et de comparer la réponse du mannequin à celle d'un animal vivant.

Finalement, un dernier problème de l'étude de Walsberg et Wolf réside dans leur méthode de calcul des coefficients de variation et de variance qu'ils ont apparemment définis par rapport à la différence entre la T_{es} et la température ambiante. Pourtant, l'objectif ultime de l'utilisation de mannequins taxidermiques est de déterminer le coût métabolique de l'exposition à un environnement thermique en particulier. Dans ce cas, il est plus approprié de mesurer les incertitudes expérimentales relativement à ce coût ou, de façon équivalente, relativement au gradient d'échange de chaleur, défini par la différence entre T_b et T_{es}. La méthode de calcul utilisée par Walsberg et Wolf résulte en apparence en une variabilité extrême dans la réponse des mannequins et laisse croire que les mannequins taxidermiques constituent des instruments de mesure très imprécis, ce qui n'est pas du tout le cas.

En résumé, puisque la grande variabilité entre les mannequins ainsi que leur faible concordance avec des animaux vivants observées par Walsberg et Wolf (1996) peut s'expliquer par des erreurs de méthodologie, leur étude ne constitue pas une réfutation acceptable de la technique des mannequins taxidermiques (Larochelle, 1998). En dépit des critiques du genre, de nombreuse études réalisées ces dernières années ont utilisé avec succès des mannequins taxidermiques comme "thermomètres" pour décrire à l'aide de températures opérantes des environnements naturels complexes, en raison de la simplicité d'utilisation des mannequins et de leur relative efficacité (Chappell, 1980; Bakken, 1992; Bakken *et al.*, 1981, 1985; Walsberg et Weathers, 1986; Greek *et al.*, 1989; Klaassen *et al.*, 1989b; Chappell *et al.*, 1990; Piersma et Morrison, 1994; Wiersma et Piersma, 1994; Fortin, 1995).

OBJECTIFS DE L'ÉTUDE

Dans cette étude, nous nous sommes intéressés à une des questions fondamentales en écophysiologie identifiée par Walsberg (1983a). Cette question est la suivante: "Quels sont les coûts énergétiques associés au stress thermique chez les homéothermes ?" Ainsi, l'objectif principal de cette étude était d'obtenir, à l'aide de mannequins taxidermiques, un estimé des coûts énergétiques associés à l'effort thermorégulateur chez les jeunes de la Grande Oie des neiges en croissance à l'île Bylot.

L'atteinte de plusieurs objectifs spécifiques était essentielle à la réalisation de notre objectif général. Dans un premier temps, il s'agissait de valider nos instruments de mesure, les mannequins taxidermiques. Cette partie plus technique de l'étude, que l'on retrouve au chapitre II, visait l'atteinte des objectifs suivants:

1) Évaluer la variabilité dans la réponse des mannequins taxidermiques et examiner la possibilité de vieillissement des mannequins;
2) Comparer les équations de prédiction de la T_{es} des mannequins taxidermiques obtenues à partir de données de laboratoire à celles obtenues à partir de données de terrain afin d'évaluer notre capacité à reproduire, en laboratoire, des environnements naturels;
3) Calibrer, en laboratoire, les mannequins taxidermiques avec des oisons vivants dans des conditions représentatives du milieu naturel.

Au chapitre III, on retrouve la portion écologique de l'étude dont les objectifs étaient les suivants:

1) Comparer les prédictions du taux métabolique des oisons obtenues à l'aide des mannequins taxidermiques à celles obtenues par une analyse biométéorologique;

2) Décrire, en termes de T_{es} et de variables météorologiques, l'environnement thermique dans lequel croissent les jeunes de la Grande Oie des neiges;
3) Comparer l'effet du régime des vents sur l'environnement thermique de deux sites représentatifs de ceux utilisés par les oies pour se reposer et se nourrir durant la période d'élevage des jeunes ainsi que l'effet de la période de la journée (jour/nuit) sur l'environnement thermique des oisons;
4) Évaluer les coûts énergétiques associés à l'effort thermorégulateur des oisons en croissance dans leur milieu naturel;
5) Tester l'hypothèse proposée par Fortin (1995) selon laquelle un environnement thermique plus défavorable en fin d'été est en partie responsable de la diminution du taux de croissance observée chez les oisons éclos tard en saison.

CHAPITRE II

USE OF TAXIDERMIC MOUNTS FOR ESTIMATING THE ENERGETIC COST OF THERMOREGULATION

RÉSUMÉ

Cette partie de l'étude visait à valider nos instruments de mesure, quatre mannequins taxidermiques chauffés de quatre âges différents représentatifs des stades importants du dévelopement des oisons de la Grande Oie des neiges. Pour ce faire, nous avons mesuré la puissance de chauffage des mannequins dans différentes conditions thermiques tant au laboratoire que sur le terrain. Nous avons aussi calibré les mannequins en laboratoire avec des oisons vivants dans des conditions représentatives du milieu naturel. Les résultats sont les suivants:

1. La réponse des quatre mannequins taxidermiques était hautement reproductible, tant à court qu'à long terme.
2. Les équations de prédiction de la T_{es} des mannequins taxidermiques obtenues à partir des données de laboratoire et de terrain étaient différentes, en partie parce qu'il est difficile de reproduire une ambiance radiative naturelle en laboratoire.
3. À des températures ambiantes de moins de 15°C, la conductance thermique des mannequins simulait adéquatement celle des oisons vivants.
4. La réponse des mannequins à une exposition à différentes vitesses de vent simulait adéquatement celle des oisons vivants, ce qui n'était pas le cas lors d'une exposition à différentes intensités de rayonnement. Ainsi, les équations de prédiction du taux métabolique des oisons donnaient de meilleurs résultats lorsque ces variables étaient incluses dans les modèles de régression.

ABSTRACT

The objective of this section of the study was to validate the use of the four heated taxidermic mounts of four ages representative of development stages of Greater Snow Goose goslings. To do this, we measured heating power of mounts under different thermal conditions both in the laboratory and in the field. We also calibrated the taxidermic mounts against live goslings in the laboratory under conditions representative of what is found in nature. Here are the results:

1. Short and long term repeatability of measurements made with the 4 taxidermic mounts used was very high.
2. Predictive models of T_{es} of mounts from laboratory and field experiments were different, partly because a natural radiative environment is difficult to reproduce in the laboratory.
3. At T_a below 15°C, the thermal conductance of the mounts adequately replicated that of live goslings.
4. Mounts exposed to different wind speeds adequately replicated the response of live goslings which was not the case for radiation. Thus, gosling metabolic rate predictions were improved when these variables were included in the regression models.

INTRODUCTION

Estimating the impact of a thermal environment on the energy expenditure of an animal is a difficult task because of the complexity of the interactions between the animal and its microenvironment. A useful tool in studies of ecological energetics is the concept of standard operative temperature (T_{es}), a thermal index that allows air temperature, radiation intensity, wind speed and their interactions to be combined into a single value expressed in temperature units (Gagge, 1940; Bakken, 1976). Thus, T_{es} integrates the effects of convective and radiative heat transfer, the dominating modes of heat transfer in cold environments, on the thermal balance of an animal in nature. Environments resulting in the same net heat flow are considered to be thermally equivalent (Bakken *et al.*, 1981). The scale of T_{es} is defined by the temperature of a reference environment consisting of an isothermal blackbody enclosure with fixed convection conditions (Bakken *et al.*, 1981). Mathematically, T_{es} is defined as follows:

$$T_{es} = T_b - \frac{(M - E)}{K_{es}} \tag{1}$$

where T_b is the body temperature (°C), M is the metabolic heat production (W), E is the evaporative heat dissipation (W), and K_{es} is the overall thermal conductance (W °C^{-1}) of the animal (Bakken *et al.*, 1981; Bakken *et al.*, 1985; Bakken, 1992). Note that all variables are defined in Appendix A.

As suggested by Bakken (1976), T_{es} can be measured directly with a heated taxidermic mount thermostated at body temperature (T_b). This procedure has two principal applications: (1) to describe the thermal environment as perceived by the animal at the same scale as the animal itself (Bakken, 1976), and (2) to measure the energy expenditure associated with thermoregulation. The heating power (P) of the mount measured in a complex environment can be related to the T_{es} by placing the mount in a reference environment and varying the air temperature (T_a) until P is the same as in the complex environment. T_a of the reference environment is then equal to T_{es}. The taxidermic mount can be used as a "T_{es} thermometer" in outdoor environments, and this method has become increasingly popular (Chappell *et al.*, 1990; Bakken, 1992; Piersma and Morrison, 1994; Wiersma and Piersma, 1994; Fortin, 1995).

The adequacy of the T_{es} estimate obtained from a taxidermic mount is critically dependent upon the assumption that the mount effectively reproduces the external properties of a live animal such as size, shape, color, and coat structure. A good taxidermic mount generally replicates well these properties (Bakken *et al.*, 1981). However, the conductance of the mount is not necessarily equal to that of a live animal because the mount cannot replicate its postural, pilo/ptilomotor, and vasomotor responses or its complete anatomy (Bakken *et al.*, 1981). Hence, it cannot be assumed, as it has been done in the past (*e.g.* Chappell, 1980), that the heating power of the mount (*P*) is equal to the dry heat dissipating rate (*M* - *E*) of a live animal. However, *P* can be used to estimate (*M* - *E*) after calibrating the mount against live animals in the laboratory (Bakken *et al.*, 1981).

A recent article by Walsberg and Wolf (1996) has seriously questioned the validity of taxidermic mounts as "T_{es} thermometer". In their study, these authors have evaluated inter-mounts variability and found substantial variation in the responses of different replicates. They have also compared mount responses with those of live animals to examine the adequacy of mounts' predictions. They found that, depending on the species, type of mount (heated or not), and environmental conditions, mounts' predictions ranged from very good to very poor. On the basis of these results, they concluded that mounts are imprecise instruments and that they are not worth the investment of time and resources.

However, this conclusion was criticized by Larochelle (1998) who argued that the poor performance obtained by Walsberg and Wolf (1996) with their taxidermic mounts can be easily explained by methodological errors. For example, their mounts were not properly constructed, their comparisons with live animals were not always theoretically justified, and the statistical parameters used to report variability were inadequate (see Larochelle, 1998 for details). Hence, Larochelle concluded that the negative appraisal of the technique of taxidermic mounts made by Walsberg and Wolf (1996) is not sufficient to reject its use in studies of ecological energetics. Their study, on the other hand, did raise some important points. One of these is that taxidermic mounts should always be calibrated against live animals under an array of thermal conditions representative of natural environments. Such calibrations have sometimes been made for mounts exposed to different wind speeds (Buttemer, 1985) but had never been reported for mounts exposed to solar radiation before Walsberg and Wolf (1996) experiments.

The main objective of this study was to validate the use of taxidermic mounts for estimating the energetic cost of thermoregulation in animals living in cold environments. This was done using Greater Snow Goose goslings which grow in the Arctic environment (Lesage and Gauthier, 1997). To achieve this objective we (1) evaluated the repeatability of measurements made with taxidermic mounts and examined the possibility of mounts' aging, (2) compared predictive equations of T_{es} from laboratory and field data, and (3) compared mount responses with those of live goslings placed in laboratory conditions simulating wind speed and radiation intensity of the natural environment.

MATERIAL AND METHODS

Taxidermic mounts

The taxidermic mounts used in this study were built by Fortin (1995). Details of mount construction are described in Fortin (1995). The four mounts correspond to four ages representative of the development stages of goslings (Table 1): at the beginning of growth (3 d), before feather emergence (10 d), at the beginning of feather emergence (20 d), and at an advanced stage of feather emergence (30 d). As in other studies (Chappell, 1980; Bakken *et al.*, 1981; Wiersma and Piersma, 1994), the mounts did not have legs. However, measurements of surface temperature of legs and feet of Red Knots (*Calidris canutus*) indicated that heat loss through these parts is negligible at air temperatures below the thermoneutral zone (Wiersma and Piersma, 1994). The mounts were supported by wood dowels inserted in the middle of the body cores, 5 cm above the ground for the two smaller mounts and 8 cm for the two larger ones. Heat loss through these dowels was considered negligible.

Experiments with the mounts

Both laboratory and field experiments were performed with the four mounts. During all experiments, the heating wires of the mounts were connected to a regulated DC power supply (15 V, 30 A, model RS-300, Daiwa) from which the voltage output was typically set between 12 and 13.5 V. Mounts' T_b were maintained at about 40.5°C (95 % CI in the laboratory: 40.42-40.57°C, in the field: 39.0-41.8°C), the mean body temperature of goslings (Fortin, 1995). Voltage pulses were applied to the mounts via relays driven by a datalogger (CR10, Campbell Scientific Inc.) programmed to act as a time-proportional controller (Appendix D). The voltage applied to the mounts was automatically recorded every second by the datalogger, and mean values were saved every 5 min. The heating power of the mounts (*P*) was calculated using Ohm's law. The resistance of the heating wires of the mounts was determined using a precision multimeter (model 199, Keithley Instruments Inc.).

In the laboratory, all measurements were averaged over a period of one hour of stability in mounts' T_b and *P*. Over this period, the coefficient of variation (CV) for T_b was less than 0.4 %. The CV for *P* was less than 5.2 % except for the experiments performed at T_a above 30°C because of the very low voltage values in these experiments.

Ambient conditions and their measurement

During all laboratory experiments, the mounts were placed facing the wind in a closed-circuit metabolic wind tunnel (volume = 100 L). The wind (from 0 to 5 $\mathrm{m\,s^{-1}}$) was produced with a cage blower driven by a 300 W DC electrical motor. The uniformity of wind velocity was ensured by a series of adjustable baffles, and turbulence was reduced by placing a honeycomb in front of the working section (20 x 25 x 31 cm). Wind speed was measured in the middle of the wind tunnel by a hot-wire anemometer (model 441S, Kurz Instruments Inc.).

Artificial radiation (from 0 to 500 W m^{-2}) was provided by a lamp (model Fresnelite 2000, Strand Lighting) with a 1000 W tungsten-quartz-halogen bulb (model BVT, General Electric Lighting). The lamp was placed behind an infrared filter consisting of two 0.5 cm Plexiglas sheets with 1.5 cm of distilled water in between. This filter blocks enough infrared wavelengths to ensure that the proportion of infrared radiation reaching the mount is close to the solar radiation (Fortin, 1995). The intensity of the filtered radiation was adjusted by varying the spread of the light beam and the distance between the lamp and the wind tunnel. Radiation was routinely measured with a pyranometer (model Li-200SA, LI-COR) placed in the middle of the wind tunnel and facing the radiation source. The pyranometer was calibrated for use with our radiation source with a power meter (model PS-310, Gentec) sensitive to wavelengths from 0.19 to 40 μm, placed at gosling height in the middle of the wind tunnel.

In the field, the following meteorological variables were measured at gosling height during the experiments: air temperature (T_a), radiation intensity (R), and wind speed (u). The measurements were recorded automatically every 10 s by a datalogger (CR10, Campbell Scientific Inc.), and mean values were saved every 5 min. T_a (°C) was measured 30 cm above the ground using a shielded temperature probe (model 207, Campbell Scientific Inc.), R (W m^{-2}) was obtained from a pyranometer (model Li-200SA, LI-COR) placed facing the sky at 40 cm above the ground, and u (m s^{-1}) was recorded with a hot-wire anemometer (model 441S, Kurz Instruments Inc.) at 10 cm above the ground. Within each 4-h period of field experiments, we averaged values over the 30-min period which displayed the greatest stability in all of T_b, P, T_a, R and u. We sometimes used two 30-min periods within the same

4-h measurement period when the thermal conditions had changed and stabilized sufficiently.

Basic calibration of the mounts and T_{es} determination

The basic calibration (sensitivity to air temperature) had two distinct goals: (1) to relate P to T_{es} for each mount, and (2) to evaluate aging of the mounts in terms of T_{es}. The basic calibration was obtained by measuring P during exposure to various T_a under conditions where T_{es} equals T_a. As recommended by Bakken (1992), this was done in an isothermal black chamber under fixed condition ($u \approx 0.05$ m s^{-1}) where free convection is expected to dominate. Each mount was exposed to 9 different T_a from -5 to +35°C in increment of 5°C, and the P required to maintain T_b was determined. The relationship between P and T_a (which is equal to T_{es} in these standard conditions) was slightly nonlinear. Hence, to maximize accuracy of predictions, second-degree regression equations were used to relate P to T_{es} (Table 1). For a given mount, experimental values of T_{es} were always calculated from measured values of P using its basic calibration equation.

In addition, to evaluate the repeatability of mount responses, one temperature was selected ($T_a = 10$°C) for which three additional measurements were performed with each mount. All replicate experiments were done on different days and included a complete reinstallation of the mounts and a resetting of the environmental parameters.

To evaluate aging of the mounts in terms of T_{es}, we wanted to compare our basic calibration equations with those reported by Fortin (1995) for the same taxidermic mounts. Fortin (1995) had used linear regression equations to relate P to T_{es}. Hence, we also developed a linear regression equation for each mount to be used only in this comparison with Fortin (1995).

TABLE 1. **Second-degree regression equations relating *P* to T_{es} for each taxidermic mount, with the corresponding body mass of the gosling used for mount construction.**

Mount age (d)	**Body mass (g)**	**Equation**	r^2	*n*
3	105	$T_{es} = T_b + 0.41 - 14.23P + 0.0569P^2$	0.998	9
10	275	$T_{es} = T_b + 0.11 - 6.961P - 0.1594P^2$	0.999	9
20	1200	$T_{es} = T_b + 0.07 - 3.350P - 0.0328P^2$	0.999	9
30	1575	$T_{es} = T_b - 0.27 - 3.230P - 0.0529P^2$	0.998	9

Meteorological calibrations of the mounts

Meteorological calibrations (sensitivity to air temperature, wind and radiation) of the mounts were made under both laboratory and field conditions. These calibrations had the following objectives: (1) to compare laboratory and field environments in terms of T_{es}, and (2) to further evaluate aging of the mounts.

In the laboratory, an array of combinations of T_a, R, and u representative of field conditions were used. Mount sensitivity to air temperature had already been evaluated through the basic calibration. Hence, all experiments involving wind and/or radiation were performed at constant T_a around 10°C. Calibration experiments were performed on the 3, 10 and 20 d mounts only (the 30 d mount was not used in the calibrations because no experiments were done on live goslings of this age class).

Three general conditions were chosen: wind alone, radiation alone and a combination of the two. In the experiments involving only wind (u), the mounts were exposed to 5 different u from 0 to 5 m s^{-1} in increment of 1 m s^{-1}, and for those involving only radiation (R), 4 different R were used, 0, 200, 300, and 500 W m^{-2}. Two angles of elevation for R were used, 15 and 90° from the ground level. The 15° angle was used because it is close to the mean solar elevation above the horizon found at our field site in July and early August (20°) calculated from equation 2.1 of Kreider and Kreith (1982). The 20 d mount was not used at 15° as it would not fit inside the wind tunnel at this angle. For the 3 and 10 d mounts exposed to the two angles of elevation, the combinations of radiation and wind used involved two R (200 and 500 W m^{-2}) and one u (5 m s-1). For the 20 d mount, exposed to only the 90° angle of elevation, more combinations were used (R of 200 and 500 W m^{-2} and u of 1 and 5 m s^{-1}).

In addition, to evaluate the repeatability of mount responses, four replicate experiments of one combination (u of 5 m s^{-1} and R of 200 W m^{-2} at 90° angle) were performed with each mount. All replicate experiments were done on different days and included a complete reinstallation of the mounts and a resetting of the environmental parameters.

Field experiments were conducted on Bylot Island (73°08'N-80°00'W, Nunavut Territory, Canada), which is a major breading area for Greater Snow Geese (Bellrose, 1980). In the field, experiments with the mounts lasted 4 h and were performed twice a day (day and night). The two measurement periods were chosen to be representative of the extreme daily conditions goslings would encounter in terms of radiation. The periods used were from 10h00 to 14h00 (standard time) and from 22h00 to 2h00. All experiments used the four taxidermic mounts simultaneously (see Chapter 3 for more details on field experiments).

Biological calibrations of the mounts

The principal objective of the biological calibration was to establish a correspondence between the response of the mounts and that of live goslings when exposed to the same conditions. To achieve this, we compared the response of the mounts to different thermal environments to that of 8 live goslings exposed to exactly the same set of radiative and convective conditions (Rioux, in preparation). We also compared the response of the mounts to different ambient temperatures to that of 7 live goslings (Ratté, 1998). Goslings were raised in captivity from eggs taken in nests on Bylot Island and flown to the laboratory. Experiments with goslings at different ambient temperatures were conducted between 1 and 40 d of age while those including the presence of radiation and/or wind were conducted from 3 to 21 d of age, as beyond this age, the goslings were too large to fit inside the metabolic wind tunnel. Metabolic rate values were obtained by indirect calorimetry (see Rioux, in preparation and Ratté, 1998 for details).

