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Patron d'incubation et régime thermique des oeufs chez la Grande Oie des neiges *Anser caerulescens atlantica*

Mémoire
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du grade de maître ès sciences (M. Sc.)

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RÉSUMÉ DU MÉMOIRE

La présente étude visait à documenter le patron d'incubation de la Grande Oie des neiges et le régime thermique des oeufs durant l'incubation, ainsi que leurs conséquences sur la synchronie d'éclosion. Les résultats ont été obtenus à partir de la température d'oeufs artificiels ajoutés aux couvées. La présence au nid des femelles et la température des oeufs ont graduellement augmenté au cours de la ponte, bien que le développement embryonnaire ne semblait pas débuter avant que tous les oeufs aient été pondus. Les femelles ont été assises sur leur couvée 91 % de la période d'incubation, quittant 5 ou 6 fois par jour pour s'alimenter. Les absences ont duré en moyenne 23 min et elles ont eu lieu plus souvent l'après-midi que la nuit. Le pourcentage de temps que les femelles passaient à couver a diminué avec la progression de la période d'incubation, bien qu'il ait augmenté une fois l'éclosion amorcée. Les femelles ont quitté leur nid plus souvent lorsque la vitesse du vent était faible et, dans une moindre mesure, lorsque la température de l'air et le rayonnement solaire étaient élevés. Les oeufs ont été incubés à une température moyenne de 37,1 ± 0,1 °C, une valeur élevée pour une espèce d'Anatidae. Lors des absences des femelles, la température des oeufs a chuté d'environ 3 °C, soit un taux de refroidissement de 0,24 ± 0,02 (°C/h)/°C. L'écart d'éclosion entre les jeunes d'un même nid dans la majorité des couvées suivies était inférieur à 24 h. Ceci suggère que le développement embryonnaire à l'intérieur d'une couvée était homogène et que donc la présence de la femelle sur ses oeufs lors de la ponte ne représente pas une incubation active.

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THESIS ABSTRACT

The present study was designed to document Greater Snow Goose incubation pattern, eggs thermal regime during the incubation period and their consequences on hatching synchrony. Results were inferred from variations in temperature recorded by artificial eggs added to clutches. Female nest attentiveness and egg temperature increased gradually during the laying period, although embryonic development did not seem to start until clutch completion. Females sat on their clutch 91 % of the incubation period, leaving the nest to feed 5 or 6 times per day. Recesses averaged 23 min and were initiated more often during the afternoon than at night. Nest attentiveness decreased with the progression of the incubation period, although it rapidly increased with the onset of hatching. Females left the nest more often when wind velocity was low and, to a smaller extent, when air temperature and solar radiation were high. Eggs were incubated at 37.1 ± 0.1 °C and eggs dropped 3 °C when the incubating parent left the nest, for a cooling rate of 0.24 ± 0.02 (°C/h)/°C. Young hatched less than 24 h apart in most clutches monitored. This indicates that embryonic development is rather uniform inside a clutch and that female presence on the eggs during laying does not provide effective incubation.

AVANT-PROPOS

Ce mémoire comprend 5 chapitres et 4 annexes. Le chapitre 1 offre au lecteur un résumé des connaissances actuelles sur la période d'incubation chez les oiseaux. Les chapitres 2 et 3 sont rédigés en anglais, sous forme d'articles scientifiques qui seront soumis pour publication. Le chapitre 2 regroupe les résultats obtenus lors de la période de ponte ainsi que le régime thermique des oeufs durant l'incubation. Le chapitre 3 présente le comportement des femelles au nid durant l'incubation, incluant les variations journalières et saisonnières, en association avec les conditions météorologiques du milieu. Le chapitre 4 a également été rédigé en anglais, mais sous forme de note, et comprend les données recueillies durant l'éclosion. Le chapitre 5 fait une synthèse des principales conclusions de l'étude. Quatre annexes ont aussi été ajoutées pour permettre au lecteur de voir un faux oeuf et le matériel utilisé sur le terrain (Annexe A), d'apprécier la validité de l'utilisation de faux oeufs pour étudier le comportement des femelles (Annexe B) ainsi que celle de la calibration des faux oeufs (Annexe C) et enfin de connaître la distribution des absences des femelles (Annexe D).

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CHAPITRE 1

INTRODUCTION GÉNÉRALE

Les oiseaux pondent des oeufs qui nécessitent un apport de chaleur externe pour que les embryons se développent. Ainsi, le terme «incubation» est utilisé pour désigner le processus par lequel un adulte s'assoit sur ses oeufs afin de leur transmettre la chaleur nécessaire au développement embryonnaire. La «période d'incubation» est, quant à elle, généralement définie comme étant le temps entre la ponte du dernier oeuf, alors que le parent débute l'incubation, et l'éclosion des jeunes. Durant l'incubation, les oiseaux doivent donc réchauffer leur couvée de façon continue pour l'amener à terme.

Les premières divisions embryonnaires ont lieu dans l'oviducte de la femelle lors des dernières étapes de la formation de l'oeuf. Le développement cesse entre la ponte de l'oeuf et le début de l'incubation car, pendant cette période, la température de l'oeuf s'équilibre essentiellement avec celle de l'environnement. La poursuite du développement embryonnaire dépend du patron d'incubation des parents. Chez la majorité des oiseaux, les parents ne débutent l'incubation que lorsque toute la couvée est pondue, ce qui permet de synchroniser l'éclosion en uniformisant le développement de tous les oeufs dans le nid.

Haftorn (1988) et Lee *et al.* (1993) ont démontré qu'un seuil minimal de 25 °C devait être atteint pour qu'il y ait un développement dans l'oeuf. Toutefois, chez la plupart des espèces, la température optimale d'incubation, c'est-à-dire celle où le développement embryonnaire est le plus rapide et le pourcentage d'éclosion est maximal, se situe entre 32 et 40 °C (Webb 1987). Au-dessous du seuil minimal, l'embryon ne se développe plus et risque de mourir s'il est exposé à un tel régime thermique trop longtemps. De plus, si l'oeuf est soumis à une température supérieure à 25 °C mais inférieure à l'optimum, l'embryon ne se développe pas normalement et la durée de la période d'incubation risque fortement d'être augmentée. Il en ressort donc une importance capitale pour les parents de maintenir une température élevée et optimale afin de minimiser la mortalité des embryons et assurer une période d'incubation la plus courte possible. Une telle stratégie diminue également l'exposition des oeufs aux prédateurs.

Par ailleurs, l'incubation est une activité incompatible avec la quête de nourriture, surtout dans les milieux froids tel l'Arctique où les oeufs se refroidissent très vite en l'absence d'un parent incubateur. Les oiseaux ont adopté plusieurs stratégies face à ce problème. Chez les Alcidae, par exemple, les deux parents participent à l'incubation. La relève d'un adulte par le second permet donc aux parents de se nourrir en alternance tout en maintenant les oeufs au chaud en permanence, ou presque. Néanmoins, l'incubation chez la majorité des espèces d'oiseaux est le plus souvent accomplie par un seul des membres du couple, habituellement la femelle. Dans une telle situation, le mâle peut nourrir la femelle, comme c'est le cas chez plusieurs espèces de passereaux et de rapaces. Ceci réduit les périodes d'absence de l'adulte incubateur, et les oeufs se trouvent ainsi couvés et protégés pendant la majorité de la période d'incubation. Le mâle peut aussi ne pas nourrir sa partenaire, et la femelle doit alors assurer seule la responsabilité d'incuber et de subvenir à ses besoins énergétiques. Cette stratégie est commune chez les espèces de grande taille telles les canards et les oies. Les femelles parviennent à répondre à tous leurs besoins en utilisant leurs réserves corporelles et en ne s'alimentant que pendant de très courtes périodes, à raison de quelques fois par jour seulement. Ce jeûne, plus ou moins important selon l'espèce, permet une assiduité élevée au nid de la part des femelles.

Cette dernière stratégie est celle utilisée par le sujet de la présente recherche, soit la Grande Oie des neiges *Anser caerulescens atlantica*, qui niche dans un milieu très froid, le haut-arctique canadien.

LA PONTE

Le nombre d'oeufs que pond un oiseau diffère beaucoup selon l'espèce. Certains n'en pondent qu'un seul par saison de reproduction tandis que d'autres ont des couvées de plusieurs oeufs dont la masse totale peut parfois dépasser celle de la femelle. Certaines espèces pondent toujours le même nombre d'oeufs par couvée, et les oeufs perdus au nid ne sont alors pas remplacés. Ceci se retrouve notamment chez plusieurs espèces de pluviers. Par contre, la majorité des espèces d'oiseaux ont une taille de couvée variable à l'intérieur d'un écart relativement fixe. Par exemple, les canards peuvent avoir de 6 à 12 oeufs par couvée (Owen et Black 1990) tandis que les oies pondent en moyenne de 3 à 5 oeufs (Newton 1977). Ces espèces, dont les jeunes sont nidifuges, ont aussi des oeufs de grande taille et également riches en vitellus, ce qui représente pour la femelle un investissement énergétique considérable. En général, les femelles âgées ont des couvées plus importantes que les jeunes qui sont à leur première saison de reproduction (Robertson *et al.* 1994). De plus, celles en bonne condition physique (ayant une masse corporelle élevée) sont plus en mesure d'investir dans de grosses couvées. La date initiale de ponte influence quant à elle la taille des couvées car on observe généralement un déclin de la taille de couvées avec la progression de l'été (Eisenhauer et Kirkpatrick 1977, Hamann et Cooke 1989, Dalhaug *et al.* 1996).

La taille des oeufs d'oiseaux est également très variable entre les espèces, s'étalant de 0,5 g chez les colibris jusqu'à 1,36 kg chez les autruches. On observe une relation positive entre la masse des oeufs et la grosseur de l'oiseau. Il existe aussi une variation intraspécifique relativement importante dans la taille des oeufs. Ainsi, les femelles plus âgées, donc avec une plus grande expérience reproductrice, pondent souvent des oeufs plus gros que les adultes qui tentent de se reproduire pour la première fois (Dow et Fredga 1984, Robertson *et al.* 1994). À l'intérieur d'une couvée, la taille des oeufs varie généralement selon un patron typique. Chez les canards et les oies, le premier oeuf dans la séquence de ponte est plus petit que le deuxième qui est le plus gros de la couvée; la taille des oeufs subséquents est généralement assez semblable au deuxième quoiqu'elle diminue graduellement durant la ponte. Finalement, la taille diminue abruptement au dernier oeuf, lequel est presque toujours le plus petit de la couvée (LeBlanc 1987, Flint et Sedinger 1992, Robertson et Cooke 1993, Williams *et al.* 1993). Cette séquence est généralement maintenue même lorsque les femelles doivent réduire la taille de leur couvée en réponse à de mauvaises conditions météorologiques.