Additionally, thermal conductance of taxidermic mounts was compared to that of live goslings between 1 and 40 d of age. For this comparison, data of live goslings came from Ratté (1998). Mounts' and goslings' thermal conductance was calculated from the results of laboratory experiments performed at different ambient temperatures using the following equations:

$$K_{es}^{m} = \frac{P}{(T_b - T_{es})} \tag{2}$$

$$K_{es} = \frac{M}{(T_b - T_{es})} \tag{3}$$

where K_{es}^{m} and K_{es} are overall thermal conductance of mounts and goslings, respectively (W °C^{-1}), P is mount heating power (W), and M is gosling metabolic rate (W). The evaporative cooling of goslings was considered negligible as shown by Ratté (1998) for ambient temperatures below 25°C. To facilitate comparisons between body sizes, conductance values were expressed per unit of body surface area (A_b) which was calculated from:

$$A_b = k_{Meeh} * m_b^{2/3} \tag{4}$$

where A_b is in m^2, k_{Meeh} is Meeh empirical constant which is 0.081 for birds (Walsberg and King, 1978), and m_b is body mass (kg). Finally, because taxidermic mounts of only four ages were available, each mount had to be assigned to a broader age class to allow this comparison with live goslings of different ages. We used the same classes as Fortin (1995). The 3 d mount represented goslings from 0 to 6 d of age, the 10 d mount those from 7 to 15 d, the 20 d mount those from 16 to 25 d, and the 30 d mount those from 25 to 40 d.

Predictions of T_{es} with mounts

Meteorological calibrations of the mounts were used to develop two identical predictive models of T_{es}, one from laboratory experiments and the other from field ones. The following multiple regression model was used for each mount:

$$T_{es} = \beta_1 T_a + \beta_2 (T_b - T_a) u + \beta_3 R + \beta_4 R u^{0.1} \qquad (5)$$

where β_n are regression coefficients. This model was inspired from Fortin (1995). The regressions were forced through the origin and hence had no intercept term. In the β_2 term, applying to u an exponent different from unity did not improve the regressions and hence, the unity exponent was retained. The β_4 values associated with the multiplicative interaction between R and u were almost always negative (except for the 20 d mount in the field). This was expected because when both R and u are present, the effect of the wind is to reduce the heat gain by radiation. However, under high wind speeds, an increase in radiation intensity would reduce T_{es}, an impossible situation. To avoid this incoherence, Fortin (1995) empirically applied an exponent of 0.1 to u.

Predictions of metabolic rate

Two other multiple regression models were developed. The first one predicted heating power of mounts (P) from meteorological calibration experiments in the laboratory. The other one predicted metabolic rate of goslings (M) from metabolic measurements with live goslings performed in the laboratory by Rioux (in preparation) and Ratté (1998) under similar conditions. Both models were based on the same equation:

$$\hat{P} \text{ or } \hat{M} = \beta_0 + \beta_1 m_b + \beta_2 T_a + \beta_3 (T_b - T_a)\, u + \beta_4 R \qquad (6)$$

where m_b is body mass of either mounts or goslings (kg). In contrast to the predictive equations of T_{es} which were mount specific, only one equation was developed to predict P of all mounts by including body mass as a variable. The β_4 term in the model predicting M, while being nonsignificant, was retained for consistency with the model predicting P in which it was significant. The interaction between R and u was nonsignificant and hence was not retained in the models. The regression models (equation 6) were used to calculate the ratio between predicted gosling metabolic rate and predicted mount heating power ($\hat{M} / \hat{P}$) at different R and u for the four taxidermic mounts.

The model predicting gosling metabolic rate from measurements made on live goslings was in fact a biometeorological analysis because the prediction was based only on goslings body mass (m_b) and meteorological variables (T_a, R, and u). An additional model was developed to predict gosling metabolic rate but this time including mount heating power along with body mass and meteorological variables. This last model will be referred to as the complex mount model.

Data analysis

All regression models were developed using the REG procedure of SAS (SAS Institute Inc., 1988). Independent variables were considered statistically significant at $p < 0.05$. To compare linear regression models developed in this study to those of Fortin (1995), we verified if the values of the intercepts and slopes of the models from this author were included in 95 % CI of the estimates from our study. Similarly, to compare T_{es} predictive equations developed in the laboratory to those developed in the field, we verified if the coefficient of each independent variables of the laboratory models was included in the 95 % CI of that of the field models.

RESULTS

Stability in mount responses

Short term repeatability (intervals ranging from 1 to 83 d) of heating power measurements with the taxidermic mounts in laboratory experiments was high (Table 2), with most coefficients of variation being smaller than 3 % (range: 0.5-3.4 %). Long term repeatability

TABLE 2. Short term repeatability (intervals ranging from 1 to 83 d) of heating power measurements for Greater Snow Goose taxidermic mounts in laboratory experiments (meteorological calibrations). Mounts were exposed to a combination of wind and radiation at T_a of 10°C in a metabolic wind tunnel.

Mount age (d)	**Wind speed ($m\,s^{-1}$)**	**Radiation intensity ($W\,m^{-2}$)**	***n***	**Heating power**	
				Mean (W)	**CV (%)**
3	0	0	4	2.2	1.0
	5	200	4	2.8	3.4
10	0	0	4	4.0	1.9
	5	200	4	5.2	2.1
20	0	0	4	8.4	1.0
	5	200	4	12.5	0.5
30	0	0	4	8.1	2.5

was investigated by comparing our basic calibration with that performed three years earlier by Fortin (1995) with the same taxidermic mounts. The values of the slopes and intercepts of the regression lines obtained in this study were not statistically different from those found by Fortin (1995), except for the value of the intercept for the 30 d mount which was lower (Table 3). The regression lines were almost identical for all mounts (Fig. 1) and, over the calibrated range of T_a (-5 to 20°C), the average and maximum deviations in T_{es} between lines were 1.0 and 3.7°C, respectively. Moreover, the resistance of the heating wires of the mounts changed less than 2 % over an 18-month period.

Effects of meteorological variables on *P*

In basic calibration experiments where $T_{es} = T_a$, P of taxidermic mounts increased almost linearly as T_a decreased (Fig. 1, dots). Although we used a second-degree regression to predict T_{es} from P, the relationship was only slightly nonlinear and the linear regression also provided a good fit to the data (Table 3).

Similarly, calibrations in presence of wind or radiation alone showed that P was linearly related to wind speed (range of r^2: 0.939-0.997) and radiation intensity (range of r^2: 0.883-0.994) for the three smaller mounts (Fig. 2). Thus, between $u = 0$ and 5 m s^{-1}, P increased by 28, 31, and 34 % while it decreased by 56, 58, and 34 % between $R = 0$ and 500 W m^{-2} for the 3, 10, and 20 d mounts respectively ($T_a = 10$°C). Adding a wind of 5 m s^{-1} in presence of radiation increased P by a mean of 45 and 59 % for $R = 200$ and 500 W m^{-2}, respectively, close to the values of P observed in absence of radiation (Fig. 2).

Predictions of T_{es} with mounts

Predictive equations of mounts' T_{es} obtained from laboratory calibrations explained a very high proportion of the observed variation in T_{es} (range of r^2: 0.993-0.999, Table 4). Independent variables were all highly significant. For the 3 and 10 d mounts, three equations

TABLE 3. Comparison of regression models ($T_{es} = T_b - \beta_1 P - \beta_0$) obtained from laboratory experiments (basic calibration) repeated at an interval of about three years using the same taxidermic mounts of Greater Snow Goose goslings. Mounts were exposed to 6 different T_a in an isothermal black chamber under fixed convection condition (0 m s^{-1} in 1994 and 0.05 m s^{-1} in 1997). In 1994, T_a of -10, -5, 0, 5, 10, 15°C were used and in 1997, T_a of -5, 0, 5, 10 15, 20°C were used.

Mount age (d)		This study			Fortin (1995)		
		β_0	β_1	r^2	β_0	β_1	r^2
3	**Estimate**	-0.26	14.06	0.992	0.99	14.81	0.985
	95% CI	4.19	1.74		----	----	
10	**Estimate**	-3.42	8.45	0.998	-2.04	8.03	0.999
	95% CI	2.09	0.48		----	----	
20	**Estimate**	-3.10	4.01	0.995	-3.28	3.93	0.993
	95% CI	3.52	0.39		----	----	
30	**Estimate**	-5.76*	4.38	0.993	-0.98	4.09	0.999
	95% CI	4.71	0.53		----	----	

* This value is different from that of Fortin ($p < 0.05$).

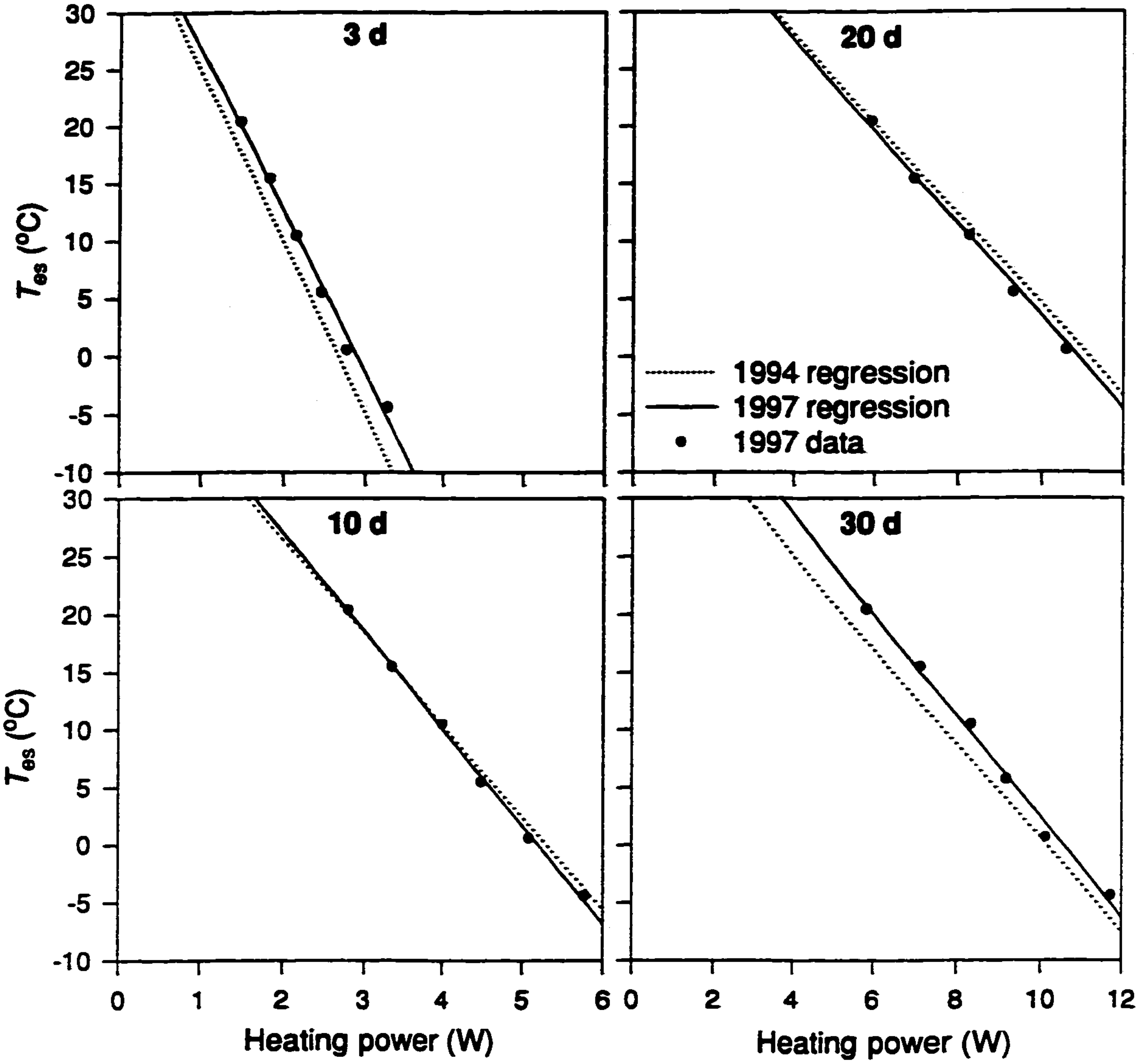

FIG. 1. Comparison of regression models relating heating power to T_{es} obtained from laboratory experiments (basic calibration) repeated at an interval of three years with the same taxidermic mounts of Greater Snow Goose goslings (1997 data and regressions are from this study, 1994 regressions are from Fortin, 1995).

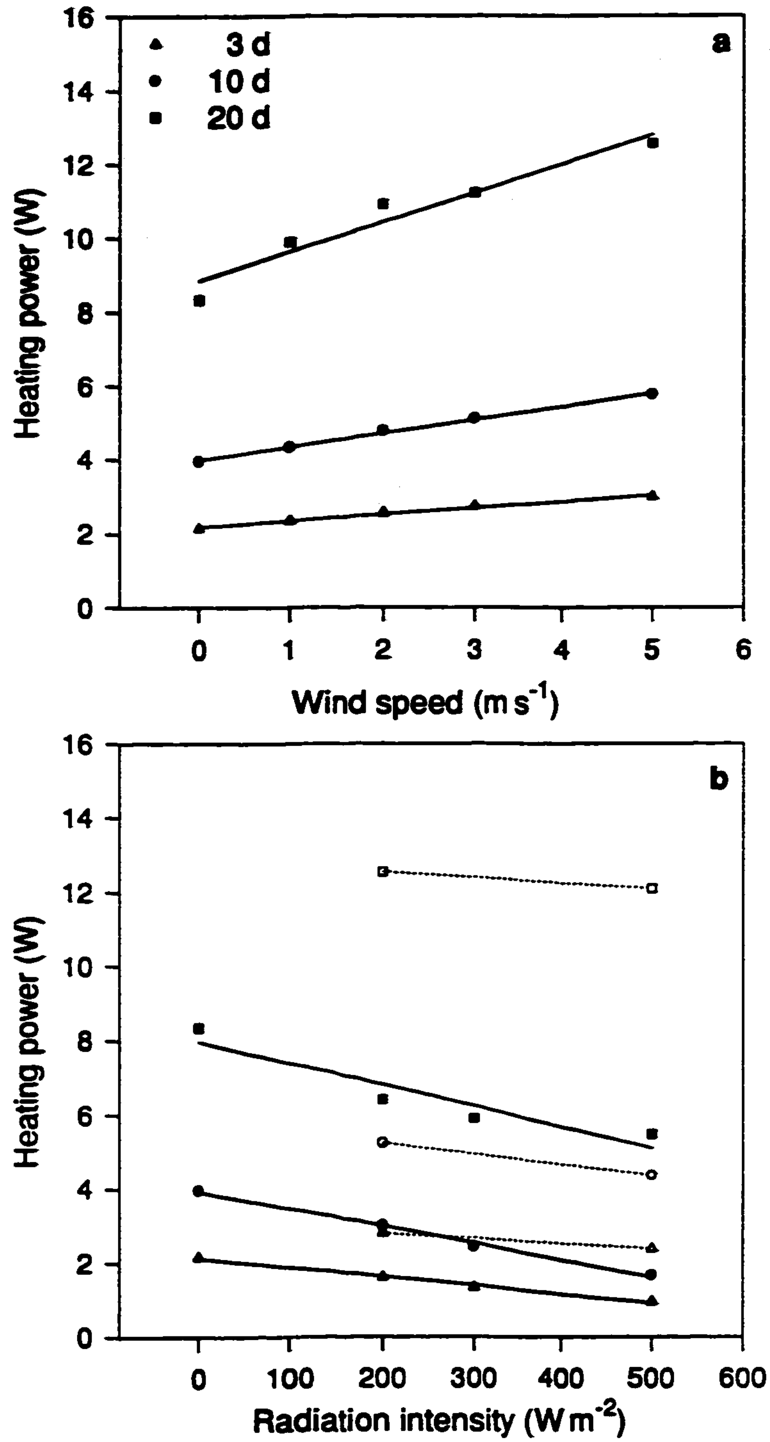

FIG. 2. Impact of wind (u) and radiation (R) on the heating power required to maintain mounts' T_b in laboratory experiments (meteorological calibrations). (a) $R = 0$, (b) $u = 0$ except for open symbols where $u = 5$ m s^{-1}. Lines are linear regressions (all $p < 0.05$). T_a= 10°C in all cases.

TABLE 4. Predictive equations of T_{es} obtained from laboratory calibrations of Greater Snow Goose taxidermic mounts of 3 ages based on air temperature (T_a), wind speed (u), radiation intensity (R), and their interaction (equation 5). All β values are statistically significant at $p < 0.005$.

Elevation angle of radiation	**Independent variables**	**Mount age (d)**					
		3		**10**		**20**	
		β	partial r^2	β	partial r^2	β	partial r^2
90°	T_a	0.996	0.832	1.001	0.778	0.999	0.650
	$u(T_b-T_a)$	-0.084	0.098	-0.103	0.132	-0.129	0.294
	R	0.031	0.065	0.035	0.087	0.026	0.042
	$Ru^{0.1}$	-0.011	0.003	-0.010	0.003	-0.013	0.006
	global r^2		0.998		0.999		0.993
	(n)		(26)		(26)		(28)
15°	T_a	0.998	0.844	1.002	0.819		
	$u(T_b-T_a)$	-0.083	0.049	-0.105	0.069		
	R	0.040	0.098	0.040	0.108		
	$Ru^{0.1}$	-0.018	0.007	-0.011	0.003		
(n = 23)	**global r^2**		0.998		0.999		
Combined	T_a	0.999	0.777	1.003	0.733		
	$u(T_b-T_a)$	-0.085	0.094	-0.105	0.123		
	R	0.035	0.118	0.037	0.138		
	$Ru^{0.1}$	-0.014	0.006	-0.011	0.004		
(n = 31)	**global r^2**		0.995		0.998		

were developed depending on the elevation angle of the radiation. Whether the angle was 90°, 15°, or both, the models obtained were very similar (Table 4).

Predictive equations of mounts' T_{es} obtained from field calibrations also explained a very large fraction of the observed variation in T_{es} (range of r^2: 0.944-0.959, Table 5). Independent variables were all significant, except for the interaction term between R and u which was significant only for the 3 d mount. The nonsignificant interactions were nonetheless retained for consistency with equations obtained in the laboratory.

Because it is easier to perform laboratory experiments than field ones, equations to predict T_{es} in the field are often derived only from laboratory calibrations. It was therefore interesting to compare T_{es} predictive equations obtained from laboratory data to those obtained from field data. In the laboratory models (Table 4), all β values associated with u and R were not statistically different from those of the field models (Table 5), except for the β values associated with R for the 3 d mount. In contrast, all β values associated with T_a in the laboratory models were significantly higher than those of the field models. Moreover, the relative importance of the independent variables was different between the two models. In the laboratory, it was T_a alone that explained most of the variation in T_{es} (range of partial r^2 for T_a: 0.650-0.844) whereas in the field it was both T_a (range of partial r^2: 0.322-0.547) and R (range of partial r^2: 0.386-0.529) that explained most of the variation in T_{es}.

To illustrate the differences between the laboratory and field models, we plotted the relationship between T_{es} and R in absence of wind (Fig. 3), and T_{es} and u in absence of radiation (Fig. 4) for T_a = 0°C. In presence of radiation, lines derived from laboratory equations were all statistically different from those derived from field ones. With radiation at 15°, which is close to the mean solar elevation above the horizon found on Bylot Island in July and August (about 20°), lines derived from laboratory equations fell slightly closer to those derived from field equations compared with radiation at 90° (Fig. 3). The greatest differences between laboratory and field lines were observed for the 3 d mount followed by the 10 d mount. In presence of wind, the relationship between u and T_{es} was very similar

TABLE 5. Predictive equations of T_{es} obtained from field calibrations of Greater Snow Goose taxidermic mounts of 4 ages based on air temperature (T_a), wind speed (u), radiation intensity (R), and their interaction (equation 5). All β values are statistically significant at $p < 0.05$ except those associated with partial $r^2 = 0$ which are nonsignificant.

Independent variables	**Mount age (d)**							
	3		**10**		**20**		**30**	
	β (95%CI)	partial r^2	β (95%CI)	partial r^2	β (95%CI)	partial r^2	β	partial r^2
T_a	0.711 (0.244)	0.526	0.706 (0.173)	0.547	0.491 (0.223)	0.322	0.661 (0.164)	0.415
$u(T_b\text{-}T_a)$	-0.091 (0.021)	0.031	-0.104 (0.017)	0.003	-0.141 (0.019)	0.092	-0.118 (0.014)	0.102
R	0.088 (0.041)	0.386	0.056 (0.030)	0.424	0.037 (0.037)	0.529	0.043 (0.028)	0.442
$Ru^{0.1}$	-0.041 (0.038)	0.003	-0.004 (0.029)	0.000	0.011 (0.034)	0.000	0.005 (0.026)	0.000
global r^2		0.946		0.947		0.944		0.959
(n)	(79)		(85)		(88)		(88)	

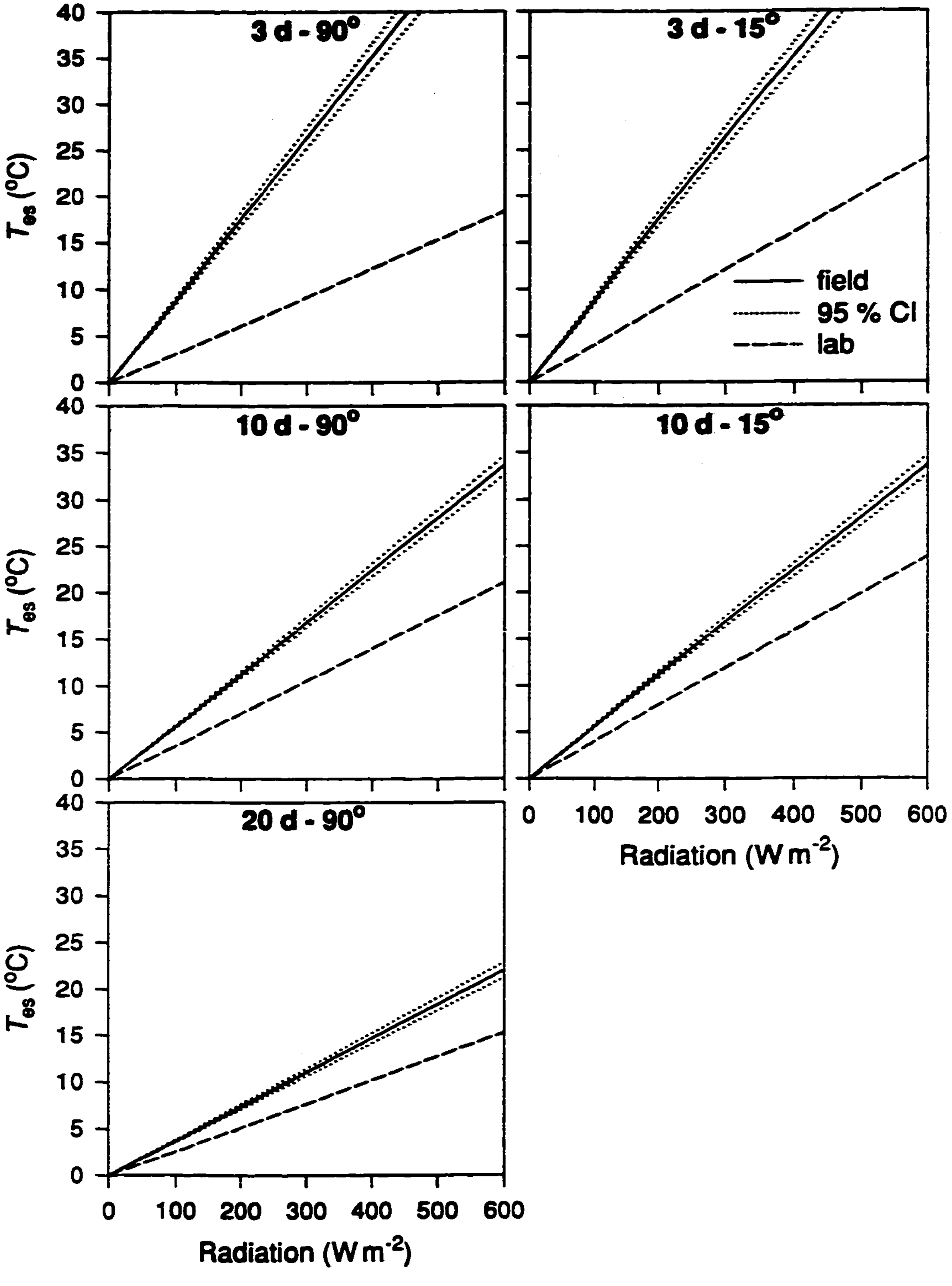

FIG. 3. Impact of radiation on T_{es} at 0°C in absence of wind. Regression lines are derived from the predictive equations of T_{es} developed in the laboratory (Table 4) and in the field (Table 5). 95 % CI are plotted for field data (for laboratory data, CI are indistinguishable from the regression lines).

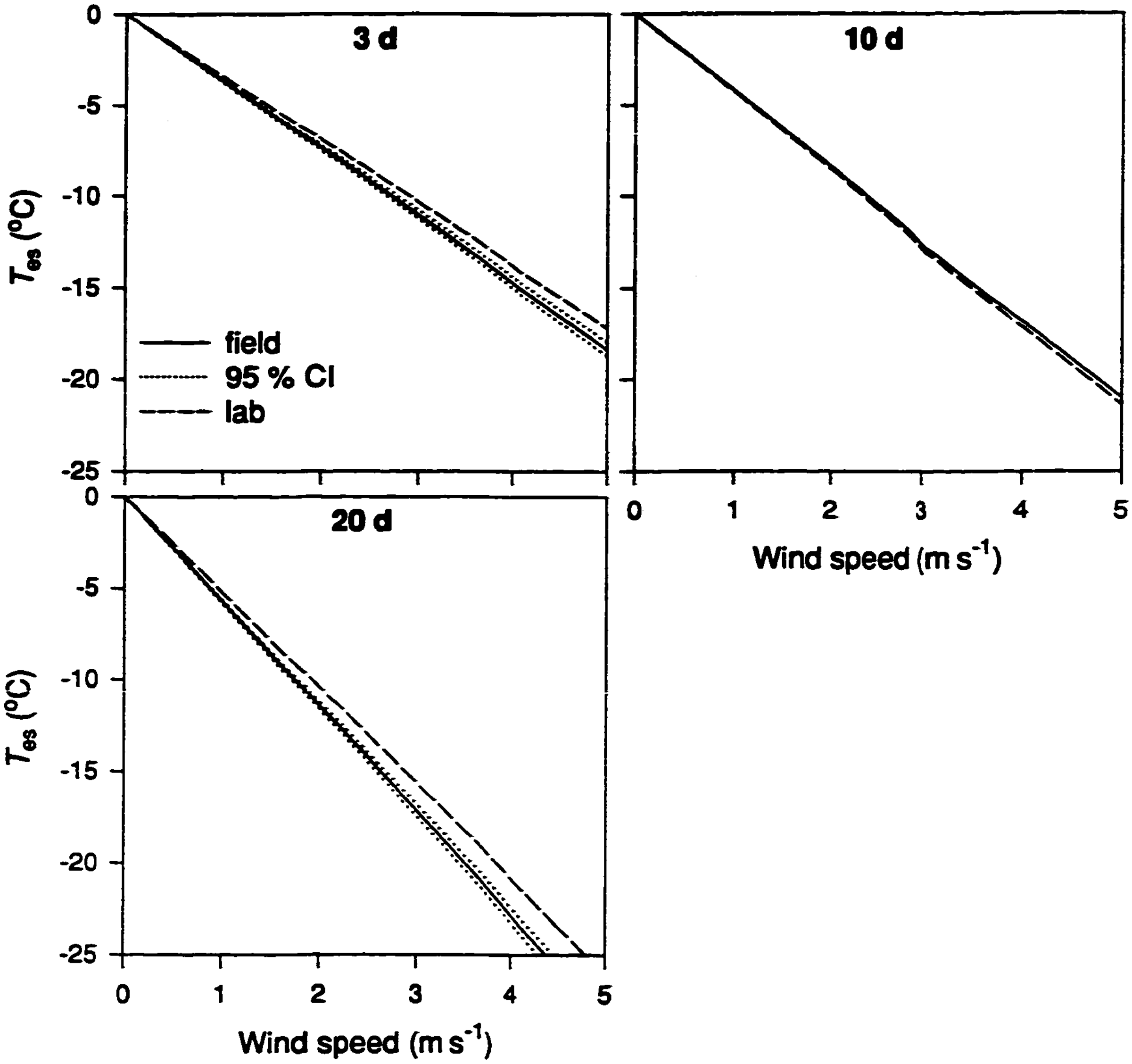

FIG. 4. Impact of wind on T_{es} at 0°C in absence of radiation. Regression lines are derived from the predictive equations of T_{es} developed in the laboratory (Table 4) and in the field (Table 5). 95 % CI are plotted for field data of 3 and 20 d mounts (other CI are indistinguishable from the regression lines).

between the laboratory and the field (Fig. 4). For the 10 d mount, the two lines were not statistically different.

Comparisons between mounts and live goslings

Mounts' thermal conductance per unit surface area calculated from biological calibration experiments was compared to that of live goslings of the same age class at different ambient temperatures (Fig. 5). In contrast to the constancy observed in taxidermic mounts, the thermal conductance of live goslings increased as the temperature warmed. However, at temperatures colder than about 15°C, the thermal conductance of the mounts generally fell within ± 1 SD of that of live goslings of the same age class.

The two regression models developed from laboratory experiments to predict mount heating power and gosling metabolic rate were:

$$P = 3.84 + 4.69m_b - 0.181T_a + 0.0197(T_b - T_a)\,u - 0.00316R;\ r^2 = 0.855;\ n = 105 \qquad (7)$$

$$M = 4.34 + 5.66m_b - 0.123T_a + 0.0151(T_b - T_a)\,u - 0.000679R;\ r^2 = 0.761;\ n = 596 \qquad (8)$$

The ratio $(\hat{M} / \hat{P})$, as predicted from equations 7 and 8, was plotted against wind speed and radiation intensity to examine variations in the influence of these two variables on goslings and mounts (Fig. 6). Mounts and goslings reacted similarly to an increase in wind speed independently of age such that the ratio varied only slightly. The mean ratio was 1.26 at 0 m s^{-1} (range: 1.23-1.29) compared to 1.07 (range: 1.02-1.12) at 5 m s^{-1}. However, mounts and goslings reacted very differently to an increase in radiation intensity, as the mean ratio passed from 1.26 (range: 1.23-1.29) at 0 W m^{-2} to 1.79 (range: 1.42-2.31) at 500 W m^{-2}. Age also had a strong influence on the ratio: for example, at 500 W m^{-2} the ratio was 1.42 for the 30 d mount (m_b = 1575 g) compared to 2.31 for the 3 d mount (m_b = 105 g).

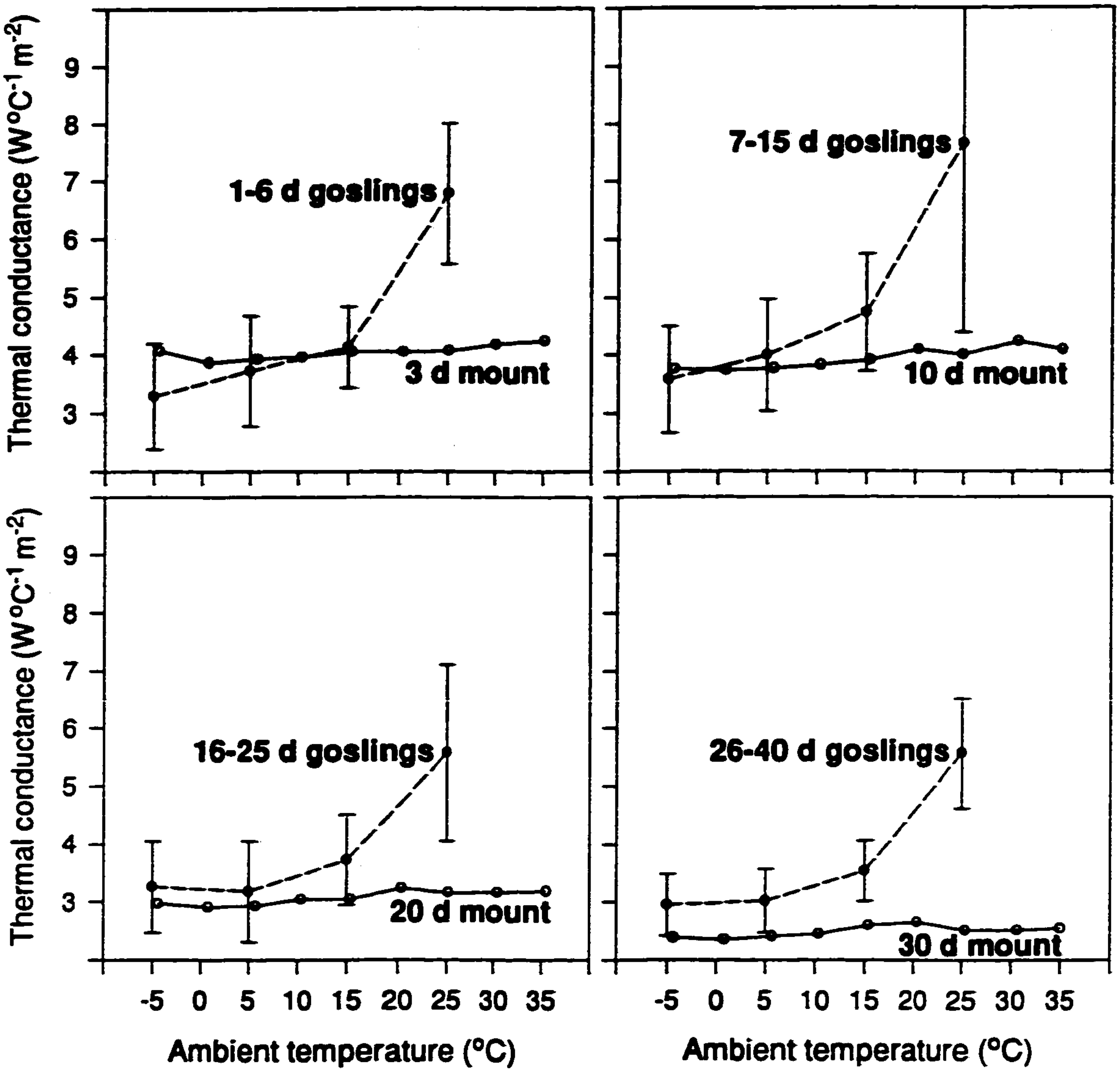

FIG. 5. Comparison of mounts' thermal conductance per unit surface area (K_{es}/A_b) with that of live goslings in laboratory experiments at different ambient temperatures. For goslings, means ± SD are given ($n = 7$; data from Ratté, 1998).

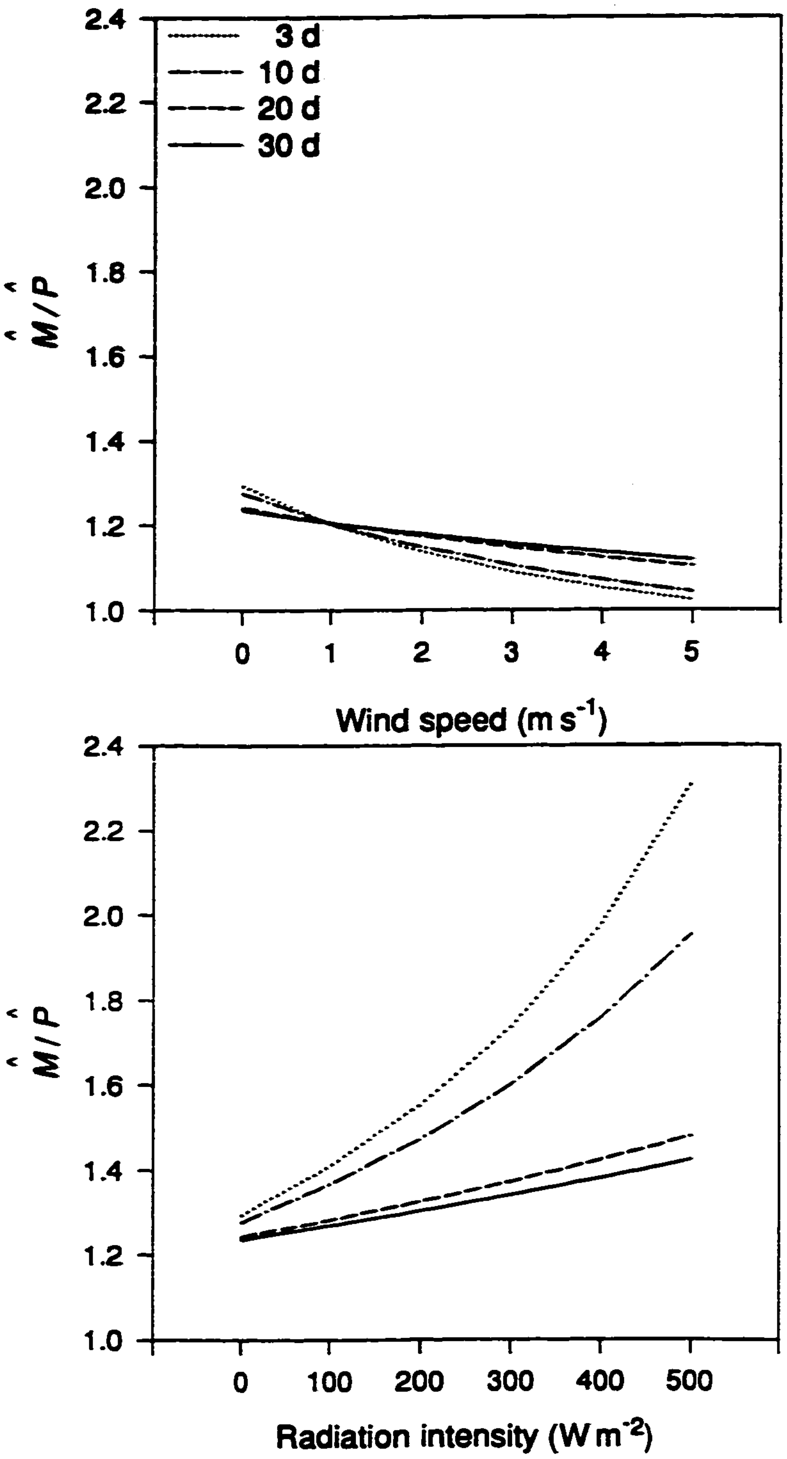

FIG. 6. Impact of wind and radiation on the ratio between predicted gosling metabolic rate and predicted mount heating power ($\hat{M}$ / $\hat{P}$) at 6°C for goslings of 4 ages corresponding to those of the taxidermic mounts. Predictions are from equations 7 and 8.

These observations on the influence of wind and radiation on the ratio ($\hat{M} / \hat{P}$) led us to conclude that a predictive equation of gosling metabolic rate from taxidermic mounts should include data on u and especially R in addition to P, m_b and T_a. We developed such predictive equation (complex mount model) and compared it to the one obtained from the biometeorological analysis. Both models explained a high proportion of the variation in gosling metabolic rate with the complex mount model giving a slightly better fit ($r^2 = 0.793$) than the biometeorological analysis ($r^2 = 0.761$; Table 6).

DISCUSSION

Stability in mount responses

Our basic laboratory calibration showed that taxidermic mounts properly built and carefully handled give remarkably consistent results over periods ranging from days to years, even after several hundred hours of exposure to laboratory and natural environments. Short term variability in replicate experiments was small (≤ 3.4 %) and may not solely be due to variation in mounts themselves but also to slight variations in air temperature, wind speed, artificial radiation and positioning of the mounts in the set up.

The comparison between our basic calibration and that performed about three years ago by Fortin (1995) with the same taxidermic mounts suggest that aging of the down/feather coats and of the heating systems had little effect on mounts' performance. The 30 d mount, the only one for which the intercept value of the regression line differed significantly from that found by Fortin (1995), possessed movable wings (unlike other mounts) such that wing position may have added to the variability.

TABLE 6. Regression models developed from laboratory experiments to predict the metabolic rate of Greater Snow Goose goslings. All β values are statistically significant at $p < 0.05$ except the one in parentheses which is nonsignificant.

Independent variables	**Complex Mount Model**		**Biometeorological Analysis**	
	β	partial r^2	β	partial r^2
intercept	2.70	-----	4.34	-----
P	0.344	0.599	-----	-----
m_b	4.41	0.176	5.66	0.655
T_a	-0.0588	0.008	-0.123	0.068
$u(T_b\text{-}T_a)$	9.99×10^{-3}	0.007	0.0151	0.037
R	1.16×10^{-3}	0.001	(-6.79×10^{-4})	0.001
Ru	-5.63×10^{-4}	0.003	-----	-----
global r^2		0.793		0.761
(n)	(596)		(596)	

Predictions of T_{es} with mounts

The comparison of T_{es} predictive equations developed from laboratory experiments with those developed from field experiments may be used to evaluate our capacity of reproducing natural environments in the laboratory. The results show that the relative importance of the meteorological variables (T_a, u, and R) in explaining variations in T_{es} is different between the laboratory and the field. In the laboratory, T_a was the single most important variable whereas in the field, T_a and R were almost equally important. This might reflect the difficulty of reproducing the radiative environment adequately in the laboratory, presumably because radiation provided by a single lamp source cannot duplicate the diffuse and reflected portion of natural radiation.