L'intervalle de ponte entre deux oeufs successifs chez les oiseaux est le plus souvent de 24 h (ex. Martin-Pêcheur d'Amérique, *Ceryle alcyon*; Mésange à tête noire, *Parus atricapillus*; Phalarope de Wilson, *Phalaropus tricolor*). Les canards respectent assez bien cet ajout au nid d'un oeuf par jour (Johnsgard 1978). Par contre, chez quelques espèces dont les oies, le temps entre la ponte successive de deux oeufs est supérieur à 24 h. Chez l'Oie de Ross (*Chen rossii*), Ryder (1967) a décelé un intervalle de ponte de 1,5 d. Chez l'Oie empereur (*Chen canagica)*, Eisenhauer et Kirkpatrick (1977) ont enregistré un intervalle de 28 h tandis que chez la Petite Oie des neiges (*Anser caerulescens caerulescens*), celui-ci est de 33 ± 3 h (Schubert et Cooke 1993). Un intervalle de ponte de 48 h ou plus est parfois observé chez des oiseaux rapaces.

L'INCUBATION

Le patron de réchauffement des oeufs est influencé par le comportement du parent qui incube. L'absence prolongée du parent peut provoquer le refroidissement des oeufs au-dessous du seuil de développement embryonnaire et réduire la probabilité d'éclosion, laquelle dépend directement du régime thermique subi par l'oeuf pendant l'incubation (Booth 1987). De plus, un nid laissé sans surveillance risque d'être détruit partiellement ou complètement par un prédateur (Madsen *et al.* 1989). Les adultes doivent donc ajuster leurs absences du nid en fonction des moments de la journée qui occasionnent le moins de risques pour le développement de l'embryon ou la perte d'oeufs (Haftorn 1988).

Début de l'incubation

Pour les couvées comprenant plus d'un oeuf, le moment du début de l'incubation varie selon l'espèce. Le parent peut commencer à réchauffer ses oeufs dès la ponte du premier, avant la ponte du dernier ou, le plus souvent, attendre que la couvée soit complète. Chaque espèce observe généralement le même patron, bien qu'une expérience de manipulation d'abondance de nourriture une fois la ponte amorcée a révélé que les femelles de la Mésange bleue (*Parus caeruleus*) pouvaient devancer l'initiation de l'incubation lorsque le milieu offrait davantage de nourriture (Nilsson et Svensson 1993). Débuter l'incubation avant la fin de la ponte entraîne une éclosion plus précoce que prévu, mais risque de l'étaler sur un plus grand laps de temps à cause de la présence d'oeufs pondus après le début de l'incubation.

Pendant longtemps, on a cru que l'incubation chez les oies et les canards ne débutait qu'une fois la couvée complétée. Aujourd'hui, plusieurs études démontrent que l'incubation n'est pas initiée de façon abrupte mais qu'elle débute plutôt progressivement vers la fin de la période de ponte (Cooper 1978, Afton 1979, Cargill et Cooke 1981, Kennamer *et al.* 1990, Flint *et al.* 1994). Il y aurait plusieurs avantages à cette incubation hâtive, notamment le maintien de la viabilité des oeufs non incubés, laquelle diminue avec le temps dans les grosses couvées (Arnold *et al.* 1987), la réduction des risques de parasitisme intraspécifique qui peuvent parfois être élevés (Semel et Sherman 1986), et la diminution des risques de prédation. Une incubation hâtive peut écourter la période de nidification et favoriser une éclosion également hâtive, ce qui peut être un avantage chez les espèces nichant dans l'Arctique, où la saison de reproduction est brève. Chez les oies, une éclosion précoce permet une meilleure croissance et une plus grande survie des jeunes à cause de la quantité et de la qualité supérieures de la nourriture disponible au début de l'été (Sedinger et Flint 1991, Lindholm *et al.* 1994, Lepage 1997).

Le réchauffement périodique des oeufs lorsque la femelle visite le nid pour pondre un nouvel oeuf peut transmettre une chaleur suffisante pour entraîner un certain développement embryonnaire, bien que le phénomène soit encore mal connu (Afton 1980, Flint *et al.* 1994). Ceci peut engendrer une différence dans le développement qui peut persister jusqu'à l'éclosion entre les premiers et les derniers oeufs pondus (Cargill et Cooke 1981). Dans ce cas, l'ordre d'émergence des jeunes est le même que celui de la ponte puisque les premiers oeufs pondus ont déjà amorcé leur développement au moment où les derniers sont ajoutés à la couvée. Par contre, comme une trop grande asynchronie à l'éclosion augmente les risques d'abandon des jeunes au nid (voir L'éclosion, page 9), une incubation trop hâtive peut devenir coûteuse.

Patron d'incubation et facteurs qui l'influencent

Chez les Anserinae, la tâche d'incuber est accomplie seulement par les femelles. Les mâles restent à proximité du nid pour défendre leur couvée et leur partenaire, sans toutefois nourrir cette dernière. Il existe chez ce groupe d'oiseaux une relation positive entre l'assiduité au nid et la taille corporelle. Ceci découle de la plus grande capacité d'emmagasiner des réserves corporelles pour la période de nidification chez les espèces de grande taille et d'un rapport surface / volume réduit. Les Anatidae sont très fidèles à leur nid durant la période d'incubation, soit de 73 à 98 % du temps pour les canards et de 89 à 99 % chez les oies (voir revue dans Afton et Paulus 1992). Cette présence soutenue de la part des femelles leur permet de nicher avec succès dans des environnements froids.

En moyenne, les femelles oies quittent leur nid de 0,5 à 7 fois par jour, selon l'espèce. Ces absences permettent à l'adulte de s'alimenter (ex. Grande Oie des neiges, Bernache du Canada *Branta canadensis*) et de se toiletter (ex. Bernache cravant, *B. bernicla hrota*). Chez plusieurs espèces dont la Bernache du Canada (Cooper 1978), l'Oie rieuse (*Anser albifrons flavirostris*, Stroud 1982), la Bernache cravant (Madsen *et al.* 1989), et la Grande Oie des neiges (Reed *et al.* 1995), le nombre d'absences par jour augmente avec la progression de la période d'incubation. Un tel comportement pourrait être relié à une diminution des réserves énergétiques des femelles durant l'incubation.

Chez les oies, les périodes d'absence hors du nid ont une durée moyenne de 20 min. La durée des absences peut varier en fonction de l'heure de la journée. Ainsi, certaines espèces profitent des moments les plus chauds pour s'absenter plus longuement (Aldrich et Raveling 1983, Madsen *et al.* 1989, mais voir Thompson et Raveling 1987, Reed *et al.* 1995). Par contre, la progression de la période d'incubation n'entraîne que très peu de changements dans la durée de ces absences (Prop *et al.* 1978, Madsen *et al.* 1989, Reed *et al.* 1995, mais voir Cooper 1978, Spaans *et al.* 1993), quoique, les femelles sont parfois moins attentives à leur nid vers la fin de la saison de reproduction. Plusieurs auteurs rapportent néanmoins que, lors des quelques jours précédant l'éclosion, l'assiduité des femelles au nid atteint presque 100 %. Cette attention particulière semblerait être reliée à la communication entre les poussins et leur mère lorsque les oeufs commencent à éclore.

Jusqu'à ce jour, les études ne semblent pas démontrer un lien étroit entre le patron d'incubation des femelles et les conditions météorologiques. Les Garrots à oeil d'or (*Bucephala clangula*) ont réagi aux températures ambiantes élevées en s'absentant plus longuement, bien que la vitesse du vent et les chutes de pluie n'aient eu aucune influence sur les allées et venues au nid (Mallory et Weatherhead 1993). Les Oies empereurs (Thompson et Raveling 1987), tout comme les Bernaches du Canada (Aldrich et Raveling 1983) et la Grande Oie des neiges (Reed *et al.* 1995), quittent quant à elles plus souvent leur nid en après-midi. Toutefois, chez cette première espèce, aucune différence significative n'a été décelée entre la durée des absences et le moment de la journée. De plus, la durée et la fréquence des absences n'étaient pas reliées aux températures ambiantes ou aux vitesses journalières moyennes du vent. Cooper (1978) a, quant à lui, démontré une corrélation positive entre la durée des absences du nid des femelles de la Bernache du Canada et l'indice éolien (wind chill) au moment du départ.

Les conditions extrêmes peuvent, par contre, jouer un rôle prépondérant sur le comportement des femelles incubatrices. Chez la Petite Oie des neiges, une tempête de neige aurait forcé les adultes à rester au nid pendant 60 h sans interruption (Krechmar et

Syroechkovsky 1978), malgré que durant des conditions analogues, les femelles de la Bernache cravant auraient plutôt abandonné leur nid (Madsen *et al.* 1989). Bien que les femelles essaient vraisemblablement de minimiser les pertes de chaleur des oeufs, leur comportement ne semble pas être entièrement «contrôlé» par les conditions environnementales du moment. D'autres facteurs pourraient donc influencer les moments et les durées d'absence des femelles. Le temps nécessaire pour remplir complètement le jabot lorsque les femelles s'alimentent et les périodes d'activité des prédateurs pourraient être de tels facteurs.

Température d'incubation

Les chercheurs s'intéressent depuis longtemps aux températures d'incubation des espèces d'oiseaux commerciales. Plus récemment, les températures d'incubation ont été mesurées chez plusieurs espèces de sauvagine en milieu naturel (voir la revue par Afton et Paulus 1992). En insérant une sonde dans la poche d'air de vrais oeufs, Afton (1979) a mesuré une température moyenne d'incubation chez le Canard souchet (*Anas clypeata*) de 36,1 ± 0,1 °C tandis que Caldwell et Cornwell (1975) ont mesuré une température moyenne de 36,3 ± 0,1 °C chez le Canard colvert (*Anas platyrhynchos*). Au moyen d'une sonde insérée à l'intérieur d'un oeuf artificiel, Miller (1976) a, quant à lui, enregistré une température d'incubation moyenne de 38,2 ± 1,9 °C chez la Sarcelle à ailes bleues (*Anas discors*). Quelques chercheurs ont aussi mesuré les températures d'incubation chez les oies. À partir d'une sonde implantée dans un oeuf de la Bernache du Canada, Cooper (1978) a établi la température moyenne de la poche d'air pendant 24 jours d'incubation à 34,3 °C. À l'aide d'oeufs artificiels en paraffine, Krechmar et Syroechkovsky (1978) ont mesuré une température moyenne de 32,9 °C pendant l'incubation chez la Petite Oie des neiges. De même, la température d'incubation chez l'Oie empereur et l'Oie rieuse a été évaluée, aussi avec de faux oeufs, à 31,8 et 33,9 °C, respectivement (Krechmar et Kondratiev 1982, Krechmar 1986 dans Afton et Paulus 1992). Ces résultats suggèrent que les températures optimales d'incubation pourraient être plus basses chez les oies que chez les canards.