To investigate further this question, we isolated the impact of radiation and wind on T_{es}. For all mounts, the impact of R on T_{es} was very different between the laboratory and the field and the difference was accentuated for the smaller mounts. The laboratory T_{es} predictions for the 3 and 10 d mounts were slightly closer to the field ones when the angle of elevation of radiation was 15° rather than 90°. However, even by using a realistic angle of elevation for artificial radiation (such as 15°), differences between laboratory and field conditions were large, suggesting that natural radiation is a difficult parameter to recreate in the laboratory. As opposed to radiation, the laboratory T_{es} predictions at different wind speeds were very similar to the field ones. Thus, wind appears to be reproduced well in the laboratory.

Additional factors may have been partly responsible for the large differences observed between laboratory and field radiative environments. In the laboratory, the radiation was measured perpendicular to the light source whereas in the field, the pyranometer was always oriented horizontally (facing the sky), regardless of sun's elevation. Moreover, the pyranometer we used in the field underestimates radiation intensity by about 10 % when the angle of elevation of radiation is around 5° (LI-COR company calibrations). In the field, during night experiments, the mean elevation of the sun was around 5° in July (n = 23) and

1° in August ($n = 8$). Hence, the intensity of radiation we measured in the field may have underestimated that experienced by the mounts.

Mount sensitivity to meteorological variables

The different taxidermic mounts were not equally sensitive to variations in meteorological variables. In the laboratory, predictive equations of T_{es} with radiation at 90° showed a trend for an increased sensitivity of the mounts to wind speed and a decreased sensitivity to air temperature with age. At hatch, goslings are covered with down which provides an immediate and efficient insulation (Fortin, 1995; Ratté, 1998). During the period of feather emergence, which begins by 20 d (Fortin, 1995), the insulation value of goslings downy coat may be reduced by the presence of feather sheaths within which new feathers are growing. At this stage of development, goslings may be the most sensitive to mechanical disturbance of their plumage by the wind and hence susceptible to a greater convective heat loss.

Comparisons between mounts and live goslings

The thermal conductance of mounts was essentially constant over a wide range of air temperatures, in contrast to that of live goslings which increased with T_a. This result is similar to the one obtained by Bakken *et al.* (1981) in calibrating taxidermic mounts against live American Goldfinches (*Carduelis tristis*). Lower critical temperature in Greater Snow Goose goslings is around 15°C for 2-40 d goslings (Ratté, 1998). Hence, below the thermoneutral zone, mounts' conductance approximates well that of live goslings of the same age. Above the thermoneutral zone, it is expected that goslings' conductance will deviate from those of mounts because taxidermic mounts cannot reproduce the postural, ptilo- and vasomotor responses (and evaporative responses when applicable) of live birds to thermal stress. Below 15°C, the difference in thermal conductance between live goslings and mounts of 10, 20, and 30 d was progressively larger. Since our taxidermic mounts had no legs, this observation is possibly explained by a greater importance taken by the legs as a site for heat dissipation as goslings grow.

In laboratory calibrations, taxidermic mounts and live goslings reacted differently to variations in wind speed and radiation intensity as demonstrated by changes in the ratio $(\hat{M} / \hat{P})$. Under wind- and radiation-free conditions, $\hat{P}$ underestimated $\hat{M}$ by about 25 %. As u increased, the ratio $(\hat{M} / \hat{P})$ decreased slightly indicating that mounts heating power was more affected by the change in u than goslings metabolic rate. In the presence of a wind of 5 $\mathrm{m\,s^{-1}}$, $\hat{P}$ underestimated $\hat{M}$ by only 7 %. The fact that our mounts were more sensitive to an increase in wind speed than live goslings again suggests that postural, ptilo- and vasomotor responses in goslings attenuated the effect of wind. This result is also similar to the one obtained by Bakken *et al.* (1981) with goldfinches.

When radiation intensity increased, mounts' reactions were very different from those of live goslings and the difference was greatly accentuated in the smaller mounts. As R increased, the ratio $(\hat{M} / \hat{P})$ increased because $\hat{P}$ decreased while $\hat{M}$ changed little. The decrease in heating power requirements with increasing R was expected because radiation, by increasing T_{es}, reduces thermostatic demands. In contrast, as R increased, live goslings maintained a relatively high metabolic rate indicating that their heat production was higher than the minimum required to maintain T_b. In the presence of a radiation of 500 W $\mathrm{m^{-2}}$, $\hat{P}$ underestimated $\hat{M}$ by an average of 79 %, indicating that mount heating power was much more affected than gosling metabolic rate. The greatest underestimation of $\hat{M}$ by $\hat{P}$ was associated with the smaller body masses. Since taxidermic mounts give an estimate of the minimum heat production required for basic temperature regulation, it can be expected that the heating power of the mounts will underestimate the metabolic rate of live goslings under certain circumstances, particularly during growth.

Because taxidermic mounts and live goslings react differently to wind and radiation, we included those variables in the equation predicting gosling metabolic rate from heating power of the mounts, the complex mount model. However, in this model, the partial r^2 associated with R was very low, and this can be explained by the fact that, as opposed to the heating power of the mounts, the metabolic rate of goslings is almost unaffected by an increase in radiation intensity.

The calibration of taxidermic mounts with live goslings enabled us to refine the predictive equation of gosling metabolic rate obtained by the biometeorological analysis. The slightly better fit offered by the complex mount model over the biometeorological analysis suggests that the method might incorporate additional interactions in the exchange of heat between the goslings and their environment. In order to determine under what circumstances the complex mount model would prove superior to the biometeorological analysis, we examined the plots of the residuals of each model against the independent variables. In the laboratory, the performance of the two models were similar. We did not have metabolic measurements in the field and so we could not examine the residuals of the models. However, field conditions potentially include more interactions in the exchange of heat between a body and its environment Hence, the hypothesis that the complex mount model might be slightly superior to the biometeorological analysis will be investigated further in Chapter 3 under field conditions.

CONCLUSION

This study demonstrates that taxidermic mounts, when properly constructed and used, are not grossly imprecise instruments as suggested by Walsberg and Wolf (1996) and that, on the contrary, they can provide accurate and reproducible results. Both Bakken (1994) and Walsberg and Wolf (1996) emphasized that to obtain valid estimates of metabolic heat production of live animals, heated taxidermic mounts should be calibrated against live animals in the laboratory. Such calibrations involving different wind speeds have rarely been made and, for mounts exposed to solar radiation, had never been conducted before Walsberg and Wolf (1996). In the present study, we calibrated our mounts against several live goslings over a wide range of air temperatures, radiation intensities, and wind speeds representative of what is found in nature. The differences obtained in the reactions of mounts and goslings to variations in wind speed and radiation intensity confirmed the necessity of calibrating taxidermic mounts against live animals, particularly during growth. Thus, we believe that the taxidermic mounts used in this study constitute a valuable tool for quantifying the complex thermal environment of animals living in cold environments such as Greater Snow Goose goslings in the Arctic.

CHAPITRE III

ENERGETIC COST OF THERMOREGULATION IN GREATER SNOW GOOSE GOSLINGS

RÉSUMÉ

Cette partie de l'étude visait à mesurer les coûts énergétiques associés à la thermorégulation chez les jeunes de la Grande Oie des neiges en croissance à l'île Bylot. Sur le terrain, nous avons mesuré la puissance de chauffage de quatre mannequins taxidermiques d'âges différents ainsi que divers paramètres météorologiques représentatifs de l'environnement thermique des oisons. Le taux métabolique des oisons a été estimé à partir des équations de prédiction obtenues au chapitre 2. Les résultats sont les suivants:

1. Le taux métabolique des oisons prédit par l'analyse biométéorologique diffère (de 0 à 20 %, selon l'âge de l'oison) de celui prédit par un modèle plus complexe incluant des données obtenues sur le terrain avec des mannequins taxidermiques.
2. L'Arctique est un environnement de croissance froid et variable pour les oisons, avec une température opérante standard (T_{es}) estivale moyenne (1994-1997) de 5.3°C.
3. Cet environnement thermique est sujet à d'importantes fluctuations journalières ainsi qu'à une détérioration progressive au cours de la période s'étalant de la naissance des oisons à 40 jours d'âge.
4. Environ 30 % de l'énergie requise pour le métabolisme de maintien doit être allouée à la thermorégulation.
5. Les oisons éclos 6 jours après le pic d'éclosion dépensent environ 6 % plus d'énergie pour la thermogenèse que ceux éclos 6 jours avant le pic d'éclosion.

ABSTRACT

The main objective of this section of the study was to evaluate the energetic cost of thermoregulation for Greater Snow Goose goslings during growth in the High Arctic. In the field, we measured the heating power of the four taxidermic mounts along with different meteorological variables representative of the thermal environment of goslings. Gosling metabolic rate was obtained from the prediction equations developed in Chapter 2. Here are the results:

1. The metabolic rate of goslings predicted by the biometeorological analysis was different (between 0 and 20 %, depending on gosling age) from that predicted by the complex mount model which included data obtained using taxidermic mounts in the field.
2. The Arctic is a cold and variable environment for growing goslings with a mean (1994-1997) summer T_{es} of 5.3°C.
3. The thermal environment experienced by goslings showed large daily variations and deteriorated between 0 and 40 d of age.
4. About 30 % of the energy allocated to maintenance was required for thermogenesis.
5. Goslings hatched 6 d after the peak day of hatch allocated about 6 % more energy to thermoregulation than those hatched 6 d before peak hatching.

INTRODUCTION

Endothermy confers important benefits such as physiological stability and escape from thermal limitations, but at a heavy metabolic cost (Welty et Baptista, 1988). Walsberg (1983b) estimated that in adult birds, the energy allocated to maintenance metabolism (basal metabolism plus thermogenesis) accounted for 40-60% of total expenditure. Because energy allocated to maintenance metabolism is an obligatory expenditure, its proportion in an animal's energy budget will determine the amount of productive energy available for reproduction or growth (Walsberg, 1983b).

The cost of thermoregulation represents an important proportion of the daily energy expenditure of chicks living in polar regions. Klaassen *et al.* (1989a and b) calculated the energy budget of Arctic Tern (*Sterna paradisaea*) chicks and found that thermostatic costs represented 16 % of total energy requirements. Several factors contribute to a high thermoregulatory demand in chicks. Being smaller than their parents, chicks have a less favorable surface/volume ratio for heat conservation. In addition, the muscles of neonates, particularly the flight muscles, are generally small and poorly developed which limits their heat production capacity (Ricklefs, 1989). Hence, in cold environments, precocial chicks allocate a large proportion of their energy to thermoregulation which may reduce the amount of energy available for growth (Chappell *et al.*, 1989; Chappell *et al.*, 1990; Olson, 1992). In polar regions, the summer is short so that time available for the growth of young is limited. This is especially critical for geese which are among the largest breeding birds of the Arctic regions. Yet, attaining adequate size and condition before the southward migration is essential for goslings because the distance to fall staging areas may be very long (Owen and Black, 1989; Menu, 1998).

Seasonal variations in growth rate and survival have been observed in several goose species. Goslings hatched late in the season often have a slower growth or a lower survival than those hatched earlier, and this is commonly associated with reduced food availability and/or quality late in the season (Cooch *et al.*, 1991b; Sedinger and Flint, 1991; Lindholm *et al.*, 1994; Lepage *et al.*, 1998). However, other factors besides food may contribute to seasonal variations in growth and survival. A seasonal decline in the thermal environment of goslings has been proposed as a factor contributing to the reduced growth rate of late-hatched goslings by increasing the proportion of energy they must allocate to thermoregulation late in the season (Lindholm *et al.*, 1994; Fortin, 1995). A reduced growth rate may have fatal consequences because body size and mass reached at the end of the summer influence survival of young in several goose species (Owen et Black, 1989; Francis *et al.*, 1992; Cooch *et al.*, 1993; Schmutz, 1993; Lindholm *et al.*, 1994; Menu, 1998).

The Greater Snow Goose (*Chen caerulescens atlantica*) is the northernmost breeding goose in America. Harsh climatic conditions characterize their breeding grounds and, being precocial, goslings of this species have to cope with the same thermal environment as their parents only a few hours after hatch. Greater Snow Goose thus constitutes an ideal subject to examine the thermal relationships between young and their natural environment under extreme conditions.

The main objective of this study was to evaluate, with the use of taxidermic mounts, the energetic cost of thermoregulation for Greater Snow Goose goslings under field conditions in the Arctic. To achieve this, we have identified five specific objectives: (1) to compare gosling metabolic rate estimated with taxidermic mounts with values estimated by a biometeorological analysis, (2) to describe the thermal environment experienced by goslings during growth in terms of meteorological variables and T_{es}, (3) to compare thermal regimes of day and night and of typical resting and feeding sites used by brood-rearing geese, (4) to evaluate the energetic cost of thermoregulation for growing goslings in the field, and (5) to test the hypothesis that a seasonal decline in the thermal environment may contribute to the slower growth of late-hatched goslings.

MATERIAL AND METHODS

Study area

This study was conducted in the summer of 1997 on Bylot Island (73°08'N-80°00'W), Nunavut Territory, Canada. The study site is located in a large glacial valley dominated by tundra polygons (Zoltai *et al.*, 1983) forming a mosaic of wetlands (see Lepage *et al.*, 1996 for details). Two microhabitats were chosen as being representative of those used by geese for resting and feeding during brood-rearing. The resting site was located along the shore of a small lake (dia. = 225 m). The feeding site was 22 m away and consisted of a wet tundra polygon (dia. = 12 m) dominated by mosses and graminoid plants. These two sites were selected because of their potentially different wind regimes. The resting site was located on a lake shore opposite to the prevalent wind direction, about 0.6 m above the water level, whereas the feeding site was located in a concave polygon bordered by ridges about 0.2 m higher than the polygon center.

Recording of meteorological variables in the field

To characterize the microenvironments used by goslings, meteorological variables were measured at gosling height (height of body trunk) within 1-2 m of the taxidermic mounts. The measured variables were air temperature (T_a), radiation intensity (R), and wind speed (u) and direction. The measurements were recorded automatically (except for wind direction) every 10 s by a datalogger (CR10, Campbell Scientific Inc.), and mean values were saved every 5 min. T_a (°C) was measured 30 cm above the ground using a shielded temperature probe (model 207, Campbell Scientific Inc.), R (W m^{-2}) was obtained from a horizontal pyranometer (model Li-200SA, LI-COR) facing the sky at 40 cm above the ground, and u was recorded with a hot-wire anemometer (model 441S, Kurz Instruments Inc.) at 10 cm above the ground. Wind direction was estimated visually to the closest 22.5° every 20 min using a wind vane located 1 m above the ground. The same meteorological variables were simultaneously recorded by an automated weather station located about

450 m from the study sites. At this station, T_a and R were measured at 2.5 m above the ground with the same instruments while u and wind direction were recorded at 3 m using a wind monitor (model 05103-10, Young Inc.).

Use of taxidermic mounts in the field

The construction of the taxidermic mounts used in this study is described in details by Fortin (1995). The four mounts correspond to four ages representative of development stages of the goslings (see Chapter 2, Table 1): at the beginning of growth (3 d, 105 g), before feather emergence (10 d, 275 g), at the beginning of feather emergence (20 d, 1200 g), and at an advanced stage of feather emergence (30 d, 1575 g). Mounts were calibrated against live goslings in the laboratory over a range of thermal conditions representative of natural environments (see Chapter 2).

During field experiments, the heating wires of the mounts were connected to a regulated DC power supply (15 V, 30 A, model RS-300, Daiwa) from which the voltage output was typically set between 12 and 13.5 V. The main power source was a 650 W generator (model EX650, Honda). Mounts' T_b were maintained at about 40.5°C (95 % CI: 39.0-41.8°C), the mean body temperature of goslings (Fortin, 1995). Voltage pulses were applied to the mounts via relays driven by a datalogger (CR10, Campbell Scientific Inc.) programmed to act as a time- proportional controller (Appendix D). The voltage applied to the mounts was automatically recorded every second by the datalogger and mean values were saved every 5 min. The heating power of the mounts (P) was calculated using Ohm's law.

Data collection was spread throughout the brood-rearing period of goslings, from 2 July to 16 August. Since geese are active during the 24-h daylight period in summer (which extends from early May to early August), two 4-h measurement periods were chosen to be representative of the extreme daily conditions goslings would encounter in terms of radiation. The periods used were from 10h00 to 14h00 (standard time) and from 22h00 to 2h00. All experiments were performed with the four mounts.

Although we intended to conduct experiments every day, bad weather (rain accompanied by high winds) or technical problems prevented data collection on some days, which resulted in a total of 33 days and 31 nights of experimentation. The two experimental sites were used in alternation every day. Experiments were initiated at least half an hour before the beginning of data recording to allow time for the mounts to attain the desired body temperature. The mounts were placed in a row side by side about 30 cm from one another. They were facing the wind most of the time because every 20 min the wind direction was recorded and the mounts reoriented accordingly. This orientation was selected because Fortin (1995) found that wild goslings in cold environments preferentially orient themselves to face the wind, especially under high wind speeds. Experiments were conducted on rainy days with light wind by placing a transparent plastic sheet horizontally 1 m above the ground to protect the mounts and the meteorological instruments from the rain. This set up was used on 9 days and 7 nights. This plastic sheet, which was supported by four poles and stretched by ropes, did not block the wind because of its horizontal position.

T_{es} determination

The nonlinear regression equations relating P to T_{es} developed from the basic calibration in the laboratory (see Chapter 2, Table 1) were used to convert the heating power of the mounts measured in the field into T_{es}. Within each 4-h period of field experiments, we averaged values over the 30-min period which displayed the greatest stability in all of P, T_b, T_a, R and u. We sometimes used two 30-min periods within the same 4-h measurement period when the thermal conditions had changed and stabilized sufficiently. These average P values were then converted into T_{es}.

The T_{es} calculated described the thermal environment experienced by goslings for only a portion of the summer, *i.e.* when experiments with the mounts were conducted. To characterize the thermal environment of goslings for the entire brood-rearing period, T_{es} had to be estimated for the whole period. This was done by converting the meteorological variables, recorded continuously by the automated weather station, into T_{es}. Weather data was available at the study site for the summers of 1994 to 1997.

The first step of this process consisted in establishing the relationships between the thermal conditions measured by the weather station well above the ground to the microenvironment of goslings near the ground. We found no significant differences between measurements of T_a and R made at 2.5 m above the ground and those made close to the ground (at 30 cm for T_a and 40 cm for R). Hence, data from the weather station could be used directly for these two variables. This was not the case for wind speed which decreased closer to the ground. The relationship between wind speed measured at 3 m above the ground (u_3) and at goslings height, 10 cm above the ground ($u_{0.1}$) was:

$$u_{0.1} = 0.519\ u_3 \tag{1}$$

($r^2 = 0.927$, $n = 2805$, $p < 0.001$). A zero intercept was imposed to the linear regression as wind must be equal to zero as it touches the ground. No evidence of a nonlinear relationship between $u_{0.1}$ and u_3 was found. The preceding equation was applied to all wind speed data from the weather station.

The second step consisted in relating T_{es} to the meteorological variables of the microenvironment of goslings (T_a, R, and u) during experiments with the mounts. The equations, developed in Chapter 2 (see Table 5; meteorological calibrations based on field experiments), could then be used to predict T_{es} of goslings throughout the summer using environmental conditions recorded by the weather station from 1994 to 1997. Because we had four equations relating T_{es} to environmental variables (*i.e.* one for each mount), a method of progressive attribution of mounts' equations was used throughout the growth of goslings (Table 1).

TABLE 1. Equations used to predict T_{es} of goslings of various ages throughout the summer by progressive attribution. The superscripts (3d, 10d, 20d, and 30d) refer to the predictive equations relating T_{es} to environmental variables for the taxidermic mounts of these four ages.

Gosling age	Equation used
0-3	$T_{es} = T_{es}^{3d}$
4-9	$T_{es} = ((\text{age} - 3)/7)*T_{es}^{10d} + ((10 - \text{age})/7)* T_{es}^{3d}$
10	$T_{es} = T_{es}^{10d}$
11-19	$T_{es} = ((\text{age} - 10)/10)*T_{es}^{20d} + ((20 - \text{age})/10)* T_{es}^{10d}$
20	$T_{es} = T_{es}^{20d}$
21-29	$T_{es} = ((\text{age} - 20)/10)*T_{es}^{30d} + ((30 - \text{age})/10)* T_{es}^{20d}$
30-40	$T_{es} = T_{es}^{30d}$

Metabolic rate prediction

The ratio of predicted gosling metabolic rate over predicted mount heating power ($\hat{M} / \hat{P}$) was calculated using the equations developed in the laboratory (see Chapter 2, equations 7 and 8), based on meteorological conditions encountered during field experiments. Field predictions of gosling metabolic rate were obtained from two multiple regression models also developed in the laboratory. The two models included, as independent variables, gosling body mass (m_b) and meteorological variables (T_a, R, and u). The complex mount model additionally included the heating power of the mounts (P) whereas the biometeorological analysis did not (see Chapter 2, Table 6). In the complex mount model, the heating power of the mounts (P) was obtained by reconverting T_{es} into P using the linear regression equations relating P to T_{es} developed in laboratory (see Chapter 2, Table 3). We used again the procedure of progressive attribution (see Table 1) of the four mounts' equations to estimate P at each day of growth.

The body mass values used to predict the metabolic rate of goslings were obtained from the following logistic growth curve (taken from Lesage, 1995):

$$m_b = \frac{2335}{1 + 16.83e^{-0.093age}} \tag{2}$$

where m_b is in g, and *age* is in d.

We estimated the energetic cost of maintenance metabolism (basal metabolism plus thermogenesis) based on metabolic rates (M) predicted by the complex mount model because this model offered the best predictions. The hourly average values of $\hat{M}$ were summed over the whole day. The summation of these daily values over the whole brood-rearing period (0 to 40 d) provided an estimate of the total energetic cost of maintenance.

Thermoneutral resting metabolic rate (*RMR*) of goslings was calculated using the following equation (from Ratté, 1998):

$$RMR = 7.88 m_b^{0.607} \tag{3}$$

where m_b is in kg. In this equation, *RMR* does not meet the strict definition of a basal metabolic rate because it was measured in growing goslings. Nonetheless, the *RMR* values obtained from the preceding equation were used in this study as an estimate for basal metabolic rate. Thus, the calculated daily *RMR* were summed over the brood-rearing period providing an estimate of the total energetic cost of basal metabolism.

Data analysis

All analyses were performed with SAS (SAS Institute, 1988). Daily differences between gosling metabolic rate predicted by the two models (complex mount model and biometeorological analysis) were calculated for each year from 1994 to 1997. The effects of year and gosling age on these daily differences were assessed with a two-way analysis of variance (ANOVA). The null hypothesis of no difference between the two models was tested by examining if the 95 % CI of the least-square means included 0. We also performed a paired *t*-test on the daily differences in $\hat{M}$ between the two models, all 4 years combined.

We examined if habitat (resting vs. feeding site) had an effect on wind speed with a two-way ANOVA on u measured at gosling height with habitat and period of the day (day or night) as independent variables. Paired *t*-tests were used to compare average daily values of T_{es} and T_a within each year (1994 to 1997) and for all years combined according to the period of the day (daytime 6h00-18h00, nighttime 18h00-6h00, and whole day). To examine seasonal variations in meteorological variables over the summer, we performed two-way analyses of covariance (ANCOVA) on hourly values of T_a, R, u, and T_{es} using year and hour as independent variables and Julian date as covariable. Since year had an effect on T_{es}, we performed a multiple comparison of means for daily T_{es} of 1994 to 1997 using Tukey's test.

In order to compare the amount of energy that goslings hatched at different dates must allocate to thermoregulation, we evaluated the thermal environment of goslings hatched at five different dates (3 and 6 d before and after the peak day of hatch and on the peak day of hatch). The peak day of hatch was identified for each year (range: 6-12 July) as the mode of the distribution of hatching dates observed for Greater Snow Goose nests on Bylot Island from 1994 to 1997. When the hatching nests of all years were combined, 6 July was the modal hatch day (Fig. 1). Goslings hatched on the peak day of hatch are referred to as peak-hatched goslings. Depending on the year, between 91 and 100 % of all nests hatched within the 13-d period comprised between 6 d before and 6 d after peak hatching. We calculated the differences in daily T_{es} and energetic cost for maintenance between goslings hatched 3 d before and 3 d after the peak day of hatch and between goslings hatched 6 d before and 6 d after the peak day of hatch. The effects of year and gosling age on the daily differences in metabolic rate were assessed with a two-way ANOVA. The 95 % CI of the least-square means were again used to test the null hypothesis of no difference.

RESULTS

Metabolic rate prediction

The mean ratio ($\hat{M} / \hat{P}$) for all sets of thermal conditions encountered in field experiments was 1.33 ± 0.02 (mean ± SE, $n = 339$). The value of the ratio increased along with T_{es} (Fig. 2). Below a T_{es} of 15°C (which corresponds to the lower critical temperature of 2-40 d goslings; Ratté, 1998), a linear regression offered a reasonable fit to the data ($r^2 = 0.609$, $n = 258$, $p < 0.001$). However, above a T_{es} of 15°C, the ratio became highly variable and thus difficult to predict.

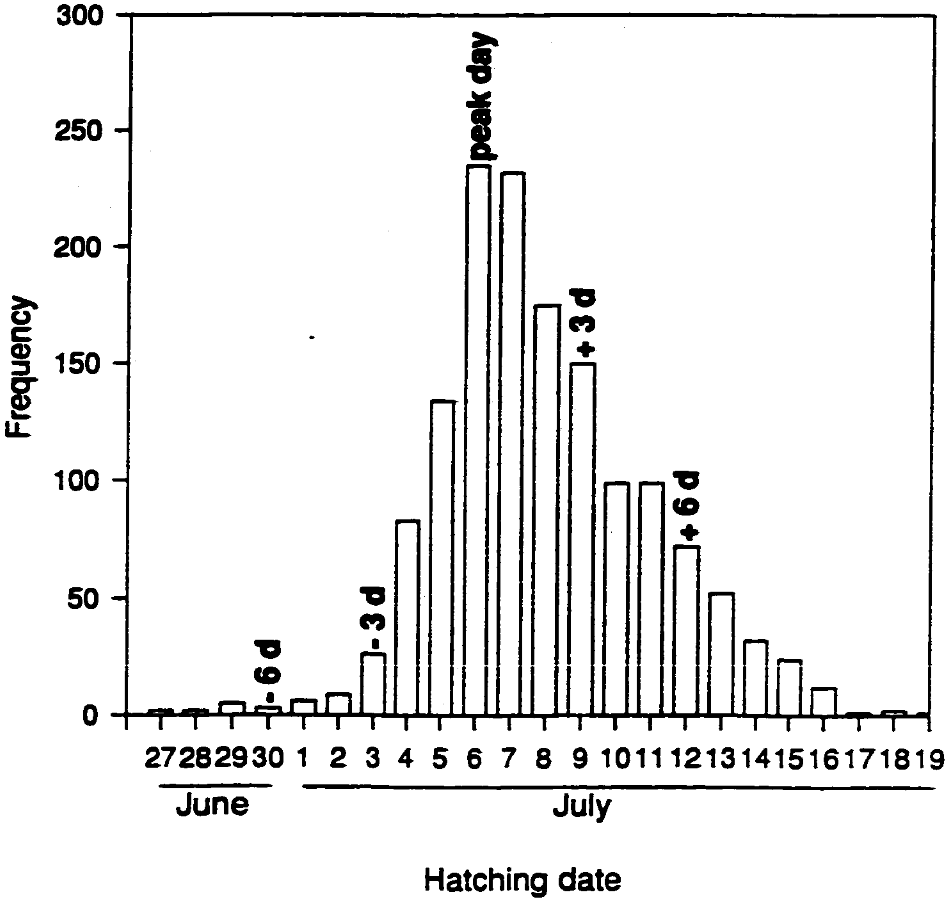

FIG. 1. Frequency distribution of hatching dates of Greater Snow Goose nests on Bylot Island for 1994-1997. The peak day of hatch (mode of the distribution) was 6 July when all years were combined (Gauthier *unpublished data*, $n = 1456$).

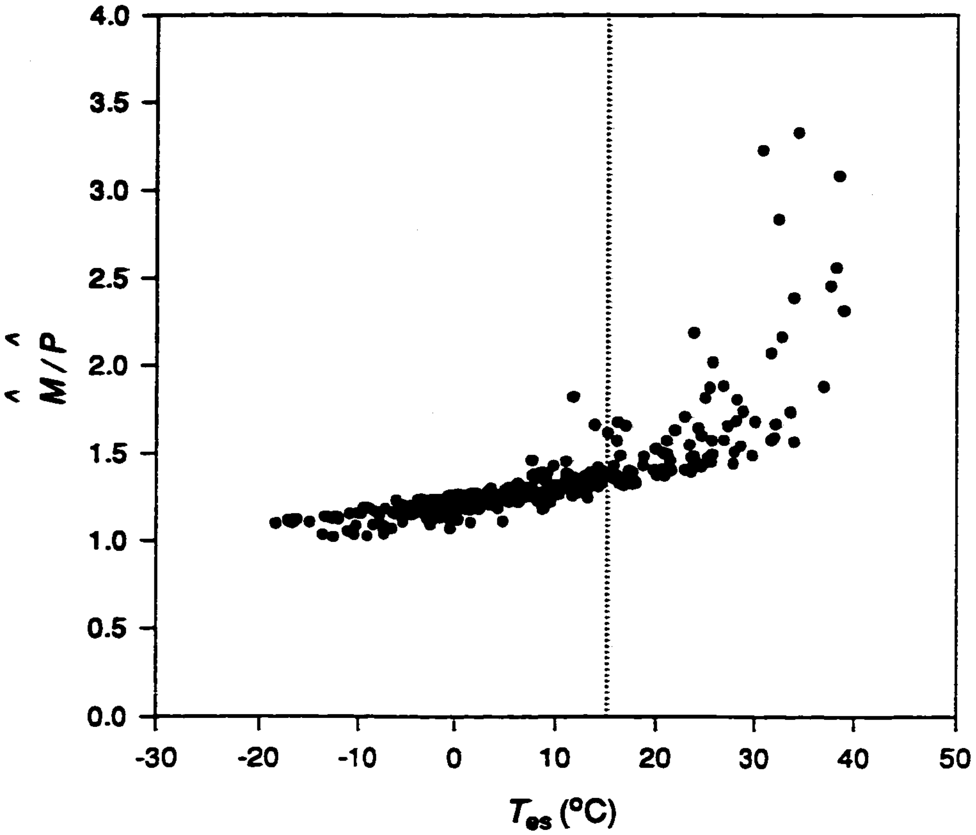

FIG. 2. Impact of T_{es} on the ratio between predicted gosling metabolic rate and predicted mount heating power ($\hat{M}/\hat{P}$). Predicted values were obtained from regression models developed in the laboratory (see Chapter 2, equations 7 and 8) and are based on meteorological data recorded in the field, as are T_{es} values. Linear regression for $T_{es} < 15$°C: $\hat{M}/\hat{P} = 9.613 \times 10^{-3} + 1.212T_{es}$ ($r^2 = 0.609$, $n = 258$, $p < 0.001$).

Daily average values (means for 1994-1997) of gosling metabolic rate (M) predicted by the two regression models (see Chapter 2, Table 6) increased with age from 4.22 W on the day of hatch to 13.85 W at 40 d of age for the complex mount model and from 5.04 W to 13.92 W for the biometeorological analysis (Fig. 3). The difference between daily average values of M predicted by the two models was consistently nonzero in all years ($p < 0.001$). Moreover, this difference varied significantly ($p < 0.001$) with gosling age. Between 0 and 8 d, gosling metabolic rate predicted by the biometeorological analysis overestimated that predicted by the complex mount model by less than 1 W, whereas between 15 and 31 d, it underestimated it by a maximum of 1.65 W. At other ages, the difference between the two models was nonsignificant.

Extreme thermal conditions often correspond to higher selective pressures than average conditions. In order to compare the performance of the two regression models (complex mount model and biometeorological analysis) in extreme thermal conditions, we selected field experiments in which the T_{es} calculated from P was less than - 5°C or over 30°C. We noted that the differences in M predicted by the two models in these extreme conditions were of the same magnitude as those observed in Fig. 3.

Thermal environment

The meteorological conditions to which goslings are exposed showed large daily variations during the summer. Important oscillations were observed between day and night values of T_a and R even though the sun remains above the horizon for the full 24-h period until early August at our study site (Fig. 4). However, at night the sun is very low even in early July. At our study site, in July and August, the elevation angle of the sun above the horizon was about 36° during the day (between 10h00 and 14h00) and about 4° at night (between 22h00 and 2h00). For the period comprised between 6 July and 15 August, 1994-1997 average value of T_a was 5.7 ± 0.2°C (mean ± SE; hourly min.: 0.9°C, hourly max.: 10.8°C) and of R 184 ± 8 W m^{-2} (mean ± SE; hourly min.: 0 W m^{-2}, hourly max.: 603 W m^{-2}). Mean daytime (6h00-18h00) values of T_a and R were 6.6 ± 0.2°C and 298 ± 11 W m^{-2} while mean

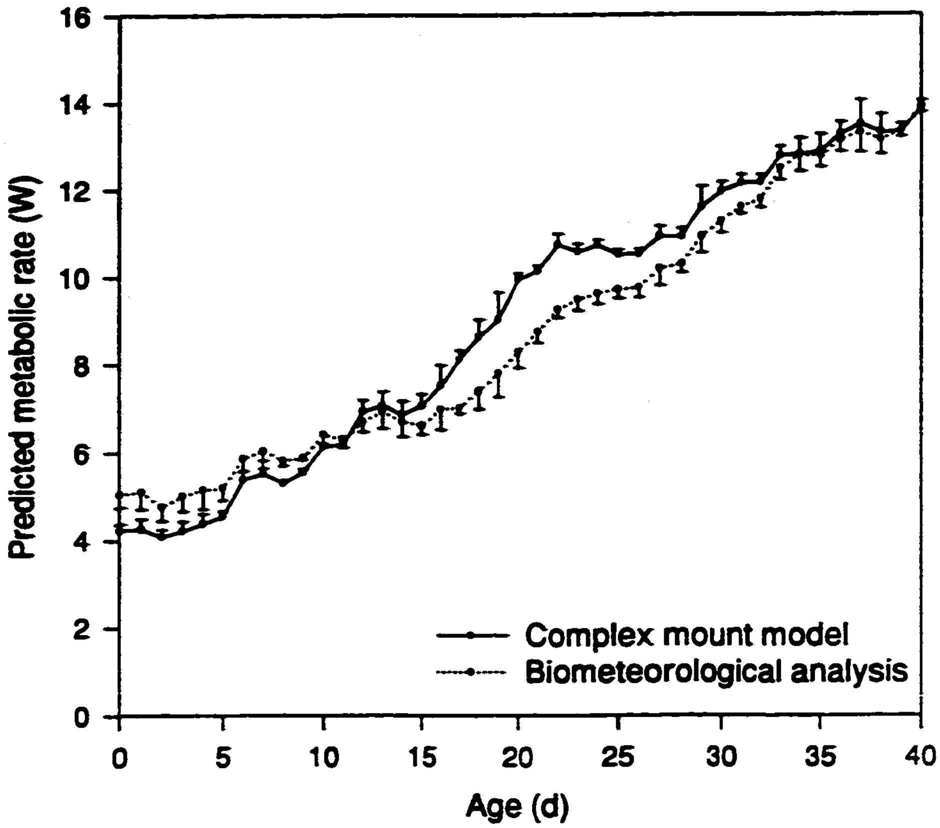

FIG. 3. Daily average values of predicted gosling metabolic rate (*M*) between 0 and 40 d of age. Predicted values of *M* (+ or - SE) were obtained from two regression models (complex mount model and biometeorological analysis, see methods), and are based on weather data recorded on Bylot Island during the summers of 1994 to 1997.

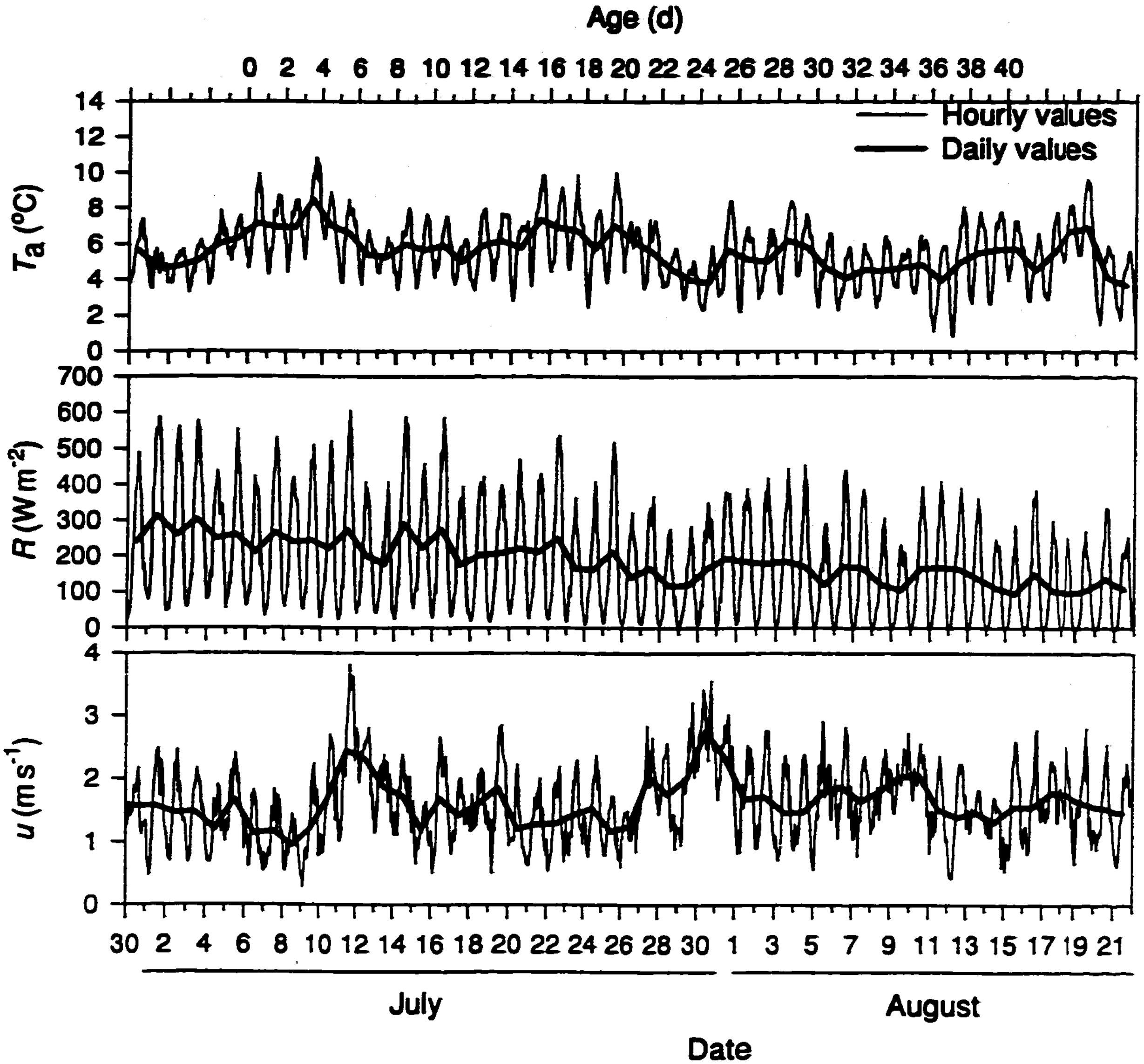

FIG. 4. Hourly and daily average values of T_a, R, and u (at gosling height) experienced by peak-hatched goslings between 0 (6 July) and 40 d of age (15 August). Mean values from 1994 to 1997.

nighttime (18h00-6h00) values were 4.8 ± 0.2°C and 71 ± 5 W m^{-2} respectively. For the entire period, mean wind speed at 10 cm above the ground was 1.6 ± 0.1 m s^{-1} (mean ± SE; hourly min.: 0.3 m s^{-1}, hourly max.: 3.8 m s^{-1}). There was no significant difference between resting and feeding sites in wind speed but the period of the day had an effect on u ($p < 0.005$), the wind being generally stronger during the day than at night. Mean daytime and nighttime u were respectively 1.9 ± 0.1 and 1.4 ± 0.1 m s^{-1}.

These daily variations in the thermal environment induced similar oscillations between day and night in the hourly average values of T_{es} experienced by peak-hatched goslings between 0 and 40 d of age (Fig. 5a). For the period comprised between 6 July and 15 August, 1994-1997, average value of T_{es} was 5.3 ± 0.8°C (mean ± SE; hourly min: -10.3°C, hourly max.: 27.5°C). Mean daytime and nighttime T_{es} were respectively 10.3 ± 1.0°C and 0.4 ± 0.6°C. During the day, T_{es} was 3.6 ± 0.8°C (mean ± SE) higher than T_a on average ($p < 0.001$, $n = 41$, all years combined) while the reverse was true for nighttime with T_{es} being 4.4 ± 0.5°C lower than T_a on average ($p < 0.001$, $n = 40$).

There was a seasonal deterioration of the thermal environment experienced by peak-hatched goslings between 0 and 40 d of age for the summers of 1994 to 1997. On average, T_a and R declined respectively by 0.046 ± 0.003 °C d^{-1} (mean ± SE) and by 3.25 ± 0.15 W m^{-2} d^{-1} (both $p < 0.001$) while u increased slightly by 0.003 ± 0.001 m s^{-1} d^{-1} ($p < 0.05$). Overall, these seasonal variations in T_a, R, and u resulted in a decline in T_{es} of 0.3 ± 0.01 °C d^{-1} ($p < 0.001$). This means that on average, daily T_{es} experienced by peak-hatched goslings declined from 11.3°C at hatch to 1.1°C at 40 d of age. The seasonal trend in T_{es} was observed in each individual year between 1994 and 1997.