Refroidissement des oeufs en l'absence de la femelle

Lorsqu'un parent incubateur s'absente du nid dans un environnement froid, la température des oeufs diminue. La vitesse d'un tel refroidissement peut être influencée par plusieurs facteurs dont la qualité isolante du nid, la masse de l'oeuf et les conditions environnementales comme la température ambiante, les précipitations, le vent et le rayonnement solaire. Puisque les oeufs se refroidissent plus vite qu'ils ne peuvent être réchauffés, un parent ne peut pas se permettre de quitter ses oeufs trop longtemps (Krechmar et Syroechkovsky 1978). Le taux de refroidissement des oeufs est souvent déterminé en laboratoire puisque de telles données sont plus faciles à obtenir qu'en milieu naturel, où la sonde doit être à l'intérieur d'un des oeufs de la couvée ou dans un oeuf artificiel. Dans ce dernier cas, on devra appliquer un facteur de correction pour ajuster l'inertie thermique des faux oeufs à celle des vrais oeufs. Cooper (1978) a évalué en laboratoire le taux de refroidissement d'oeufs de Bernache du Canada. Chez cette espèce, un oeuf recouvert de duvet transféré pendant une heure d'un environnement de 38 °C à un autre de 20 °C se refroidit à un rythme de 0,26 (°C/h)/°C; ce même oeuf, non recouvert de duvet, perd sa chaleur à un taux deux fois plus élevé, soit 0,53 (°C/h)/°C. Thompson et Raveling (1988) ont également documenté la perte de chaleur des oeufs de trois espèces d'oies. Transférés pendant 30 min d'un milieu sans vent à 38,7 °C vers un autre à 6,4 °C, les oeufs se refroidissent de 4,09 ± 0,14 °C chez l'Oie empereur et de 4,84 ± 0,13 °C chez la Bernache cravant, soit des taux de refroidissement variant entre 0,25 et 0,30 (°C/h)/°C. Leur étude confirme aussi que les oeufs exposés à un vent de 10 km/h se refroidissent plus vite que ceux soumis à un environnement calme.

L'ÉCLOSION

Chez les oiseaux qui ont des couvées de plus d'un oeuf, l'éclosion peut être ou non synchronisée selon le laps de temps entre l'émergence du premier et du dernier poussin de la couvée. Une éclosion est dite «synchronisée» lorsque tous les poussins d'une couvée éclosent dans un intervalle de temps restreint, habituellement en-deçà d'une seule journée. Bien que l'éclosion chez les oiseaux tende à être relativement synchrone, il existe une grande variabilité dans ce phénomène.

Le degré de synchronie dans l'éclosion d'une couvée est principalement influencé par deux facteurs: le comportement du parent qui va réchauffer les oeufs et la communication entre les embryons. Ainsi, l'adulte qui débute l'incubation dès la ponte du premier oeuf provoquera un développement asynchrone des oeufs par opposition au parent qui commence l'incubation une fois la ponte achevée. De même, les vocalises et les cognements émis par les premiers poussins perçant leur coquille peuvent être perçus par les autres et entraîner une éclosion plus hâtive que prévue chez ces derniers (Vince 1964, Davies et Cooke 1983). L'accélération du développement des embryons les moins développés pour permettre une éclosion synchrone a récemment été confirmée chez la Foulque d'Amérique (*Fulica americana*). Chez cette espèce, les poussins issus des petits oeufs produits à la fin de la séquence de ponte avaient des tissus moins matures que ceux émergeant des plus gros oeufs (Alisauskas 1986).

Parmi les espèces d'oiseaux qui nourrissent leurs jeunes, l'éclosion est souvent asynchrone. Ceci serait la conséquence d'une incubation active amorcée pendant la ponte, ce qui donnerait aux parents une plus grande flexibilité face à des conditions environnementales défavorables imprévisibles durant l'élevage des jeunes (Clark et Wilson 1981). En effet, le décalage dans la naissance des poussins réduirait la compétition entre les jeunes à l'intérieur d'une couvée (Hahn 1981) et étalerait la durée d'élevage des jeunes, diminuant ainsi la demande énergétique journalière pour les parents. De plus, lorsque les ressources alimentaires sont insuffisantes, une éclosion étalée sur quelques jours aiderait à réduire la taille de la couvée par la mort des derniers oisillons éclos, plus petits et donc moins aptes à s'emparer de la nourriture apportée par le parent (Mock et Parker 1986).

Synchronie d'éclosion chez les oiseaux nidifuges

Les avantages d'une éclosion asynchrone discutés plus haut ne s'appliquent pas aux espèces dont les jeunes sont précoces comme les Anatidae. Chez ces espèces, les poussins quittent le nid avec leurs parents peu de temps après leur sortie de l'oeuf (environ 24 h), ce qui nécessite un degré de synchronie élevé dans l'éclosion des jeunes. Une éclosion étalée sur une très courte période diminue également la vulnérabilité de la couvée à la prédation et facilite le départ de tous les jeunes vers les sites d'alimentation et d'élevage. Un jeune éclos trop hâtivement et devant demeurer au nid plusieurs jours en attendant que les autres poussins éclosent doit survivre sur ses réserves lipidiques (Kear 1965) et risque alors de mourir de faim puisque les parents ne nourrissent pas les jeunes nidifuges (Ankney 1980). À l'inverse, un jeune qui éclôt plus tard que les autres dans une couvée risque davantage d'être abandonné au nid par les parents qui vont vraisemblablement partir avec les jeunes déjà éclos (Williams *et al.* 1993).

Pour ces raisons, l'éclosion chez les oies est relativement synchrone à l'intérieur d'une couvée. Par des expériences de manipulation de couvées, Davies et Cooke (1983) ont démontré que l'accélération du développement des embryons les plus tardifs était un mécanisme favorisant la synchronie dans l'éclosion des oeufs d'une même couvée chez l'Oie des neiges. En dépit de ce mécanisme, certains auteurs rapportent un intervalle d'éclosion supérieur à 24 h chez cette espèce (Syroechkovsky 1975, Schubert et Cooke 1993).

Après leur naissance, les oisons restent habituellement au nid quelques heures pour leur permettre de sécher et de s'imprégner aux parents. Toutefois, lorsque la majorité des jeunes sont nés, les femelles semblent préférer quitter le nid avec les jeunes pour les amener vers les sites d'alimentation, et ce sans attendre l'éclosion des derniers oeufs. Plus l'éclosion des derniers oeufs est retardée, plus leur chance d'abandon au nid est grande. Le ou les derniers jeunes à éclore sont généralement des poussins de petite taille, car il semble que la séquence d'éclosion respecte celle de la ponte (Syroechkovsky 1975, Cargill et Cooke 1981) et qu'il existe souvent une relation positive entre la taille de l'oeuf et celle du jeune à l'éclosion (Ankney 1980). Certains auteurs ont suggéré que la survie réduite du dernier jeune éclos dans une couvée d'oies était principalement une conséquence de sa plus petite taille (Ankney 1980, Slattery et Alisauskas 1995). Cependant, il est difficile de séparer en milieu naturel les effets de la taille de l'oeuf et ceux de l'ordre d'éclosion sur la survie du jeune, à cause de la corrélation inverse entre la taille de l'oeuf et la séquence de ponte et donc, la séquence d'éclosion. Récemment, Williams *et al.* (1993) ont démontré que, lorsqu'ils contrôlaient pour la taille de l'oeuf, la survie des jeunes oisons de la Petite Oie des neiges était associée à l'ordre de ponte mais qu'à l'inverse, lorsqu'ils contrôlaient pour l'ordre de ponte, il n'y avait plus d'effet de la taille de l'oeuf sur la survie.

LE CAS DE L'OIE DES NEIGES

L'Oie des neiges se divise en deux sous-espèces, soit la Petite Oie des neiges qui niche dans les régions sub-arctiques et la Grande Oie des neiges qui se reproduit un peu plus au Nord. Certaines observations semblent indiquer que les femelles de la Petite Oie des neiges débutent l'incubation avant la fin de la ponte. Les oeufs artificiels remplis de paraffine placés par Krechmar et Syroechkovsky (1978) dans les nids de cette espèce au début de la ponte démontrent, en effet, que les couvées sont maintenues plus chaudes que la température ambiante. De même, les résultats de Cargill et Cooke (1981) démontrant que la séquence d'éclosion est identique à celle de la ponte suggèrent que la présence des femelles au nid lors de la période de ponte pourrait amorcer le développement des premiers oeufs pondus. Chez la Grande Oie des neiges, aucune donnée n'est encore disponible, bien que des observations visuelles semblent indiquer que les femelles passent une certaine partie de la période de ponte sur leur nid.

Chez les deux sous-espèces, la période d'incubation dure en moyenne 24 d. À partir d'observations visuelles de femelles de la Grande Oie des neiges durant quatre stades différents de la période d'incubation, Reed *et al.* (1995) ont établi que les femelles étaient sur leur nid 93 % du temps. Elles s'absentaient en moyenne 5 ou 7 fois par jour, à raison de 15 min à la fois. Ces données diffèrent quelque peu de celles obtenues chez la Petite Oie des neiges qui couve ses oeufs 97 % du temps et ne quitte son nid qu'environ deux fois par jour, pour une durée moyenne de 27 min à la fois (Krechmar et Syroechkovsky 1978). Cette assiduité plus faible chez la Grande Oie des neiges est surprenante et va à l'encontre du patron interspécifique d'une association positive entre le degré d'assiduité et la taille corporelle chez les oies (Thompson et Raveling 1987), la Grande Oie des neiges étant 25 % plus grosse que la Petite Oie des neiges. Les femelles quittent principalement leur nid pour aller se nourrir. Ces moments d'absence semblent quelque peu influencés par la présence de prédateurs car, lorsque les femelles repèrent un prédateur avien au-dessus de la colonie, elles reviennent immédiatement à leur nid, et lorsqu'elles aperçoivent un renard, elles restent assises sur leur couvée pour une durée minimale d'une heure (Reed *et al.* 1995).