Energetic cost of thermoregulation

Energetic cost associated with maintenance for peak-hatched goslings increased between 0 and 40 d of age (Fig. 5b). This was expected because resting metabolic rate (including

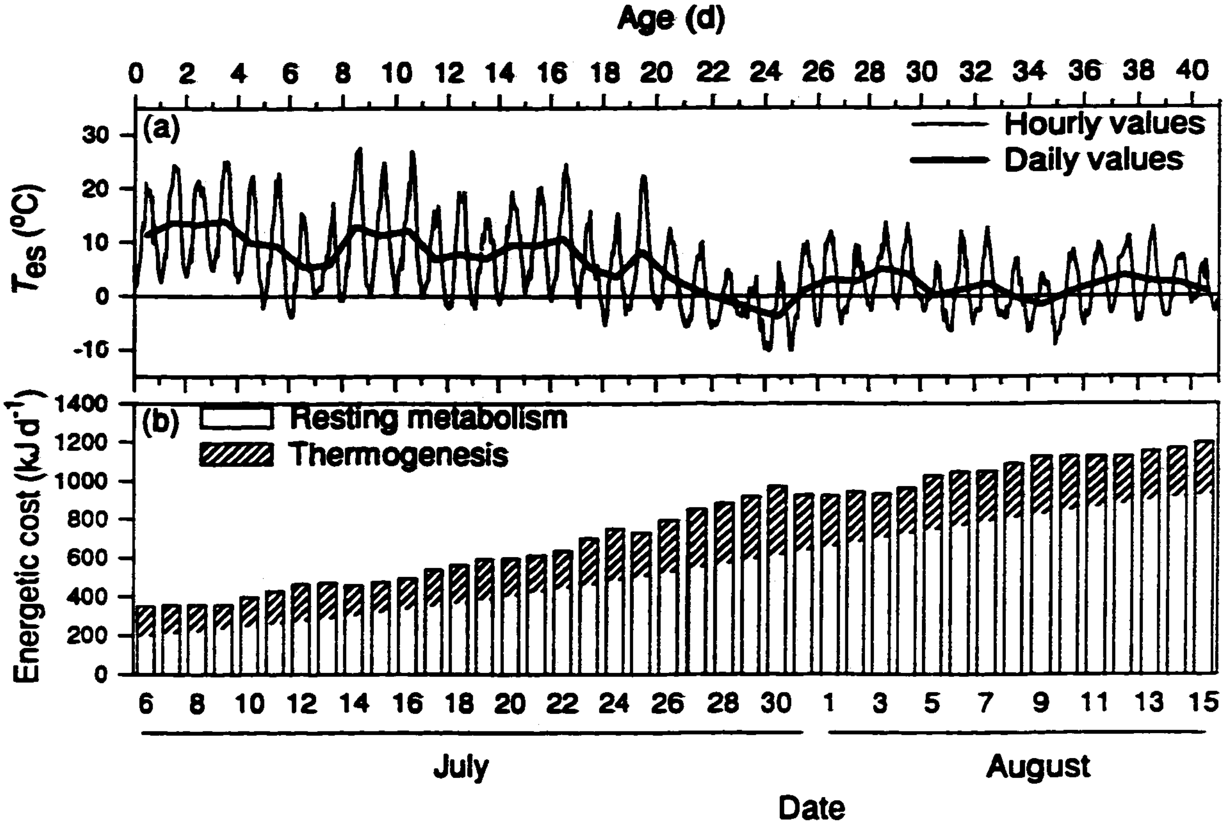

FIG. 5. (a) Hourly and daily average values of T_{es} experienced by peak-hatched goslings between 0 (6 July) and 40 d of age (15 August). (b) Daily maintenance metabolic rate of peak-hatched goslings between 0 and 40 d of age. Mean values from 1994 to 1997.

growth) is a function of body mass. The difference between the energetic costs associated with maintenance and resting metabolic rates is the energetic cost of thermoregulation. For 1994-1997, this cost represented on average 30.7 ± 0.9 % (mean ± SE) of maintenance metabolic rate. This proportion declined with age from 42 % at hatch to 22 % at 40 d of age ($p < 0.001$).

The estimates of the total energetic cost of maintenance for peak-hatched goslings between 0 and 40 d of age ranged from a high of 33 254 kJ in 1996 to a low of 31 391 kJ in 1997 (Fig. 6). For the same group of goslings, the energetic cost associated with thermoregulation represented 29 % of maintenance metabolic rate in 1994 and 1995, 32 % in 1996, and 28% in 1997. In 1996, T_{es} experienced by peak-hatched goslings was much lower ($p < 0.05$) than in the other 3 years being 1.7°C compared to 5.5°C in 1994, 6.2°C in 1995, and 5.9°C in 1997 (Fig. 6).

Effect of hatching date

No difference was found in daily T_{es} and daily cost for maintenance between goslings hatched 3 d before and 3 d after the peak day of hatch. For goslings hatched 6 d before (-6 d) and 6 d after (+6 d) the peak day of hatch, a significant difference ($p < 0.001$) was found in both variables for 1996 but not for the other 3 years. On average, in 1996, -6 d goslings experienced a daily T_{es} of 5.7 ± 1.0°C (mean ± SE) warmer than +6 d goslings. Thus, -6 d goslings spent on average 186 ± 15 kJ d^{-1} less than +6 d goslings. Between 0 and 40 d of age, -6 d goslings experienced a mean T_{es} of 6.3°C and spent 3296 kJ for thermoregulation, peak-hatched goslings a T_{es} of 1.7°C and spent 10,788 kJ, and +6 d goslings a T_{es} of 0.6°C and spent 10,931 kJ (Fig. 6).

For all years combined (1994-1997), between 0 and 40 d of age, -6 d goslings spent 8974 kJ for thermoregulation, peak-hatched goslings 9205 kJ, and +6 d goslings 9525 kJ. Thus, on average goslings hatched 6 d before peak hatching allocated 2.5 % less energy into

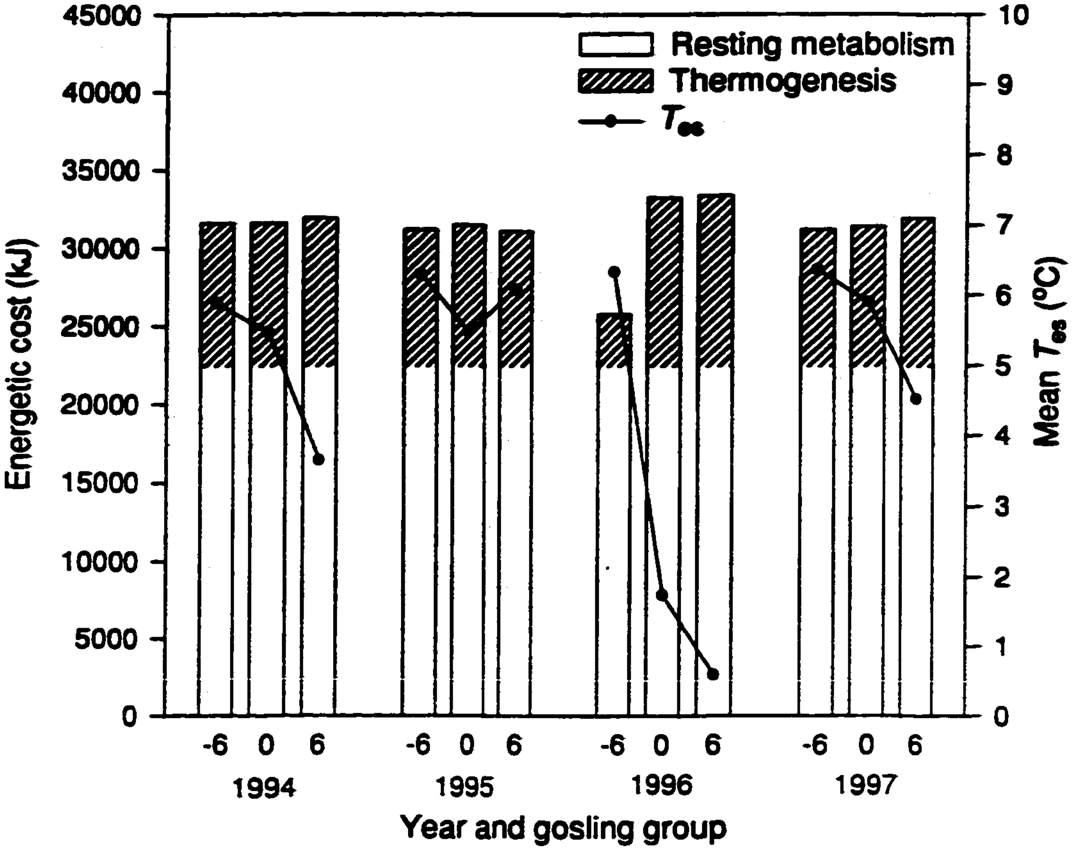

FIG. 6. Total energetic cost of maintenance metabolism between 0 and 40 d of age for goslings hatched 6 d before (- 6), 6 d after (+ 6), and on the peak day of hatch (0) for 1994 to 1997. Dots are mean T_{es} for each group and year.

thermoregulation than peak-hatched goslings whereas those hatched 6 d after peak hatching allocated 3.5 % more energy into thermoregulation.

DISCUSSION

Predictive models for metabolic rate

In this study, we predicted gosling metabolic rate from a regression model that included the heating power of the taxidermic mount, gosling body mass and meteorological variables (T_a, R, and u), *i.e.* our complex mount model. Thus, the predictions obtained using this model were based on field data including measurements from taxidermic mounts which had been calibrated against live animals in the laboratory. Because this method offered the highest r^2 and included field measurements, it appeared to us as the best available estimate for maintenance metabolic rate in Greater Snow Goose goslings under natural conditions.

Another method commonly used for predicting metabolic rate in the field is the biometeorological analysis (Mugaas and King, 1981). To apply this method, we measured in the laboratory the metabolic rates of live goslings exposed to different air temperatures, radiation intensities, and wind speeds, the meteorological variables known to affect the metabolism of homeotherms (Cartar and Morrison, 1997). We subsequently related metabolic rates to prevailing meteorological variables by regression.

This approach was compared to the one that included the heating power of the taxidermic mounts (complex mount model). We found that the metabolic rates predicted by the two models differed significantly, and that this difference was age-dependent. The determination of which method offers the best predictions would require measurements of the metabolic rate of live goslings in the field, a very complex task. Looking at extreme thermal conditions did not help us in discriminating between the performance of the two methods. However, we suggest that the biometeorological analysis was incomplete because it was based on a few discrete meteorological variables and hence did not incorporate all interactions between goslings and their environment. On the other hand, the complex mount model included measurements from taxidermic mounts exposed to natural environments which possibly incorporated more interactions in the exchange of heat between an animal and its microenvironment.

Our conclusion is somewhat different from that of Cartar and Morrison (1997) who compared metabolic rates for the Red Knot (*Calidris canutus*) predicted by a biophysical model (a series of equations based on simple meteorological and morphological variables) with estimates produced using heated taxidermic mounts (Wiersma and Piersma, 1994). They found that the metabolic rates predicted by the two methods were similar and highly correlated although the estimates from the biophysical model were slightly lower (mean: 2.09 W) than those obtained from the taxidermic mounts (mean: 2.19 W). They concluded that their biophysical prediction of metabolic rate for the Red Knot was similar to that predicted by an equation based on a heated taxidermic mount (Cartar and Morrison, 1997).

Our data also show that heating power measurements of taxidermic mounts in the field are sufficient by themselves to obtain a quick approximation of gosling metabolic rate by using a ratio of 1.3 between gosling metabolic rate and mount heating power. If T_{es} calculations are performed, a more refined approximation is available in the form of a regression equation relating T_{es} to the ratio $(\hat{M} / \hat{P})$ which is valid at T_{es} below 15°C. While simple, these two methods offer only crude estimates of gosling metabolic rate and become less valid as T_{es} increase above 15°C.

Thermal environment

Despite the continuous daylight conditions prevailing from early May to early August in our study area, strong daily variations were observed in most weather variables. The very low angle of elevation of the sun at night was responsible for the large daily variations observed in T_a and R, and to a lesser extent in u, which resulted in large oscillations in standard operative temperature (T_{es}). The difference between mean daytime and nighttime T_{es} was almost 10°C, despite a mean daily difference of only 1.8°C in T_a. Similar variations were also observed in other field studies of the thermal environment of birds in polar regions (Chappell *et al.*, 1990; Piersma and Morrison, 1994).

Between 0 and 40 d age, the average T_a experienced by peak-hatched goslings (5.7°C) is a good estimate of their average thermal environment (T_{es} of 5.3°C for the same period). However, daily variation in air temperature (1.8°C) is a very poor estimate of the daily variation in the thermal environment experienced by goslings (daily variation in T_{es} of 9.9°C). Hence, this demonstrates the importance of using taxidermic mounts in the field to obtain T_{es} as this variable offers a much better evaluation of the thermal environment of an animal.

As previously reported by Fortin (1995), the difference between T_{es} and T_a systematically varied according to the period of the day, T_{es} being significantly higher than T_a during the day and lower at night. The same differences were reported by Mugaas and King (1981) in their study of the thermal environment of the Black-billed Magpie (*Pica pica hudsonia*). These results indicate the importance of wind and radiation in determining T_{es}. During the day, the radiative heat gain from the surroundings is more important than the convective heat loss through wind in the thermal budget of goslings while at night the opposite prevails. These observations suggest that goslings' allocation of energy may be different between day and night. At night, more energy must be allocated to thermoregulation while during the day more energy may be available for other needs such as growth.

The Arctic is a cold environment for growing goslings, as shown by an average summer T_{es} (5.3°C) well below their lower critical temperature of about 15°C (Ratté, 1998). However, the radiative heat gain from the sun during the day is of major importance in the energy budget of goslings as it can considerably increase T_{es}. On clear days, when radiation intensities were at their maximum (above 600 W m^{-2}), T_{es} as high as 38°C (30-min average) have been observed in this study. Under such conditions, Fortin (1995) observed signs of heat stress like panting and intensive water consumption in Greater Snow Goose goslings. Klaassen (1994) found similarly elevated operative temperatures (reaching up to 34°C on sunny days around noon) for Antarctic Tern (*Sterna vittata*) chicks on King George Island.

Energetic cost of thermoregulation

We found that the proportion of the energy budget that goslings allocate to thermoregulation declined with age between hatch and 40 d. Thus, younger goslings have higher thermoregulatory costs even if they benefit from milder weather conditions than older goslings. Their small size must be partly responsible for these elevated costs. Younger goslings lose heat more rapidly because of their greater surface/volume ratio, and their heat production capacity is presumably limited by the small size of their flight muscles which are still undeveloped (Lesage and Gauthier, 1997). In a comparative study on growth and energetics of tern chicks of several species, Klaassen (1994) found that mass-specific thermoregulatory costs were highest at hatching and decreased sharply afterwards, stabilizing at around 10 d of age. This result is consistent with our finding that younger chicks face higher thermoregulatory costs.

On average, regulatory thermogenesis represented about 30 % of maintenance metabolic rate of peak-hatched goslings between 0 and 40 d of age. Maintenance metabolic rate is defined as basal metabolic rate plus cost of thermoregulation. In this study, as previously mentioned in the methods, we used resting metabolic rate (*RMR*) as an estimate of basal metabolic rate even though it was measured in growing goslings. Drent *et al.* (1992) who summarized chicks energy budgets for 28 species of birds reported that, for the four energy budgets in which thermoregulatory costs could be separated from activity, the cost of temperature regulation accounted for only 10 % of the total expenditure under field conditions. These authors also reported that, on average, half of the total expenditure was accounted by basal metabolism (excluding the cost of biosynthesis) such that maintenance cost represented 60 % of total energy budget.

This result lies at the upper end of the range reported by Walsberg (1983b) who pointed out that 40-60 % of the total expenditure in adult birds is allocated to maintenance. Hence, if we assume a value of 60 % for Greater Snow Goose goslings, the cost of thermoregulation would represent 18 % of the energy budget. In comparison, it was estimated that the energy required for thermoregulation accounted for 16 % of total energy requirements in Arctic Tern (*Sterna paradisaea*) chicks (Klaassen *et al.*, 1989a and b). In adult White-crowned Sparrows (*Zonotrichia leucophrys*), thermostatic demand during the breeding season in montane and subarctic sites ranged from 14 to 21 % of total daily energy expenditure (Mahoney, 1976 cited in Ettinger and King, 1980).

The total cost of thermoregulation during growth correlated well with T_{es}, being lower in years (9153 kJ in 1994, 8998 kJ in 1995, and 8925 kJ in 1997) other than 1996 (10,788 kJ) which was the coldest ($T_a = 4.4°C$), the cloudiest ($R = 161$ W m^{-2}), and the windiest ($u = 2.0$ m s^{-1}) of all four years investigated. Piersma and Morrison (1994), who measured the daily energy expenditure of Ruddy Turnstones (*Arenaria interpres*) breeding in the High Arctic using the doubly-labeled water technique, also found that energy expenditure correlated well with T_{es}.

Our estimate of the proportion of the energy budget that goslings must allocate to thermoregulation probably represents a maximum, because thermoregulatory requirements may be partly compensated by heat production from sources other than cold-induced thermogenesis. Goslings are active for about 70 % of the day (Poirier, 1992), and hence, thermogenic costs can possibly be reduced by heat production associated with activity. The heat increment of feeding is another potentially important source of heat that can partly compensate for cold thermogenesis. However, Ratté (1998) who measured oxygen consumption of goslings during periods of up to 8 h after a meal, failed to find any significant decline in metabolic rate. In addition, behavioral thermoregulation is used by Greater Snow Goose goslings to reduce the energy allocated to thermoregulation (Fortin, 1995). Goslings use both parental brooding and huddling in their rest phase, which accounts for up to 30% of the total activity budget (Poirier, 1992). Goslings may also orient themselves favorably with respect to wind and sun to minimize their heat loss through convection and maximize the heat gain by radiation (Fortin, 1995).

Effect of hatching date

Significant differences in T_{es} and maintenance metabolic rate were found between goslings hatched 6 d before and after peak hatching only in 1996. Although T_{es} experienced by -6 d goslings between 0 and 40 d of age was comparable to that of other years (6.3°C in 1996, 5.9°C in 1994, 6.3°C in 1995, and 6.4°C in 1997), their energy cost of maintenance was very much lower (3296 kJ in 1996, 9138 kJ in 1994, 8705 kJ in 1995, and 8727 kJ in 1997). However, the average T_{es} experienced by -6 d goslings in 1996 was not representative of the entire growth period, as the average value was elevated by a warm spell that lasted the first six days of the period (mean T_{es} for days 0-5 = 15.0°C, and for days 6-40 = 4.8°C). Hence, the energy savings associated with this warm spell explain the very low maintenance cost for -6 d goslings in 1996.

No differences in T_{es} and maintenance metabolic rate were found between goslings hatched 6 d before and after peak hatching in the other three years, although trends existed in 1994 and 1997. For these two years, we could not detect significant differences because of the large variability in daily cost of maintenance throughout the summer (daily cost ranging from around 350 kJ at hatch to above 1100 kJ at 40 d of age). However, by pooling the four years together, we found that goslings hatched 6 d after the peak allocated about 6 % more energy to thermoregulation than those hatched 6 d before the peak. This was likely a consequence of the seasonal decline in the thermal environment that goslings experienced between 0 and 40 d of age. Although small, these differences in the proportion of energy that goslings hatched at different dates must allocate to thermoregulation can possibly contribute to the slower growth rate observed in late-hatched goslings (Lepage *et al.*, 1998). The energy allocation hypothesis predicts a reduced growth for birds with higher thermoregulatory costs (Olson, 1992). Moreover, the difference in the allocation of energy to thermoregulation between early- and late-hatched goslings could be amplified by the seasonal decline observed in the availability and/or quality of food (Cooch *et al.*, 1991b; Sedinger and Flint, 1991; Lindholm *et al.*, 1994; Lepage *et al.*, 1998). However, we cannot yet evaluate this effect on gosling growth because we lack a complete energy budget of goslings.

The differences that we found between -6 and + 6 d goslings were much smaller than those reported in the preliminary analysis of Fortin (1995). Using weather data from a nearby weather station for the period 1989-1994, Fortin (1995) concluded that goslings hatched 3 d after the peak could potentially allocate 22 % more energy to thermoregulation than those hatched 3 d before the peak. We believe that this percentage was overestimated due to several faulty assumptions. For example, T_{es} values were from taxidermic mounts not calibrated on live goslings, all experiments with the mounts were performed only in the laboratory, and metabolic rate predictions were based on a small number of preliminary experiments on live goslings (Thibault, Larochelle, and Gauthier, *unpublished data*).

CONCLUSION

In this study, we estimated that for growing goslings of the Greater Snow Goose, 30 % of the energy required for maintenance had to be allocated to thermoregulation. This proportion might appear low for chicks living in such extreme environment as the high Arctic although it is comparable to that of other studies on birds breeding in polar regions. Goslings have very high growth rates (Lesage and Gauthier, 1997) and as a result they maintain high metabolic rates and produce a lot of heat. Hence, even if a rapid growth imposes several constraints, it may be advantageous in terms of thermoregulation by diminishing the amount of energy required for cold-induced thermogenesis. Finally, to complete our knowledge of the energy budget of goslings, we would need estimates of the metabolic costs associated with the different activities that goslings engage in, as reported for adults (Thibault, 1994).

CHAPITRE IV

CONCLUSION GÉNÉRALE

La première partie de notre étude était consacrée à la validation de nos instruments de mesure, soit quatre mannequins taxidermiques d'oisons de la Grande Oie des neiges représentatifs de quatre âges différents. La réalisation de cette étape essentielle à la poursuite de notre projet de recherche a été motivée en partie par l'article de Walsberg et Wolf, paru en 1996, qui discréditait l'utilisation de mannequins taxidermiques comme outil d'évaluation de l'environnement thermique des animaux en milieu naturel. Ces auteurs soutenaient que, en général, l'utilisation de mannequins taxidermiques violait deux principes fondamentaux de l'échantillonnage biologique. La violation du premier de ces principes se résume au fait que la plupart des études sont réalisées avec un seul exemplaire de mannequin taxidermique, et qu'ainsi, elles négligent l'importance de la variabilité biologique. Le deuxième de ces principes concerne la calibration des mannequins taxidermiques qui devrait être effectuée pour un ensemble de conditions représentatives du milieu naturel. À ce sujet, Walsberg et Wolf rapportent que peu d'études ont comparé la réponse des mannequins à celle d'animaux vivants exposés à différentes conditions thermiques. De telles calibrations, rarement effectuées en présence de vent, n'auraient jamais été réalisées en présence de rayonnement (Walsberg et Wolf, 1996).

À la lumière de ces critiques, nous avons décidé de calibrer nos mannequins taxidermiques avec des oisons vivants dans différentes conditions météorologiques représentatives de leur milieu naturel, le Haut Arctique. Pour ce faire, les mannequins ont été exposés, en laboratoire, à différentes températures ambiantes, intensités d'irradiance et vitesses de vent, de même qu'à certaines combinaisons de ces variables. Ces mêmes conditions météorologiques ont été utilisées lors de mesures de consommation d'oxygène chez des oisons vivants. Sept oisons, entre les âges de 1 et 40 d, ont été exposés à différentes températures ambiantes (Ratté, 1998) alors que, pour les combinaisons de vent et de rayonnement, huit oisons ont été utilisés entre 4 et 21 d (Rioux, en préparation). Avec ces nombreuses calibrations, les mannequins taxidermiques utilisés dans l'étude respectent le deuxième principe de l'échantillonnage biologique énoncé plus haut. Quant au premier principe, notre intention initiale était de construire trois répliques de chacun des mannequins taxidermiques que nous possédions déjà. Mais, malheureusement, des difficultés techniques ont empêché la réalisation de cet objectif. Par contre, en calibrant les mannequins avec plusieurs oisons différents, ils deviennent représentatifs d'une variabilité biologique que l'on aurait possiblement retrouvée chez plusieurs exemplaires d'un même mannequin taxidermique.

Dans la première partie de notre étude, nous avons de plus démontré que les mannequins taxidermiques utilisés ne s'étaient pas détériorés depuis leur construction par Fortin (1995), et ce malgré les nombreuses manipulations qu'ils ont subies (dont deux voyages dans l'Arctique). La conductance des mannequins n'a pas été modifée de façon significative depuis leur fabrication. De même, leurs réponses à des variations de la température ambiante sont demeurées constantes.

Nous avons aussi comparé la conductance des mannequins à celle d'oisons vivants exposés à différentes températures ambiantes. En milieu froid, c'est-à-dire pour des températures ambiantes sous les 15°C, la conductance des mannequins est similaire à celle d'oisons vivants. Pourtant, à mesure que la température ambiante augmente, la conductance des oisons augmente aussi, et ce de façon importante. Les mannequins taxidermiques, quant à eux, conservent une conductance constante puisqu'ils ne peuvent la modifier. En effet, les mannequins ne peuvent reproduire les réactions typiques du stress thermique des oisons vivants, comme la ptiloérection et la vasodilatation. On peut donc considérer que lorsque la température ambiante ne dépasse pas la température critique inférieure des oisons (qui se situe autour de 15°C pour des oisons de 2-40 d, Ratté 1998), la réponse thermique des mannequins taxidermiques représente bien celle d'oisons vivants. Ainsi, les mannequins taxidermiques sont de très bon outils pour évaluer les coûts de la thermorégulation chez des animaux vivant en milieu froid.

À l'île Bylot (73°08'N-80°00'W), où l'on retrouve la plus forte densité d'oiseaux nicheurs de la Grande Oie des neiges (Bellrose, 1980), la température de l'air dépasse rarement les 15°C (c'est arrivé une fois entre 1994 et 1997 lors d'une vague de chaleur de quatre jours en juillet 1994). Les mannequins taxidermiques peuvent donc être utilisés sans crainte dans un tel environnement. Il est toutefois important de prendre en considération le fait que les mannequins taxidermiques et les animaux vivants réagissent aux fluctuations de l'ensemble des variables météorologiques (représenté par la T_{es}) et pas seulement à celles de la température de l'air.

Un autre des objectifs spécifiques de la première partie de notre étude était d'évaluer notre capacité à reproduire, en laboratoire, des environnements thermiques naturels. Pour ce faire, nous avons comparé les résultats de la calibration météorologique effectuée en laboratoire avec ceux que nous avons obtenus des expériences réalisées sur le terrain avec les mêmes mannequins taxidermiques. Nous avons ainsi observé que les effets du vent peuvent être reproduits efficacement en laboratoire mais que l'ensemble du rayonnement en provenance d'un environnement naturel est beaucoup plus difficile à recréer à partir d'une simple lampe. De plus, nous avons observé que l'utilisation en laboratoire d'un angle réaliste d'élévation du rayonnement (15° dans cette étude) rapprochait légèrement les résultats de laboratoire de ceux de terrain mais que cette mesure était largement insuffisante pour recréer les effets du rayonnement naturel.

Les calibrations en présence d'une source de rayonnement simulant le soleil ont aussi permis de mettre en évidence un phénomène intéressant. Les mannequins et les oisons répondent similairement, quel que soit leur âge, à une augmentation de la vitesse du vent, ce qui n'est pas le cas pour une augmentation de l'intensité du rayonnement. En présence de rayonnement, les mannequins diminuent leur consommation d'énergie électrique en fonction de l'intensité du rayonnement tandis que les oisons maintiennent plus ou moins leur métabolisme constant. Par exemple, dans le noir à 10°C, les oisons entre 7 et 15 d ont un métabolisme moyen de 5,3 W. À la même température ambiante mais exposés au rayonnement, ils maintiennent un métabolisme moyen de 6 W à 200 W m^{-2}, de 5,6 W à 300 W m^{-2} et de 5 W à 500 W m^{-2}(Rioux, en préparation). Il apparaît ainsi que les oisons n'utilisent pas nécessairement la chaleur rayonnante pour diminuer leur production de chaleur métabolique et ainsi économiser de l'énergie.

La deuxième partie de notre étude a été réalisée à partir de données obtenues des expériences avec les mannequins taxidermiques placés en milieu naturel, à l'île Bylot dans le territoire du Nunavut. L'objectif principal de cette partie de l'étude était de mesurer les coûts énergétiques de la thermorégulation chez les jeunes de la Grande Oie des neiges.

Deux équations de prédiction du taux métabolique des oisons, l'une issue d'un modèle complexe impliquant les mannequins et l'autre de l'analyse biométéorologique, avaient été établies à partir des expériences réalisées en laboratoire à la fois avec les mannequins taxidermiques et les oisons vivants ainsi que celles réalisées sur le terrain. En utilisant, dans ces deux équations, les données de terrain provenant des expériences avec les mannequins taxidermiques ainsi que les données météorologiques, nous avons obtenu des différences significatives entre les valeurs de taux métabolique prédites par les deux méthodes. Puisque l'analyse biométéorologique prédit le taux métabolique des oisons à partir des mêmes variables que le modèle complexe mais avec le taux de chauffage des mannequins en moins, nous croyons que cette méthode est incomplète. En effet, en incluant des mesures du taux de chauffage des mannequins exposés à des environnements thermiques naturels, le modèle complexe incorpore un plus grand nombre d'interactions existant dans les échanges de chaleur entre un animal et son microenvironnement.

L'île Bylot constitue un environnement de croissance relativement froid pour les jeunes de la Grande Oie des neiges. La température opérante standard (T_{es}) mesurée dans le microenvironnement des oisons a été en moyenne de 5,3°C pour les saisons estivales (du 6 juillet au 15 août) de 1994 à 1997. Cette T_{es} se situe bien en-dessous de la température critique inférieure des oisons de 2-40 d qui est d'environ 15°C (Ratté, 1998). De plus, malgré la présence ininterrompue du soleil jusqu'au début août, il existe des variations journalières importantes de la T_{es} qui peuvent causer des différences entre le jour et la nuit dans la quantité d'énergie que les oisons doivent allouer à la thermorégulation. De telles variations journalières ont aussi été observées dans d'autres études relatives à l'évaluation de l'environnement thermique d'espèces d'oiseaux nichant en régions polaires (*e.g.* Chappell *et al.*, 1990; Piersma et Morrison, 1994).

Ainsi, l'environnement froid de l'Arctique impose des contraintes thermiques majeures aux oisons de la Grande Oie des neiges. Dans cette étude, nous avons estimé que pour les oisons entre les âges de 0 et 40 d, environ 30 % de l'énergie allouée au métabolisme de maintien devait être consacrée à la thermorégulation. De plus, cette proportion augmente lors des années plus froides, comme ce fut le cas en 1996. Walsberg (1983b) a estimé que chez les oiseaux adultes, les coûts énergétiques associés au métabolisme de maintien peuvent accaparer de 40 à 60 % du budget énergétique total. Si cet estimé était valide pour les oisons de la Grande Oie des neiges, cela impliquerait que les coûts énergétiques associés à la thermorégulation pourraient représenter de 12 à 18 % du bilan énergétique total des oisons. Un pourcentage similaire a été obtenu par Klaassen *et al.* (1989a et b). Ces derniers ont estimé les coûts associés à la thermorégulation à 16 % du bilan énergétique total des jeunes de la Sterne Arctique (*Sterna paradisaea*).

L'allocation à la thermorégulation de 30 % de l'énergie requise par le métabolisme de maintien représente probablement un estimé maximum. En effet, la chaleur perdue au profit de l'environnement peut être remplacée en partie par de la chaleur provenant de sources autres que la thermogenèse de régulation. Les oisons étant actifs environ 70 % de la journée (Poirier, 1992), l'importante production de chaleur associée à l'activité peut être l'une de ces sources. De plus, la thermorégulation comportementale, via la couvaison parentale ou le blottissement thermique, est utilisée par les oisons de la Grande Oie des neiges pour diminuer le plus possible les pertes de chaleur à l'environnement (Fortin, 1995). Les oisons vont aussi, dans certaines conditions, s'orienter par rapport au vent et au rayonnement solaire afin de diminuer leurs pertes convectives et augmenter leurs gains radiatifs (Fortin, 1995).

Finalement, nous avons observé une détérioration saisonnière significative de l'environnement thermique des oisons. Ainsi, les oisons éclos tardivement doivent faire face à un environnment thermique plus défavorable que ceux qui ont éclos plus tôt en cours d'été. Pourtant, seule l'année 1996 a révélé des différences significatives dans la T_{es} journalière moyenne ainsi que dans la dépense journalière d'énergie associée au métabolisme de maintien pour des oisons éclos 6 d avant et après le pic d'éclosion. Nous avons tout de même estimé qu'en moyenne, pour les saisons estivales 1994-1997, les oisons éclos 6 d après le pic d'éclosion ont dû allouer environ 6 % plus d'énergie à la thermorégulation que ceux qui ont éclos 13 d auparavant, *i.e.* 6 d avant le pic d'éclosion.

Malgré que les différences de T_{es} et de dépense d'énergie observées entre des oisons éclos 6 d avant et après le pic d'éclosion soient faibles, il est tout à fait possible qu'elles contribuent à la diminution du taux de croissance observé chez les oisons éclos tardivement (Lepage *et al.*, 1998). En effet, lorsque l'accès à l'énergie est limité, l'hypothèse de l'allocation de l'énergie prédit un taux de croissance plus faible aux oiseaux ayant des coûts de thermorégulation plus élevés (Olson, 1992). De plus, cette différence dans l'allocation de l'énergie à la thermorégulation entre les oisons éclos très tôt et ceux éclos tardivement pourrait être amplifiée par le déclin saisonnier observé dans la disponibilité ou la qualité de la nourriture (Cooch *et al.*, 1991b; Sedinger and Flint, 1991; Lindholm *et al.*, 1994; Lepage *et al.*, 1998).

En terminant, rappelons que cette étude nous a permis d'établir un bilan énergétique partiel des oisons de la Grande Oie des neiges en mesurant les coûts associés à la thermorégulation. Évidemment, l'étude de Ratté (1998) avait déjà permis d'évaluer les coûts énergétiques associés au métabolisme de repos des oisons (ce qui incluait la croissance). Toutefois, nous ne sommes pas encore en mesure de séparer l'entretien basal et le métabolisme de croissance. De plus, le bilan énergétique des oisons de la Grande Oie des neiges demeure incomplet, puisque nous ne connaissons pas encore la quantité d'énergie allouée par les jeunes aux différentes activités quotidiennes.

ANNEXES

ANNEXE A

Mathematical symbols and definitions

A_b : Body surface area (m^2)
β : Regression coefficient
E : Evaporative heat dissipation (W)
G : Overall thermal conductance of a live animal (W °C^{-1})
K_e : Overall thermal conductance of a whole animal or a taxidermic mount in a complex environment (W °C^{-1})
K_{es} : Overall thermal conductance of a whole animal or taxidermic mount in a reference environment (W °C^{-1})
M : Metabolic heat production or rate (W)
$\hat{M}$: Predicted metabolic rate (W)
m_b : Body mass (g or kg)
P : Electrical or heating power (W)
$\hat{P}$: Predicted heating power (W)
R : Radiation intensity (W m^{-2})
RMR : Resting metabolic rate (W)
T_a : Air temperature (°C)
T_b : Body temperature (°C)
T_e : Operative temperature (°C)
T_{es} : Standard operative temperature (°C)
T_{lc} : Lower critical temperature (°C)
T_{uc} : Upper critical temperature (°C)
u : Wind speed (m s^{-1})

ANNEXE B

Mean ± SE of air temperature (T_a), radiation intensity (R), wind speed (u) at gosling height, 10 cm above the ground, and standard operative temperature (T_{es}; calculated as in Chapter 3) for peak-hatched goslings between 0 and 40 d of age according to the period of the day (daytime 6h00-18h00, $n = 41$; nighttime 18h00-6h00, $n = 40$; whole day, $n = 41$). Data is from Bylot Island weather station.

Year	Period	T_a (°C)	R (W m^{-2})	u (m s^{-1})	T_{es} (°C)
1994	Whole day	6.0 ± 0.5	184 ± 12	1.7 ± 0.1	5.5 ± 1.2
	Daytime	7.2 ± 0.6	280 ± 17	2.0 ± 0.2	9.3 ± 1.5
	Nighttime	4.9 ± 0.5	87 ± 9	1.4 ± 0.1	1.6 ± 1.0
1995	Whole day	5.8 ± 0.2	178 ± 10	1.4 ± 0.1	6.2 ± 0.7
	Daytime	6.7 ± 0.3	296 ± 17	1.5 ± 0.1	11.5 ± 1.0
	Nighttime	5.0 ± 0.3	62 ± 5	1.3 ± 0.1	0.9 ± 0.6
1996	Whole day	4.4 ± 0.3	161 ± 14	2.0 ± 0.1	1.7 ± 1.1
	Daytime	5.1 ± 0.3	267 ± 24	2.3 ± 0.1	6.1 ± 1.5
	Nighttime	3.8 ± 0.3	56 ± 6	1.8 ± 0.2	-2.6 ± 0.9
1997	Whole day	6.1 ± 0.3	189 ± 12	1.6 ± 0.1	5.9 ± 1.0
	Daytime	7.0 ± 0.3	313 ± 20	1.9 ± 0.1	11.5 ± 1.3
	Nighttime	5.3 ± 0.3	66 ± 6	1.5 ± 0.1	0.3 ± 0.9
All years combined	Whole day	5.7 ± 0.2	184 ± 8	1.6 ± 0.1	5.3 ± 0.8
	Daytime	6.6 ± 0.2	298 ± 11	1.9 ± 0.1	10.3 ± 1.0
	Nighttime	4.8 ± 0.2	71 ± 5	1.4 ± 0.1	0.4 ± 0.6

ANNEXE C

Paired Student *t*-tests to compare averaged T_{es} (as calculated in Chapter 3) and T_a for peak-hatched goslings between 0 and 40 d of age according to the period of the day (daytime 6h00-18h00, nighttime 18h00-6h00, and whole day) within each year from 1994 to 1997 and for all years combined.

Year	**Period**	$T_{es} - T_a$ (°C)				
		Mean	**SE**	n	t	p
1994	Whole day	-0.5	0.8	41	-0.61	0.545
	Daytime	2.2	1.0	41	2.10	0.042
	Nighttime	-3.3	0.7	40	-4.42	0.001
1995	Whole day	0.4	0.7	41	0.50	0.620
	Daytime	4.8	1.0	41	4.95	0.001
	Nighttime	-4.1	0.5	40	-8.03	0.001
1996	Whole day	-2.7	0.9	41	-2.83	0.007
	Daytime	1.0	1.3	41	0.74	0.465
	Nighttime	-6.4	0.8	40	-7.62	0.001
1997	Whole day	-0.2	0.9	41	-0.28	0.783
	Daytime	4.4	1.2	41	3.81	0.001
	Nighttime	-5.0	0.8	40	-6.40	0.001
All years combined	Whole day	-0.4	0.6	41	-0.58	0.562
	Daytime	3.6	0.8	41	4.41	0.001
	Nighttime	-4.4	0.5	40	-9.04	0.001