Le régime thermique de la couvée durant la période d'incubation a été étudié chez la Petite Oie des neiges nichant à l'Île Wrangel, en Russie, par Krechmar et Syroechkovsky (1978). Avec des oeufs artificiels en paraffine contenant un thermomètre, ils ont évalué la température moyenne à 32,9 °C, de la ponte du dernier oeuf à l'éclosion. Ceci est relativement faible par rapport aux autres espèces d'oiseaux, surtout compte tenu du fait que la température moyenne de la plaque incubatrice des femelles de la Petite Oie des neiges s'élève à 40,4 °C. Ces chercheurs n'ont pas calculé de taux de refroidissement des oeufs lors de l'absence des femelles. Néanmoins, lorsque les femelles étaient chassées de leur nid par la présence d'un observateur humain, la température de l'oeuf artificiel chutait de 10 à 15 °C en 20 à 30 min, et elle n'était rétablie que de 90 à 120 min après le retour de l'oiseau sur ses oeufs. Aucune étude du régime de température des oeufs ou de leur taux de refroidissement n'a encore été réalisée chez la Grande Oie des neiges.

Les périodes d'absence des femelles pendant la période d'incubation en relation avec les conditions météorologiques n'ont pas été vérifiées chez l'une ou l'autre des sous-espèces de l'Oie des neiges. Chez la Grande Oie des neiges, le plus grand nombre d'absences surviendrait en après-midi, la portion la plus chaude de la journée (Reed *et al.* 1995). Cependant, ces chercheurs pensent que la température ambiante influence peu la durée des absences à cause de leur faible variation selon l'heure de la journée ou la période d'incubation.

Les visites périodiques aux nids de la Grande Oie des neiges pendant l'éclosion à l'Île Bylot révèlent que plusieurs couvées prennent plus d'une journée à éclore (Gilles Gauthier; observation personnelle). Ce manque de synchronisme semble être plus important que celui qui est rapporté dans la littérature pour d'autres espèces d'oies (Inglis 1977, Flint *et al.* 1994). Cette observation est surprenante compte tenu des coûts associés à une éclosion trop étalée pour une espèce nidifuge en terme de survie des jeunes. Les Grandes Oies des neiges sont les oies qui se reproduisent le plus au Nord. Il est donc possible que la température froide incite les femelles, au moment de la ponte, à passer plus de temps au nid que les autres espèces d'oies, pour éviter entre autres le gel des oeufs. Cette présence accrue de la femelle sur ses oeufs pendant la ponte pourrait alors être la cause d'une éclosion plus étalée. Bien que la présence de la femelle au nid durant la ponte puisse avoir un effet négatif sur la synchronie d'éclosion, cela aurait quand même l'effet positif d'avancer la date d'éclosion des premiers oeufs pondus. En effet, une différence de quelques jours seulement au niveau de l'éclosion peut avoir un effet bénéfique très marqué sur la croissance des jeunes (Lindholm *et al.* 1994, Lepage 1997). Ainsi, une incubation hâtive pourrait être un moyen pour la femelle de favoriser une éclosion plus hâtive. La capacité des jeunes tardifs à avancer leur éclosion (Davies et Cooke 1983) serait alors un mécanisme permettant d'atténuer les effets négatifs d'un tel comportement sur la synchronie d'éclosion.

OBJECTIFS

La présente étude visait à établir le patron d'incubation de la Grande Oie des neiges nichant sur l'Île Bylot, et le régime thermique auquel sont soumis les oeufs ainsi que leurs conséquences sur la synchronie d'éclosion. Les objectifs spécifiques étaient donc:

1. D'établir le régime thermique des oeufs lors de la ponte en relation avec l'assiduité des femelles au nid pendant cette période;
2. De déterminer le patron d'incubation journalier et saisonnier des femelles, de la ponte jusqu'à l'éclosion, et de le mettre en relation avec les conditions météorologiques de l'aire d'étude;
3. De vérifier si la séquence de ponte correspond à celle d'éclosion, et de calculer si l'éclosion est synchrone à même chaque couvée;
4. D'évaluer la température des oeufs pendant l'incubation; et
5. De déterminer le taux moyen de refroidissement des oeufs et la chute moyenne de la température des oeufs lorsque les femelles quittent leur nid, et d'évaluer les facteurs environnementaux qui influencent le taux de refroidissement.

CHAPITRE 2

THE THERMAL REGIME OF EGGS DURING LAYING AND INCUBATION IN GREATER SNOW GEESE

RÉSUMÉ

Le régime thermique auquel sont exposés les oeufs pendant les périodes de ponte et d'incubation peut influencer le développement de l'embryon et la synchronie dans l'éclosion des oeufs d'un même nid. Des oeufs artificiels ont été ajoutés à des couvées de la Grande Oie des neiges afin de déterminer la température des oeufs et leur taux de refroidissement pendant la ponte et l'incubation, ainsi que les facteurs qui les influencent. Le temps passé au nid par les femelles et la température des oeufs ont progressivement augmenté durant la période de ponte. Bien que le temps passé au nid après la ponte de l'avant-dernier oeuf était assez élevé, la température moyenne des oeufs était encore de 8 °C inférieure à la température moyenne d'incubation, ce qui suggère que le développement de l'embryon n'était pas très important avant la ponte du dernier oeuf. La température moyenne des oeufs lors de l'incubation était de 36,5 ± 0,2 °C en incluant les périodes d'absence de la femelle et de 37,1 ± 0,1 °C en les excluant. La température moyenne des oeufs a augmenté légèrement (1 °C) avec la progression de la période d'incubation, mais elle n'était pas influencée par la taille de la couvée ou la date initiale de ponte. Lorsque les femelles ont quitté leur nid, la température des oeufs a chuté de 3,2 ± 0,3 °C durant 24,7 min, ce qui correspond à un taux de refroidissement instantané de 0,24 ± 0,02 (°C/h)/°C. Le taux de refroidissement est peu influencé par la température de l'air, mais il augmente avec la vitesse du vent et diminue en présence de rayonnement solaire.

ABSTRACT

The thermal regime experienced by eggs during the laying and incubation periods can have an effect on the development of embryos and the hatching synchrony within a clutch. Snow Goose nest temperatures were monitored with dummy eggs added to naturally incubated clutches in order to evaluate egg temperature and cooling rate during laying and incubation, together with the factors influencing them. Presence on the clutch by females and average egg temperature both increased progressively during laying. Although time spent at the nest after laying the penultimate egg was relatively high, mean egg temperature was still about 8 °C lower than mean value during the rest of the incubation period. This implies that little embryonic development began before clutch completion. Egg temperature averaged 36.5 ± 0.2 °C including incubation recesses and rose to 37.1 ± 0.1 °C when only periods of female presence were considered. A slight increase (1 °C) in mean egg temperature was measured as the incubation progressed, but egg temperature was not influenced by clutch size nor by the laying date of the first egg. When females left the nest, egg temperature dropped by 3.2 ± 0.3 °C in 24.7 min, which corresponds to an instantaneous cooling rate of 0.24 ± 0.02 (°C/h)/°C. Cooling rates increased under windy conditions and decreased with high solar radiation. However, air temperature had little influence.

INTRODUCTION

During incubation in birds, parents must keep eggs at a high and constant temperature for the embryos to develop normally. Most species delay the onset of incubation until clutch completion to insure synchronous hatching, although some will start incubation before all the eggs have been laid, thereby causing asynchronous emergence of the young (Stoleson and Beissinger 1995). Because young precocial birds leave the nest soon after hatching, asynchronous emergence increases the risk of abandonment at the nest of late-hatched young (Williams *et al.* 1993). We would therefore expect females of precocial species to start incubation only after the clutch is complete. However, some studies have shown that female Anatids spend progressively more time at their nest as laying proceeds, and that nest attentiveness toward the end of the laying period can be relatively high (Afton 1980, Kennamer *et al.* 1990). It is not clear to which extent adoption of an incubation posture by the female before the end of laying warms up the eggs sufficiently to initiate development, as this behavior may not necessarily imply an effective heat transfer from the brood patch to the eggs. Sitting on the eggs during laying could be for reasons other than incubation, such as reducing predation risks (Krechmar and Syroechkovsky 1978) or maintaining egg viability (Arnold *et al.* 1987) by preventing excessive cooling of the eggs.

Development of the embryo is not only influenced by the timing of the onset of incubation but also by the thermal regime during incubation. In a cold environment like the Arctic, ambient temperatures are always well below the optimal values for embryonic development (Webb 1987). Therefore, the incubation temperature maintained during presence of the parents, as well as the temperature drop experienced by the eggs during their absence, can have a strong influence on the development of embryos. Egg temperature during incubation has been measured in several species of arctic-nesting geese including White-Fronted Geese (*Anser albifrons frontalis*; 33.9 °C), Emperor Geese (*A. canagicus*; 31.8 °C) and Lesser Snow Geese (*A. caerulescens caerulescens*; 32.9 °C; reported in Afton and Paulus 1992). These temperatures are surprisingly low in comparison with other waterfowl species (review in Afton and Paulus 1992) and with the optimum temperature reported for the development of avian embryos (35 to 40 °C; Webb 1987). Hence, low incubation temperature in geese could be an adaptation to nesting in the cold conditions of the Arctic.

We have examined the thermal regime of eggs in Greater Snow Geese (*Anser caerulescens atlantica*) during the whole nesting period. Greater Snow Geese are large body size geese (body mass ca. 3 kg) breeding in the canadian high Arctic. Visual observations have shown that, like other species of geese, females spend some time at their nest during laying (Gauthier and Tardif 1991), although the extent of egg warming occurring during this period is unknown. In contrast, nest attentiveness during incubation is relatively low for a large body size goose (Reed *et al.* 1995). The objectives of the present research were to (1) document the thermal regime of eggs during the laying period in relation to female attentiveness and determine when “effective” incubation starts, (2) measure egg temperature during incubation to verify if low egg temperature is general in arctic-nesting geese, and (3) examine the effect of environmental conditions on egg temperature and cooling rate during parental absence.

METHODS

Field work was carried out during the summers of 1995-1996 on the southwest plain of Bylot Island, Northwest Territories, Canada (73 °N, 80 °W). Data were collected at two nesting sites: a glacial valley characterized by wet polygon tundra and a low-elevation plateau 30 km south of the main study site (see description in Lepage *et al.* 1996). Geese nest colonially at each site and benefit from 24-h daylight during the entire nesting period.

Incubation temperature

Egg temperatures were measured with artificial eggs (hereafter called EGG) added to goose nests. The EGGS were made of a hollow copper shell (thickness ca. 1 mm) to insure thermal uniformity reading regardless of the orientation of the EGG with respect to the incubating bird. The shells, roughly the size and shape of a goose egg, were covered by a few millimeters of plaster to give the right texture and color to the surface. A thermistor soldered to the copper shell was read with an electronic data logger (StowAway, *Onset Computer*). In 1995, the logger was housed within the EGG. In 1996, loggers were placed in a waterproof plastic tube outside the EGGS and fastened to a metal stake driven into the ground about 0.5 m from the nest. The sensor wire between the EGG and the data logger was reinforced with a fine metal wire and hidden in the soil litter. These wires somewhat restricted movements of the EGGS in the nests although they could still be turned, to a certain extent, along their long axis (see Appendix A for picture).

A total of 11 and 12 EGGS were added to goose nests in 1995 and 1996, respectively. All females accepted the EGGS added to their nest except for two females in 1996 which rejected the EGG by rolling it outside the nest. Nests received an EGG during laying but many nests were predated and/or abandoned, and several EGGS were removed by predators (in 1995 only). As a result, the incubation temperature was monitored in only 12 nests (2 in 1995 and 10 in 1996). Loggers stored the mean temperature recorded during a given interval with an accuracy of 0.5 °C. In 1995, interval lengths were 3.2 min during early incubation, 2 min during mid-incubation and 1.6 min during late incubation. In 1996, intervals were 1.6 min (3.2 min for two EGGS) during laying and the first half of incubation (until 5 July) and 0.67 min (1.2 min for two EGGS) afterwards.

Weather parameters

An automated weather station at the main study site recorded air temperature (°C) and solar radiation (W/m^2) at 2 m above ground, and wind velocity (m/s) at 2.5 m every min. Mean hourly values were saved by a *Campbell Scientific* CR-10 data logger. Air temperature was measured with a shielded temperature probe (model 107, *Campbell Scientific*), solar radiation with a pyranometer (model LI-200 SA Pyranometer sensor, *LI-COR*) and wind velocity with an anemometer (*Young*). In 1995, nests monitored were located about 2.5 km from the weather station, but in 1996, nests were 30 km further south. A relatively flat terrain (low elevated hills) separated the two sites. Weather conditions were similar at both locations (personal observation) but a time delay between sites was possible during extreme conditions (*i.e.* strong winds, rain).

Determination of nest attentiveness by the females

Due to their low thermal inertia and high conductivity, EGGS had a rapid thermal response which facilitated the detection of the absences by incubating females from their nests (= recess). Abrupt and sustained drops in temperature (≥ 6 min) were easy to recognize on graphs of EGG temperature vs. time (see Fig. 1) and were assumed to represent absence of the female. The validity of this assumption was checked by visual observations of five nests with EGGS over a period of 54 h during which the time of departure and return of incubating females to their nest was precisely recorded. Recess duration determined by EGG temperatures was a good predictor of actual recess duration ($r^2 = 0.62$, $n = 39$, $p < 0.01$) and both measurements did not differ significantly (paired *t*-test, $df = 38$, $p > 0.86$; see Appendix B for more details).

Nest attentiveness of females during laying was calculated by summing all periods of time when EGG temperature was rising rapidly or was stable but high (≥ 10 °C above ambient air temperature). As nests were visited 2 - 7 times each during incubation (mean 4), these periods of disturbance were excluded from all calculations.

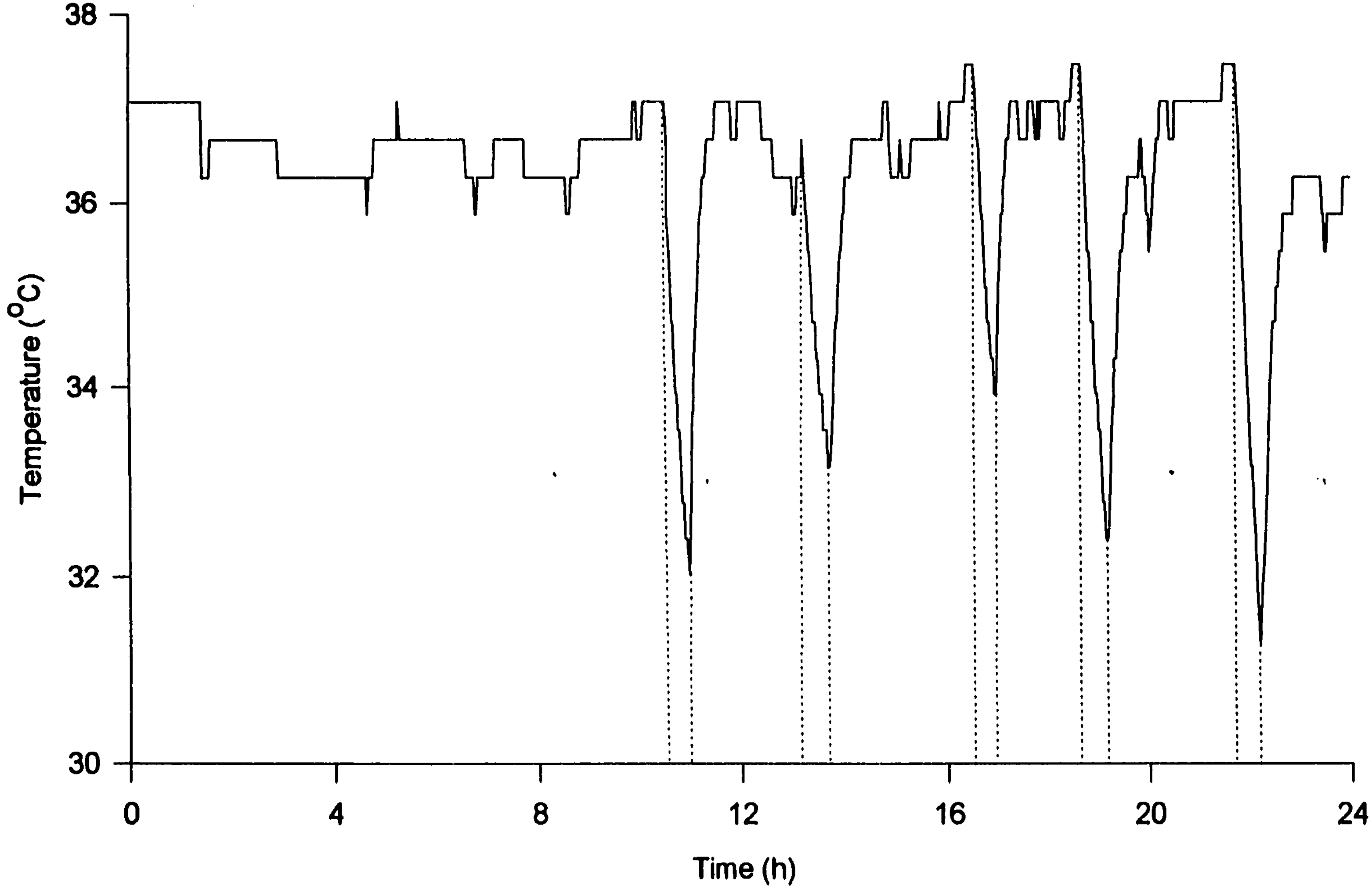

Figure 1. Typical daily pattern of EGG temperature in incubating Greater Snow Geese. In this example, five incubation recesses (enclosed by dashed lines) were determined.

A nest located close to camp (CX01) which did not receive an EGG was also used to calculate nest attentiveness during the laying period as presence or absence of the female was noted many times daily, from the laying of the second egg to the 14th day into the incubation period ($n = 99$). Nest attentiveness was expressed as the proportion of observations that the female was sitting on the nest.

Egg cooling rates

As expected, cooling and heating rates of EGGS were more rapid than those of real eggs. Therefore, thermal inertia of EGG was calibrated against freshly-laid goose eggs collected in the field (see Appendix C for more details). This enabled us to calculate time constants based on an exponential model of temperature drop over time. These time constants were used to transform the EGG final temperature at the end of a recess into values which would better represent the final temperature reached by real goose eggs. Corrections were applied to 677 recesses ≥15 min in duration. We then calculated, for each recess, (1) the temperature drop during the entire duration of the recess, (2) the average cooling rate, which represents the linearized rate of temperature drop (°C/min), and (3) the instantaneous cooling rate which takes into account the thermal gradient between the egg and the ambient air temperature during the recess [(°C/h)/°C]. Data for air temperature used in the calculation of instantaneous cooling rates were recorded at the weather station near the study site (see above) and are the mean hourly temperatures closest to the mid-point of the recess. The first and last temperature recording of each recess was included in the calculation of temperature drop but not in those of cooling rates as the data loggers measured an average temperature within each interval, therefore obscuring the exact time of departure and return by the females from the nest. We are aware that the corrected cooling rates may not account for the thermal contributions of embryos which may modify egg cooling rates late in the incubation period (Turner 1990). However, our procedure should yield cooling rates and temperature drops close to those observed in real goose eggs during most of the incubation period.

Statistical analyses

Individual nests were used as the sampling unit in all statistical analyses unless mentioned otherwise. Mean temperature of individual EGGS was calculated using all recordings, both including and excluding the absence of females from the nest. We use the word EGG to identify variables for which temperature data were not corrected to better reflect those experienced by real goose eggs. EGG temperature and nest attentiveness at the beginning of the incubation period were compared with mean values recorded during the rest of the incubation period with paired *t*-tests. Among-nest variability in incubation temperature (over periods of 3 h; including recesses) was investigated with a one-way analysis of variance (ANOVA, model II). The relationship between egg temperature and incubation stage was investigated with a forward polynomial regression. The effect of clutch size, laying date and recess duration on mean EGG temperature, cooling rate and temperature drop during recesses was examined using linear regressions. Among-nest variability for temperature drops, average cooling rates and instantaneous cooling rates were investigated with one-way analyses of variance (model II). The effect of weather conditions (air temperature, solar radiation and wind velocity) and recess duration on average cooling rates was investigated with general linear models (GLM; SAS Institute Inc. 1992). Only significant variables were retained in the final model. Analyses were performed using a significance level of 0.05 and results are presented as mean ± *SE*.

RESULTS

EGG temperature during laying

Most nests to which EGGS were added during laying were destroyed by predation. Hence, data from the laying period and the transition from laying to incubation are only available for a few nests. The most complete data are from nest 103 which received an EGG at the one egg stage and in which three additional eggs were laid (Fig. 2). Visits every other day during this period allowed us to determine a mean laying interval of 34 h, assuming a constant laying rate. Both EGG temperature and nest attentiveness gradually increased as the laying period progressed (Table 1). Once the fourth and final egg was laid, the female continuously incubated for 35 h.