ANNEXE D

Computer program developed in this study to control the datalogger (CR10, Campbell Scientific Inc.). During laboratory and field experiments, voltage pulses were applied to the taxidermic mounts via relays driven by a datalogger programmed to act as a time-proportional controller.

```
*    1     Table 1 Programs
 01: 0.5    Sec. Execution Interval

01:  P30     Z=F
 01: 40      F
 02: 00      Exponent of 10
 03: 31      Z Loc : zone inferieure de seuil 1

02:  P30     Z=F
 01: 40.2    F
 02: 00      Exponent of 10
 03: 32      Z Loc : zone inferieure de seuil 2

03:  P30     Z=F
 01: 40.4    F
 02: 00      Exponent of 10
 03: 33      Z Loc : zone inferieure de seuil 3

04:  P30     Z=F
 01: 40.6    F
 02: 00      Exponent of 10
 03: 35      Z Loc : zone superieure de seuil 3

05:  P30     Z=F
 01: 40.8    F
 02: 00      Exponent of 10
 03: 36      Z Loc : zone superieure de seuil 2

06:  P30     Z=F
 01: 41      F
 02: 00      Exponent of 10
 03: 37      Z Loc : zone superieure de seuil 1
```

```
07: P30      Z=F
 01: 30      F
 02: 00      Exponent of 10
 03: 38      Z Loc : nombre de pas par cycle

08: P30      Z=F
 01: 210     F
 02: 00      Exponent of 10
 03: 39      Z Loc : nombre de pas par periode

09: P32      Z=Z+1
 01: 40      Z Loc : compteur de pas par cycle +1

10: P32      Z=Z+1
 01: 41      Z Loc : compteur de pas par periode +1

11: P1       Volt (SE)
 01: 4       Reps
 02: 5       2500 mV slow Range
 03: 1       IN Chan
 04: 1       Loc :
 05: 0.006   Mult
 06: 0.0000  Offset

12: P1       Volt (SE)
 01: 4       Reps
 02: 5       2500 mV slow Range
 03: 5       IN Chan
 04: 5       Loc :
 05: 0.001   Mult
 06: 0.0000  Offset

13: P55      Polynomial
 01: 4       Reps
 02: 5       X Loc
 03: 5       F(X) Loc :
 04: 0.1024  C0
 05: -267.89 C1
 06: 2239.8  C2
 07: -4525.6 C3
 08: 3654.6  C4
 09: -1074.5 C5
```

```
14:  P91     If Flag/Port
 01: 21     Do if flag 1 is low
 02: 30     Then Do

15:  P89     If X<=>F
 01: 5      X Loc
 02: 3      >=
 03: 28     F
 04: 30     Then Do

16:  P89     If X<=>F
 01: 5      X Loc
 02: 4      <
 03: 38     F
 04: 30     Then Do

17:  P86     Do
 01: 11     Set high Flag 1

18:  P95     End

19:  P95     End Tb entre 28 et 38

20:  P95     End flag 1 low

21:  P91     If Flag/Port
 01: 22     Do if flag 2 is low
 02: 30     Then Do

22:  P89     If X<=>F
 01: 6      X Loc
 02: 3      >=
 03: 28     F
 04: 30     Then Do

23:  P89     If X<=>F
 01: 6      X Loc
 02: 4      <
 03: 38     F
 04: 30     Then Do
```

```
24:  P86      Do
 01: 12      Set high Flag 2

25:  P95      End

26:  P95      End Tb entre 28 et 38

27:  P95      End flag 2 low

28:  P91      If Flag/Port
 01: 23      Do if flag 3 is low
 02: 30      Then Do

29:  P89      If X<=>F
 01: 7       X Loc
 02: 3       >=
 03: 28      F
 04: 30      Then Do

30:  P89      If X<=>F
 01: 7       X Loc
 02: 4       <
 03: 38      F
 04: 30      Then Do

31:  P86      Do
 01: 13      Set high Flag 3

32:  P95      End

33:  P95      End Tb entre 28 et 38

34:  P95      End flag 3 low

35:  P91      If Flag/Port
 01: 24      Do if flag 4 is low
 02: 30      Then Do

36:  P89      If X<=>F
 01: 8       X Loc
 02: 3       >=
 03: 28      F
```

```
 04: 30     Then Do

37:  P89     If X<=>F
 01: 8      X Loc
 02: 4      <
 03: 38     F
 04: 30     Then Do

38:  P86     Do
 01: 14     Set high Flag 4

39:  P95     End

40:  P95     End Tb entre 28 et 38

41:  P95     End flag 4 low

42:  P91     If Flag/Port
 01: 11     Do if flag 1 is high
 02: 30     Then Do

43:  P32     Z=Z+1
 01: 22     Z Loc : +1 au compteur de tours entre 28 et 38

44:  P89     If X<=>F
 01: 5      X Loc
 02: 3      >=
 03: 38     F
 04: 30     Then Do

45:  P86     Do
 01: 21     Set low Flag 1

46:  P95     End Tb depasse 38

47:  P95     End flag 1 high

48:  P91     If Flag/Port
 01: 12     Do if flag 2 is high
 02: 30     Then Do

49:  P32     Z=Z+1
```

```
 01: 23    Z Loc : +1 au compteur de tours entre 28 et 38

50: P89    If X<=>F
 01: 6     X Loc
 02: 3     >=
 03: 38    F
 04: 30    Then Do

51: P86    Do
 01: 22    Set low Flag 2

52: P95    End Tb depasse 38

53: P95    End flag 2 high

54: P91    If Flag/Port
 01: 13    Do if flag 3 is high
 02: 30    Then Do

55: P32    Z=Z+1
 01: 24    Z Loc : +1 au compteur de tours entre 28 et 38

56: P89    If X<=>F
 01: 7     X Loc
 02: 3     >=
 03: 38    F
 04: 30    Then Do

57: P86    Do
 01: 23    Set low Flag 3

58: P95    End Tb depasse 38

59: P95    End flag 3 high

60: P91    If Flag/Port
 01: 14    Do if flag 4 is high
 02: 30    Then Do

61: P32    Z=Z+1
 01: 25    Z Loc : +1 au compteur de tours entre 28 et 38
```

```
62:  P89      If X<=>F
 01: 8       X Loc
 02: 3       >=
 03: 38      F
 04: 30      Then Do

63:  P86      Do
 01: 24      Set low Flag 4

64:  P95      End Tb depasse 38

65:  P95      End flag 4 high

66:  P87      Beginning of Loop
 01: 0       Delay
 02: 4       Loop Count

67:  P89      If X<=>F
 01: 5--     X Loc
 02: 3       >=
 03: 38      F
 04: 30      Then Do

68:  P89      If X<=>F
 01: 18--    X Loc
 02: 1       =
 03: 0       F
 04: 30      Then Do

69:  P37      Z=X*F
 01: 22--    X Loc
 02: 0.05    F
 03: 22--    Z Loc : compteur de tours en sec.

70:  P89      If X<=>F
 01: 22--    X Loc
 02: 4       <
 03: 50      F
 04: 30      Then Do

71:  P30      Z=F
 01: 16      F
```

```
  02: 00     Exponent of 10
  03: 18--   Z Loc : met chauffage de depart a 16

72:  P94     Else

73:  P89     If X<=>F
  01: 22--   X Loc
  02: 4      <
  03: 150    F
  04: 30     Then Do

74:  P55     Polynomial
  01: 1      Rep
  02: 22--   X Loc
  03: 18--   F(X) Loc :
  04: -17.535 C0
  05: 0.6571  C1
  06: -0.0024 C2
  07: 0.0000  C3
  08: 0.0000  C4
  09: 0.0000  C5

75:  P44     Z=FRAC(X)
  01: 18--   X Loc
  02: 26--   Z Loc :

76:  P45     Z=INT(X)
  01: 18--   X Loc
  02: 18--   Z Loc : # entier pour chauffage de depart

77:  P89     If X<=>F
  01: 26--   X Loc
  02: 3      >=
  03: 0.5    F
  04: 30     Then Do

78:  P32     Z=Z+1
  01: 18--   Z Loc : ajoute 1 si fraction depasse 0.5

79:  P95     End

80:  P95     End temps de chauffage entre 50 et 150
```

```
81:  P95     End temps de chauffage moins de 50

82:  P89     If X<=>F
 01: 22--   X Loc
 02: 3      >=
 03: 150     F
 04: 30     Then Do

83:  P30     Z=F
 01: 30     F
 02: 00     Exponent of 10
 03: 18--   Z Loc : met chauffage de depart a 30

84:  P95     End temps de chauffage plus de 150

85:  P95     End 1er passage au dessus de Tb=38

86:  P95     End Tb depasse 38

87:  P95     End fin du loop

88:  P87     Beginning of Loop
 01: 0      Delay
 02: 4      Loop Count

89:  P88     If X<=>Y
 01: 5--    X Loc
 02: 3      >=
 03: 37     Y Loc
 04: 30     Then Do

90:  P30     Z=F
 01: 0      F
 02: 1      Exponent of 10
 03: 14--   Z Loc : si Tsup1 depassee met chauffage a 0

91:  P95     End Tsup1 depassee

92:  P88     If X<=>Y
 01: 5--    X Loc
 02: 4      <
```

```
  03: 37     Y Loc
  04: 30     Then Do

93:  P88     If X<=>Y
  01: 5--    X Loc
  02: 3      >=
  03: 36     Y Loc
  04: 30     Then Do

94:  P37     Z=X*F
  01: 18--   X Loc
  02: 0.7    F
  03: 14--   Z Loc : si Tsup2 depassee met chauffage a 0.7 X taux

95:  P94     Else

96:  P88     If X<=>Y
  01: 5--    X Loc
  02: 3      >=
  03: 35     Y Loc
  04: 30     Then Do

97:  P37     Z=X*F
  01: 18--   X Loc
  02: 0.85   F
  03: 14--   Z Loc : si Tsup3 depassee met chauffage a 0.85 X taux

98:  P95     End Tsup3 depassee

99:  P95     End Tsup2 depassee

100: P95     End sous Tsup1

101: P88     If X<=>Y
  01: 5--    X Loc
  02: 4      <
  03: 37     Y Loc
  04: 30     Then Do

102: P88     If X<=>Y
  01: 5--    X Loc
  02: 3      >=
```

```
 03: 35     Y Loc
 04: 30     Then Do

103: P88     If X<=>Y
 01: 41     X Loc
 02: 1      =
 03: 39     Y Loc
 04: 30     Then Do

104: P32     Z=Z+1
 01: 46--   Z Loc : incremente compteur de sortie de zone sup.

105: P95     End fin d'une periode

106: P95     End Tsup3 depassee

107: P95     End sous Tsup1

108: P88     If X<=>Y
 01: 5--    X Loc
 02: 4      <
 03: 31     Y Loc
 04: 30     Then Do

109: P31     Z=X
 01: 38     X Loc
 02: 14--   Z Loc : si sous Tinf0 met chauffage a 30

110: P95     End sous Tinf0

111: P88     If X<=>Y
 01: 5--    X Loc
 02: 3      >=
 03: 31     Y Loc
 04: 30     Then Do

112: P88     If X<=>Y
 01: 5--    X Loc
 02: 4      <
 03: 32     Y Loc
 04: 30     Then Do
```

```
113: P37     Z=X*F
 01: 18--   X Loc
 02: 1.3    F
 03: 14--   Z Loc : si sous Tinf2 met chauffage a 1.3 X taux

114: P94     Else

115: P88     If X<=>Y
 01: 5--    X Loc
 02: 4      <
 03: 33     Y Loc
 04: 30     Then Do

116: P37     Z=X*F
 01: 18--   X Loc
 02: 1.15   F
 03: 14--   Z Loc : si sous Tinf3 met chauffage a 1.15 X taux

117: P95     End sous Tinf3

118: P95     End sous Tinf2

119: P95     End Tinf1 depassee

120: P88     If X<=>Y
 01: 5--    X Loc
 02: 3      >=
 03: 31     Y Loc
 04: 30     Then Do

121: P88     If X<=>Y
 01: 5--    X Loc
 02: 4      <
 03: 33     Y Loc
 04: 30     Then Do

122: P88     If X<=>Y
 01: 41     X Loc
 02: 1      =
 03: 39     Y Loc
 04: 30     Then Do
```

```
123: P32     Z=Z+1
 01: 42--   Z Loc : incremente compteur de sortie de zone inf.

124: P95     End fin d'une periode

125: P95     End sous Tinf3

126: P95     End Tinf1 depassee

127: P89     If X<=>F
 01: 42--   X Loc
 02: 1      =
 03: 3      F
 04: 30     Then Do

128: P32     Z=Z+1
 01: 18--   Z Loc : augmente chauffage de depart

129: P30     Z=F
 01: 0      F
 02: 1      Exponent of 10
 03: 42--   Z Loc : reset compteur de sortie de zone inf.

130: P30     Z=F
 01: 0      F
 02: 1      Exponent of 10
 03: 46--   Z Loc : reset compteur de sortie de zone sup.

131: P95     End 3 periodes sous la zone

132: P89     If X<=>F
 01: 46--   X Loc
 02: 1      =
 03: 3      F
 04: 30     Then Do

133: P34     Z=X+F
 01: 18--   X Loc
 02: -1     F
 03: 18--   Z Loc : diminue chauffage de depart

134: P30     Z=F
```

```
 01: 0      F
 02: 1      Exponent of 10
 03: 46--   Z Loc : reset compteur de sortie de zone sup.

135: P30    Z=F
 01: 0      F
 02: 1      Exponent of 10
 03: 42--   Z Loc : reset compteur de sortie de zone inf.

136: P95    End 3 periodes au-dessus de la zone

137: P88    If X<=>Y
 01: 18--   X Loc
 02: 3      >=
 03: 38     Y Loc
 04: 30     Then Do

138: P31    Z=X
 01: 38     X Loc
 02: 18--   Z Loc : assure que le chauffage ne depasse pas 30

139: P95    End

140: P89    If X<=>F
 01: 18--   X Loc
 02: 4      <
 03: 0      F
 04: 30     Then Do

141: P30    Z=F
 01: 0      F
 02: 1      Exponent of 10
 03: 18--   Z Loc : assure que le chauffage n'est pas -

142: P95    End

143: P95    End Fin du loop

144: P87    Beginning of Loop
 01: 0      Delay
 02: 4      Loop Count
```

```
145: P88    If X<=>Y ----zone de proportionalite
 01: 5--    X Loc
 02: 4      <
 03: 35     Y Loc
 04: 30     Then Do

146: P88    If X<=>Y
 01: 5--    X Loc
 02: 3      >=
 03: 33     Y Loc
 04: 30     Then Do

147: P31    Z=X
 01: 18--   X Loc
 02: 14--   Z Loc : met chauffage de depart

148: P95    End de la partie superieure de la zone

149: P95    End de la partie inferieure de la zone

150: P88    If X<=>Y
 01: 14--   X Loc
 02: 3      >=
 03: 38     Y Loc
 04: 30     Then Do

151: P31    Z=X
 01: 38     X Loc
 02: 14--   Z Loc : assure que le chauffage ne depasse pas 30

152: P95    End

153: P89    If X<=>F
 01: 14--   X Loc
 02: 4      <
 03: 0      F
 04: 30     Then Do

154: P30    Z=F
 01: 0      F
 02: 1      Exponent of 10
 03: 14--   Z Loc : assure que le chauffage n'est pas -
```

```
155: P95    End

156: P95    End fin du loop

157: P87    Beginning of Loop
 01: 0     Delay
 02: 4     Loop Count

158: P34    Z=X+F
 01: 14--   X Loc
 02: 1     F
 03: 14--   Z Loc : augmente chauffage de un

159: P88    If X<=>Y
 01: 40    X Loc
 02: 4     <
 03: 14--   Y Loc
 04: 30    Then Do

160: P86    Do
 01: 41--   Set high Port 1

161: P94    Else

162: P88    If X<=>Y
 01: 40    X Loc
 02: 3     >=
 03: 14--   Y Loc
 04: 30    Then Do

163: P86    Do
 01: 51--   Set low Port 1

164: P95    End Else ...

165: P95    End chauffe ou pas

166: P34    Z=X+F
 01: 14--   X Loc
 02: -1    F
 03: 14--   Z Loc : rediminue chauffage de un
```

```
167: P95     End fin du loop

168: P88     If X<=>Y
 01: 40     X Loc
 02: 1      =
 03: 38     Y Loc
 04: 30     Then Do

169: P30     Z=F
 01: 0      F
 02: 1      Exponent of 10
 03: 40     Z Loc : remet compteur de pas par cycle a 0

170: P95     End rezero canal 40

171: P88     If X<=>Y
 01: 41     X Loc
 02: 1      =
 03: 39     Y Loc
 04: 30     Then Do

172: P30     Z=F
 01: 0      F
 02: 1      Exponent of 10
 03: 41     Z Loc : remet compteur de pas par periode a 0

173: P95     End rezero canal 41

174: P92     If time is
 01: 0000   minutes into a
 02: 5      minute interval
 03: 10     Set high Flag 0 (output)

175: P77     Real Time
 01: 110    Day,Hour-Minute

176: P71     Average
 01: 4      Reps
 02: 1      Loc

177: P71     Average
```

```
  01: 4      Reps
  02: 5      Loc

178: P73     Maximize
  01: 4      Reps
  02: 00     Time Option
  03: 5      Loc

179: P74     Minimize
  01: 4      Reps
  02: 00     Time Option
  03: 5      Loc

180: P       End Table 1


*    2      Table 2 Programs
  01: 10     Sec. Execution Interval

01:  P11     Temp 107 Probe
  01: 2      Reps
  02: 9      IN Chan
  03: 1      Excite all reps w/EXchan 1
  04: 9      Loc : -------temperature-------
  05: 1      Mult
  06: 0.0000  Offset

02:  P12     RH 207 Probe
  01: 1      Rep
  02: 10     IN Chan
  03: 1      Excite all reps w/EXchan 1
  04: 9      Temperature Loc
  05: 10     Loc : -------humidite--------
  06: 1      Mult
  07: 0.0000  Offset

03:  P1      Volt (SE)
  01: 1      Rep
  02: 23     25 mV 60 Hz rejection Range
  03: 11     IN Chan
  04: 11     Loc : -----rayonnement------
  05: 0.807   Mult
```

```
  06: 0.0000  Offset

 04:  P1       Volt (SE)
  01: 1       Rep
  02: 25      2500 mV 60 Hz rejection Range
  03: 12      IN Chan
  04: 12      Loc : vent en mv
  05: 0.001   Mult
  06: 0.0000  Offset

 05:  P55      Polynomial
  01: 1       Rep
  02: 12      X Loc
  03: 12      F(X) Loc : ---- vent en m/s -----
  04: 0.0000  C0
  05: 3.005   C1
  06: 6.5530  C2
  07: 31.666  C3
  08: 0.0000  C4
  09: 0.0000  C5

 06:  P92      If time is
  01: 0000     minutes into a
  02: 5       minute interval
  03: 10      Set high Flag 0 (output)

 07:  P77      Real Time
  01: 110     Day,Hour-Minute

 08:  P71      Average
  01: 4       Reps
  02: 9       Loc

 09:  P       End Table 2


 *    3      Table 3 Subroutines

 01:  P       End Table 3
```

```
*   A      Mode 10 Memory Allocation
 01: 50      Input Locations
 02: 100     Intermediate Locations
 03: 0.0000  Final Storage Area 2


*   C      Mode 12 Security
 01: 0000   LOCK 1
 02: 0000   LOCK 2
 03: 0000   LOCK 3
```

Input Location Assignments (with comments):

```
Key:
T=Table Number
E=Entry Number
L=Location Number

T:  E:  L:
1: 11:  1:  Loc :
1: 12:  5:  Loc :
1: 13:  5:  F(X) Loc :
2:  1:  9:  Loc : -------temperature-------
2:  2: 10:  Loc : -------humidite--------
2:  3: 11:  Loc : -----rayonnement------
2:  4: 12:  Loc : vent en mv
2:  5: 12:  F(X) Loc : ---- vent en m/s -----
1: 90: 14:  Z Loc : si Tsup1 depassee met chauffage a 0
1: 94: 14:  Z Loc : si Tsup2 depassee met chauffage a 0.7 X taux
1: 97: 14:  Z Loc : si Tsup3 depassee met chauffage a 0.85 X taux
1:109: 14:  Z Loc : si sous Tinf0 met chauffage a 30
1:113: 14:  Z Loc : si sous Tinf2 met chauffage a 1.3 X taux
1:116: 14:  Z Loc : si sous Tinf3 met chauffage a 1.15 X taux
1:147: 14:  Z Loc : met chauffage de depart
1:151: 14:  Z Loc : assure que le chauffage ne depasse pas 30
1:154: 14:  Z Loc : assure que le chauffage n'est pas -
1:158: 14:  Z Loc : augmente chauffage de un
1:166: 14:  Z Loc : rediminue chauffage de un
1: 71: 18:  Z Loc : met chauffage de depart a 16
1: 74: 18:  F(X) Loc :
1: 76: 18:  Z Loc : # entier pour chauffage de depart
1: 78: 18:  Z Loc : ajoute 1 si fraction depasse 0.5
```

```
1: 83: 18:  Z Loc : met chauffage de depart a 30
1:128: 18:  Z Loc : augmente chauffage de depart
1:133: 18:  Z Loc : diminue chauffage de depart
1:138: 18:  Z Loc : assure que le chauffage ne depasse pas 30
1:141: 18:  Z Loc : assure que le chauffage n'est pas -
1: 43: 22:  Z Loc : +1 au compteur de tours entre 28 et 38
1: 69: 22:  Z Loc : compteur de tours en sec.
1: 49: 23:  Z Loc : +1 au compteur de tours entre 28 et 38
1: 55: 24:  Z Loc : +1 au compteur de tours entre 28 et 38
1: 61: 25:  Z Loc : +1 au compteur de tours entre 28 et 38
1: 75: 26:  Z Loc :
1:  1: 31:  Z Loc : zone inferieure de seuil 1
1:  2: 32:  Z Loc : zone inferieure de seuil 2
1:  3: 33:  Z Loc : zone inferieure de seuil 3
1:  4: 35:  Z Loc : zone superieure de seuil 3
1:  5: 36:  Z Loc : zone superieure de seuil 2
1:  6: 37:  Z Loc : zone superieure de seuil 1
1:  7: 38:  Z Loc : nombre de pas par cycle
1:  8: 39:  Z Loc : nombre de pas par periode
1:  9: 40:  Z Loc : compteur de pas par cycle +1
1:169: 40:  Z Loc : remet compteur de pas par cycle a 0
1: 10: 41:  Z Loc : compteur de pas par periode +1
1:172: 41:  Z Loc : remet compteur de pas par periode a 0
1:123: 42:  Z Loc : incremente compteur de sortie de zone inf.
1:129: 42:  Z Loc : reset compteur de sortie de zone inf.
1:135: 42:  Z Loc : reset compteur de sortie de zone inf.
1:104: 46:  Z Loc : incremente compteur de sortie de zone sup.
1:130: 46:  Z Loc : reset compteur de sortie de zone sup.
1:134: 46:  Z Loc : reset compteur de sortie de zone sup.
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