Nest 331 received an EGG when it contained three eggs and two additional ones were laid. The timing of laying was unknown for this nest. Assuming a laying interval of 34 h as in nest 103 (see also Schubert and Cooke 1993), the first 34 h interval after the initial visit and a variable portion of the second 34 h interval can be considered part of the laying period (Fig. 3). For calculation of mean EGG temperature and nest attentiveness (Table 1), we assumed that both intervals were part of laying. Although nest attentiveness was relatively high during laying, EGG temperature was quite variable and reached a high and constant value only during the second half of the last presumed laying interval.

Records of nest CX01 indicate that time taken for laying of the third and fourth eggs was more than 28 h, and between 33 and 45 h, respectively. Nest attentiveness during the last two laying intervals was 79 %, a value similar to that obtained for nest 331 (Table 1).

Although nest attentiveness was relatively high at the penultimate egg stage and even at the preceding one, mean EGG temperature at the penultimate egg stage (28.4 °C, $n = 2$) was still about 8 °C below normal incubation temperature (Table 1). EGG temperature during the first 34 h following laying of the last egg averaged 35.5 °C, about 1.1 °C lower than mean temperature observed throughout the rest of the incubation period (Table 1; $t = -3.7$, $df = 4$, $p < 0.02$), even though nest attentiveness was slightly higher (95.0 vs. 91.1 % respectively; $t = 3.3$, $df = 5$, $p < 0.02$).

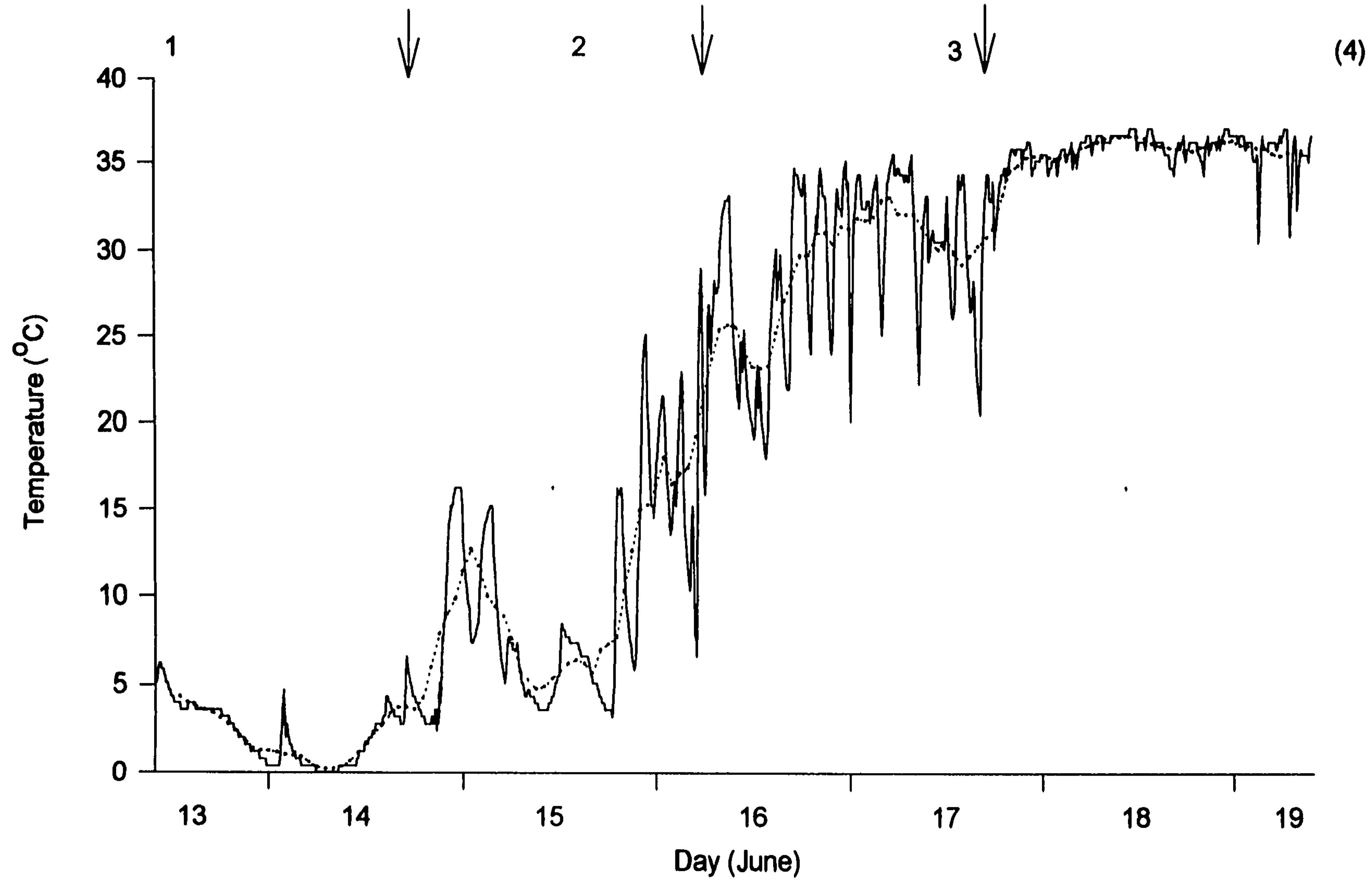

Figure 2. EGG temperature of nest 103 during laying and early incubation (continuous line) and smooth curve showing general trend (stippled line; running mean over 6 h). Numbers indicate clutch size at the time of visits and arrows show the estimated time of laying of the 2nd, 3rd and 4th egg assuming a constant laying interval (34 h).

Table 1. Mean EGG temperature (including recesses) and nest attentiveness during laying, early incubation and the rest of the incubation period in Greater Snow Geese. Each laying stage corresponds to the number of eggs remaining to lay in the nest and lasts 34 h. Stage 1 of incubation is the first 34 h interval following estimated time of clutch completion (data during only 20.5 h for nest 15).

			Laying stage			Incubation stage	
	Nest	Clutch size	-3	-2	-1	1	Others
Temperature	103	4	2.4	10.1	29.0	35.7	36.9
(°C)	331	5		21.3	27.8	33.6	35.6
	14	7				35.8	36.8
	115	5				36.8	37.0
	15	3				35.6	36.5
Attentiveness	103	4	2.8	29.7	52.1	100	93.4
(%)	331	5		78.4	72.1	89.4	90.0
	14	7				99.1	95.0
	115	5				94.2	91.1
	15	3				95.6	92.7
	CX01	4		——— 79.2 ———		91.7	84.2

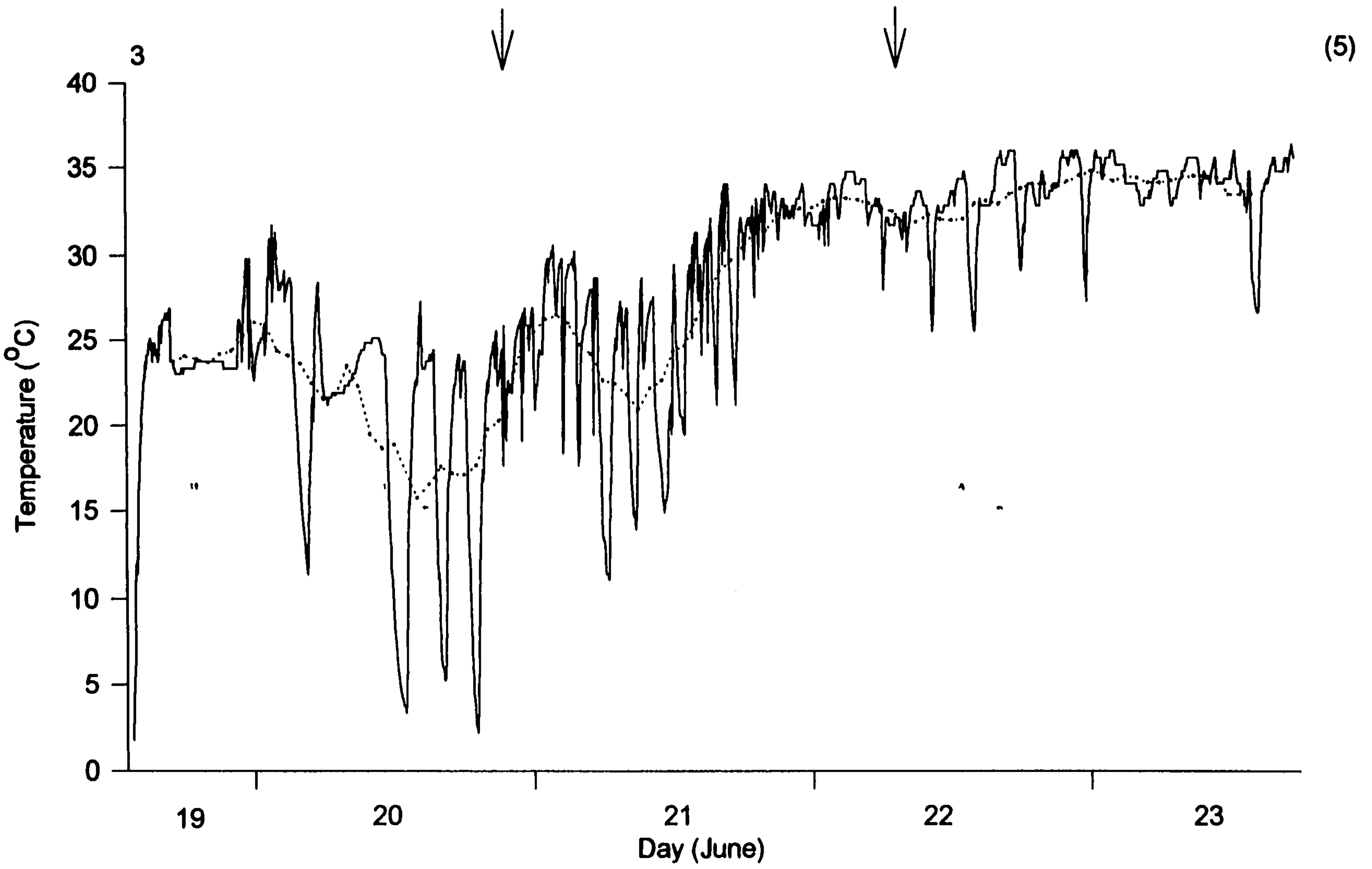

Figure 3. EGG temperature of nest 331 during laying and early incubation (continuous line) and smooth curve showing general trend (stippled line; running mean over 6 h). Numbers indicate clutch size at the time of visits and arrows show latest possible time of laying of the 4th and 5th egg assuming that an egg was laid shortly before the first visit and that the laying interval was constant at 34 h.

Length of incubation period

The interval between estimated time of laying of the last egg and hatching of the clutch allowed us to assess the length of the incubation period for three nests. Eggs in nests 103, 331 and CX01 were incubated for 23.5, 24 and 23 d, respectively.

EGG temperature during incubation

EGG temperature averaged 37.1 ± 0.1 °C when females were sitting on their clutch, and 36.5 ± 0.2 °C when incubation recesses were included in the calculation (Table 2). The difference between the highest and lowest mean incubation temperature was only 1.0 °C (1.6 °C including recesses). Variability in mean temperature was significant among nests ($F = 41.8$, $df = 11, 1662$, $p < 0.01$) although variation within nests explained 77.2 % of total variation.

Egg temperature (excluding recesses) showed a slight increase with the progression of incubation stage (Fig. 4), from a low value of 36.1 °C on the fourth day of incubation to a high of 37.4 °C on the day of hatching. The curvilinear relationship suggests that the gradual increase took place mostly during the first half of incubation and that temperature was more or less stable thereafter. Mean temperature was not related to clutch size ($r^2 = 0.09$, $df = 11$, $p > 0.34$) or laying date of the first egg ($r^2 = 0.01$, $df = 11$, $p > 0.79$) despite a large variation in both variables (Table 2).

Cooling rate and temperature drop during incubation recess

Ambient temperature during the incubation period averaged 5.2 °C. During incubation recesses, egg temperature dropped an average of 3.2 ± 0.3 °C (Table 3, $n = 677$). Mean temperature drop differed among nests ($F = 29.9$, $df = 11, 665$, $p < 0.01$) but variability was greater within nests (65.8 %). Average egg cooling rate was 0.124 ± 0.010 °C/min, corresponding to an instantaneous cooling rate of 0.243 ± 0.019 (°C/h)/°C (Table 3). Mean cooling rates differed among nests (average; $F = 18.8$, $df = 11, 665$, $p < 0.01$: instantaneous; $F = 19.0$, $df = 11, 665$, $p < 0.01$) but again variability was greater within nests (74.7 % and 75.4 %, respectively). Instantaneous cooling rates varied by more than a factor of two between nests with the lowest and highest values (Table 3).

Table 2. Laying date of the first egg, total clutch size and mean EGG temperature during the entire incubation period in Greater Snow Geese. Sample size for each nest varies from 2,787 to 12,519 individual temperature recordings (without recesses) or 4,298 to 29,109 (with recesses). All *SE* for individual nests are < 0.01 °C.

Nest	Laying date (June)	Clutch size	Incubation temperature (°C)	
			Without recesses	With recesses
14	12	7	37.0	36.8
15	10	5	36.8	36.5
103	13	4	37.2	36.9
106	15	3	37.1	36.5
107	14	4	37.5	37.0
108	17	4	37.3	37.1
114	18	2	37.5	35.6
115	16	3	37.5	37.0
118	17	3	37.0	36.2
331	17	5	36.5	35.5
363	19	3	37.2	36.9
365	14	5	36.5	36.1
Mean ± *SE*	15 ± 0.8	4 ± 0.4	37.1 ± 0.1	36.5 ± 0.2

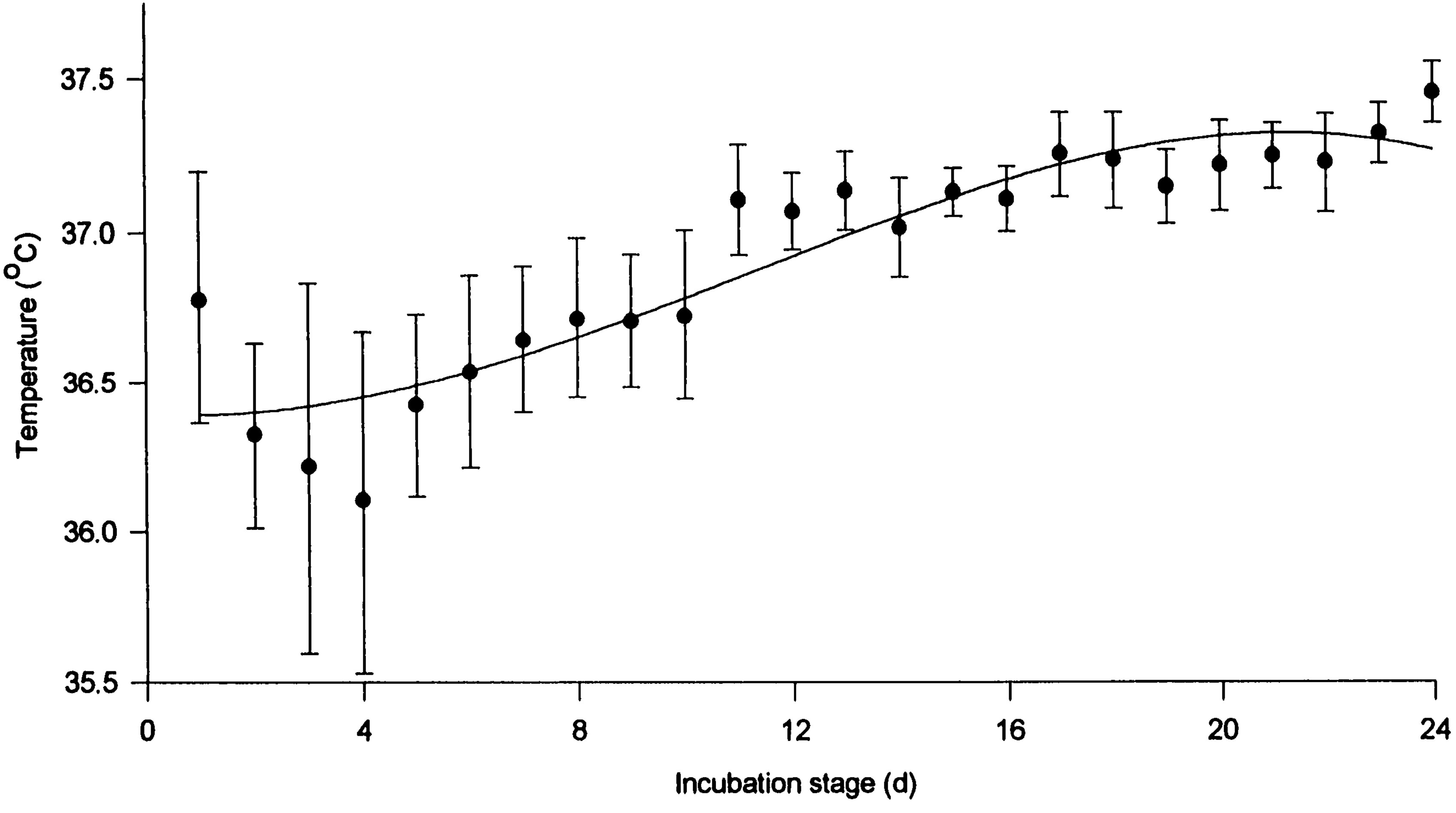

Figure 4. Time course of egg temperature (excluding recesses) with the incubation stage in Greater Snow Goose clutches. Circles (mean ± *SE*) are daily average temperature of 4 to 12 nests. Best curve fitting followed the equation $Y = 36.4 + 6.21E\text{-}3X^2 - 1.928E\text{-}4X^3$, $r^2 = 0.84$, $p < 0.01$.

Table 3.Temperature drop during recesses, recess duration and cooling rates in nests of incubating Greater Snow Geese. Only recesses ⩾ 15 min in duration were used and variables were adjusted to approximate the thermal regime experienced by real goose eggs (see Methods). Mean ambient temperature during recesses was 7.1 °C (range: 0.6 to 13.8 °C). Mean ± *SE*. *N* = number of recesses except overall mean.

Nest	Temperature drop (°C)	Recess duration (min)	Average cooling rate (°C/min)	Instant cooling rate [(°C/h)/°C]	*N*
14	3.0 ± 0.3	19.1 ± 0.6	0.146 ± 0.015	0.272 ± 0.029	31
15	3.4 ± 0.2	22.1 ± 0.5	0.149 ± 0.009	0.281 ± 0.017	71
103	2.4 ± 0.1	23.1 ± 0.6	0.096 ± 0.006	0.185 ± 0.010	69
106	4.3 ± 0.3	23.4 ± 0.9	0.202 ± 0.014	0.391 ± 0.026	43
107	3.2 ± 0.2	27.6 ± 0.9	0.113 ± 0.008	0.221 ± 0.013	58
108	1.9 ± 0.1	19.0 ± 0.7	0.089 ± 0.005	0.180 ± 0.010	25
114	4.9 ± 0.2	36.6 ± 1.2	0.129 ± 0.004	0.259 ± 0.007	92
115	2.9 ± 0.1	23.6 ± 0.5	0.117 ± 0.004	0.231 ± 0.007	80
118	2.7 ± 0.1	24.8 ± 0.7	0.101 ± 0.005	0.210 ± 0.011	59
331	4.3 ± 0.2	27.4 ± 0.9	0.157 ± 0.007	0.318 ± 0.014	61
363	2.3 ± 0.2	24.3 ± 1.0	0.081 ± 0.006	0.169 ± 0.012	26
365	2.8 ± 0.1	25.4 ± 0.8	0.102 ± 0.004	0.202 ± 0.007	62
Mean ± *SE*	3.2 ± 0.3	24.7 ± 1.3	0.124 ± 0.010	0.243 ± 0.019	12

Mean temperature drop experienced by the eggs was significantly related to the length of each recess ($Y = 0.13X - 0.10$; $r^2 = 0.46$, $df = 11$, $p < 0.02$). Nonetheless, average egg cooling rate was neither influenced by clutch size ($r^2 = 0.03$, $df = 11$, $p > 0.60$) nor by laying date ($r^2 = 0.10$, $df = 11$, $p > 0.31$).

Eggs cooled at a slower rate with high solar radiation and low wind velocity (Table 4). However, interactions were also significant between wind velocity and air temperature, and between recess duration and solar radiation. This implies that, with increasing wind velocity, egg cooling rate tended to be greater under high solar radiation but smaller with high air temperature and during long recesses. Air temperature and recess duration had no effect on cooling rate. Altogether, the model explained 30 % of the variation in cooling rate.

Table 4. The effect of weather parameters, recess duration and their interactions on average cooling rates of Greater Snow Goose eggs. The significance of each variable and its coefficient are presented (General linear model; $r^2 = 0.30$, $n = 677$, $p < 0.01$).

Variables	Coefficients	*p*
Solar radiation	-0.1899	< 0.01
Wind velocity	0.0148	< 0.01
Wind velocity * Air temperature	-0.0017	< 0.01
Wind velocity * Recess duration	-0.0004	< 0.01
Wind velocity * Solar radiation	0.0335	< 0.01
Air temperature	-	ns
Recess duration	-	ns
Air temperature * Solar radiation	-	ns
Recess duration * Air temperature	-	ns
Recess duration * Solar radiation	-	ns

DISCUSSION

Effect of using artificial eggs

All our temperature measurements were made using artificial eggs. Because EGGS warmed up and cooled down more rapidly than goose eggs (see Appendix C), fluctuations in temperature of goose eggs during laying should be less pronounced than those observed in Figs. 2 and 3. During incubation, maximum EGG temperature is limited by the amount of heat transferred by the female. We thus assumed that EGG temperature was very close to the one of goose eggs when females were sitting on their clutch. This assumption was necessary in order to adjust EGG temperature at the end of a recess to a value closer to the one expected for goose eggs and then calculate egg cooling rates and temperature drops. Temperature data collected with artificial eggs may still differ from those obtained with thermistors directly placed inside goose eggs. However, our calibration experiments (see Appendix C) suggest that any bias in the corrected data, if present, was slight.

Laying period

Even though our sample size is small, female Greater Snow Goose attended their nest during the laying period, and both presence on the clutch and egg temperature increased as clutch completion approached. A gradual increase in attentiveness or egg temperature during this period was also observed in Giant Canada Geese (*Branta canadensis*; Cooper 1978), Lesser Snow Geese (Krechmar and Syroechkovsky 1978) and Emperor Geese (Krechmar and Kondratiev 1982). However, our results indicate that temperatures putatively high enough to allow embryonic development in birds (≥ 28 °C; White and Kinney 1974, Drent 1975, Haftorn 1988) were not reached until the very end of the laying period in Greater Snow Geese. Although temperature at the penultimate egg stage was at times high enough (up to 35 °C) to allow embryonic development, mean egg temperature was still about 8 °C below the one maintained during incubation. Thus, even though presence of the female on the eggs before clutch completion warms the eggs, it should not be interpreted as functional incubation (*i.e.* embryo development). For instance, the cumulative amount of heat (in °C h) above the threshold for development (28 °C) received by the eggs in nest 103 during laying was 56.0 °C h which represents only 1.1 % of the total amount of heat received during the entire incubation period. Transition to a fully functional incubation (*i.e.* constant high temperature) occurred rapidly around laying of the last egg. Nest attentiveness during the subsequent 34-h period was slightly higher than that recorded for the rest of the incubation, and egg temperature was high (35.5 °C) and constant, though still about 1 °C below mean egg temperature during the whole incubation.

Our results do not support the conclusion of Cargill and Cooke (1981) that embryonic development occurs throughout the laying period in Snow Geese. They based their conclusion on the observed relationship between the laying and hatching sequences in Lesser Snow Goose clutches, although they did not give the time between hatching of the first and the last egg. Flint *et al.* (1994) measured egg temperature during laying in Brent clutches and reported that first laid eggs received up to 48 h of incubation (≥ 28 °C) before the last egg was laid. But again, the extent of embryonic development within clutches was not determined at the end of the laying period.

It is not surprising that Greater Snow Goose eggs are not attended very much during most of the laying process. Laying females must feed extensively in order to accumulate the energy necessary for incubation and to complete clutch formation (Gauthier and Tardif 1991, Choinière and Gauthier 1995). Brief visits to the nest during this period could be a reaction to the presence of predators, a response to cold temperatures (*i.e.* below freezing level) or an attempt to verify that eggs are still in the nest. In ducks, secretion of the hormone prolactin, which is closely associated with incubating behavior, has been shown to be stimulated by tactile signals (*i.e.* contact of eggs on the brood patch; Hall 1987). Hence, the presence of eggs under the female would trigger secretion of prolactin in the blood, which in turn would help maintain the brood patch and the incubation behavior. Such hormonal adjustment could also occur gradually in geese and consequently contribute to the females low but increasing nest attentiveness as the clutch is being laid.

Incubation temperature

Incubation temperature recorded in this study (37.1 °C) falls within the range of those reported in many other species of birds (35 to 40 °C; Webb 1987), but is higher than the mean value reported for ducks and geese (35.6 °C; Afton and Paulus 1992). Our value is also surprisingly high compared to those previously measured in several arctic-nesting geese (31.8 -

33.9 °C) by russian workers (Krechmar and Syroechkovsky 1978, Krechmar and Kondratiev 1982, Krechmar 1986 *in* Afton and Paulus 1992). Consequently, our results reject the hypothesis that all geese reproducing in the Arctic have low incubation temperatures. Although temperature recordings in the russian studies were also obtained with thermistors placed in artificial eggs, it is not known if these eggs made of paraffin were thermally uniform and properly calibrated against real eggs of the studied species. Differences could therefore come in part from divergent thermal inertia of artificial eggs used. However, thermal properties of nests may also vary between species depending, among other things, on the nesting habitat used and may account for some of the difference.

A gradual rise in egg temperature as the incubation period progresses has been observed in many waterfowl species (Caldwell and Cornwell 1975, Cooper 1978, Afton 1979, Wilson and Verbeek 1995). This increase has often been attributed to the growing embryo which occupies a greater portion of the egg, and thereby reduces egg cooling by its metabolism in absence of the incubating parent. However, our results also show this characteristic rising trend even though temperature was recorded with artificial eggs, and only periods when females were sitting on the clutch were included (*i.e.* recesses were excluded). Rising temperature could be a consequence of an increased heat transfer by the incubating parent, but this is unlikely as brood patch temperature is thought to stay constant throughout most of the incubation period (from day 4 to 20 in the Northern Shoveler *Anas clypeata*; Afton 1979). Alternatively, higher egg temperature during the second half of incubation may be a consequence of a warmer nest environment. This could be due to a larger total heat production by the growing embryos in the nest, and/or by higher ground temperature which reduces heat losses by conduction. The latter explanation, however, is unlikely in our case because mean temperature at 2 cm below ground only rose 0.2 °C during incubation at our weather station. Therefore, the contribution of the neighboring developing embryos could be the most important factor even though clutch size did not affect mean egg temperature.

Egg temperature was not related to laying date although many aspects of the reproductive behavior of Greater Snow Geese vary seasonally (*e.g.* growth; Lindholm *et al.* 1994, Lepage 1997). Time is presumably a constraint for incubating females because early-hatched birds show a higher success. However, egg temperature is apparently not a parameter which females can adjust to advance hatching.

Egg cooling rate

An average temperature drop of 3 °C during recesses lasting 25 min indicates that Greater Snow Goose eggs are far from being exposed to temperatures which could endanger the embryos development or survival. This drop is actually lower than those recorded in other naturally incubated eggs of waterfowl species nesting at lower latitudes. Drops of 5.4 °C were reported in Mallard Duck eggs (*Anas platyrhynchos*; recess duration = 24 min; Caldwell and Cornwell 1975) and 7.6 °C in Northern Shoveler eggs (recess duration = 101 min; Afton 1979). However, temperature drops were related to recess duration in Greater Snow Geese, which suggests that females taking longer recesses may have to incubate for a longer period. Adjusted instantaneous cooling rate (0.243 ± 0.019 [(°C/h)/°C]) was similar to the one measured in naturally incubated and covered eggs of Canada Geese (0.26 [(°C/h)/°C]; Cooper 1978) and Northern Shovelers (0.22 [(°C/h)/°C]); Afton 1979). In a controlled experiment with Emperor, Cackling (*Branta canadensis minima*) and Brent (*B. bernicla nigricans*) Goose eggs covered with down in natural nests, transferring them from an environment of 38.7 °C to 6.4 °C for a 30 min period yielded cooling rates slightly higher than our value (0.25 to 0.30 [(°C/h)/°C]). However, these eggs were smaller than Greater Snow Goose eggs by 14 to 36 % (Thompson and Raveling 1988). As females most often cover their eggs with down upon leaving their nest, this most likely reduces the rate at which eggs cool down in a cold environment like the Arctic.

Cooling rates were mostly influenced by wind speed and solar radiation. In contrast, air temperature alone seemed to be a poor predictor of environmental conditions experienced by eggs. Convective heat loss and radiative heat gain are thus major avenues of heat transfer for eggs. If females are sensitive to egg temperature, they should adjust their recess frequency and duration accordingly. Recesses should be longer and more frequent under sunny conditions, which help maintain a warm microclimate within the nest, and when wind speed is too low to blow down away from the eggs in the absence of an incubating parent (see Chapter 3). However, the effect of wind is complex as it is also affected by other variables. For example, with a wind of 2 m/s, eggs cooled at a mean rate of 0.16 °C/min when air temperature was 1 °C but at a rate of 0.08 °C/min only when air temperature was 11 °C. Furthermore, as wind velocity was recorded nearly 30 km from the study area and at 2.5 m above ground, the wind experienced by the eggs may have differed from the values used in our calculations.

Weather variables only explained a small portion of the variation (30 %), which implies that other factors affected the rate at which eggs cooled. Differences in the insulative properties of nests among individuals, because of variable amount of down and other materials, may play an important role in affecting the thermal relationship with the environment. Thompson and Raveling (1988) showed that under windy conditions (*i.e.* wind velocity of 2.8 m/s), eggs placed in a well insulated nest such as the one of Black Brant cooled 15 % less rapidly than those in nests built with less down and vegetation such as those of Emperor and Cackling Geese. Micro-topography around nests may also affect the microclimate that they experience under various prevailing weather conditions. For instance, nest 331 was 1 m East of a large rock, which most likely considerably reduced the effect of wind coming from the West, whereas nests 115 and 118 were on a gentle slope facing NorthWest, which may have reduced the amount of solar radiation received compared to nests on flat ground. Soil properties under the nests could have also influenced their thermal environment as those on more humid ground may have suffered greater conductive heat loss. However, it is surprising that egg cooling rate was not directly affected by the number of eggs in the nest as Frost and Siegfried (1977) found a clear negative relationship between the number of eggs in a nest and the rate at which they cooled. This suggests that the content of a nest may affect its thermal inertia at least under some circumstances.

In conclusion, our results indicate that effective incubation in Greater Snow Geese only begins after clutch completion and that incubation temperature is considerably higher than the one measured in other goose species nesting in the Arctic. Egg cooling rates are mostly affected by solar radiation and wind velocity although the amount of variation explained is low and other factors related to nest quality and micro-topography are likely to be influencial.

CHAPITRE 3

INCUBATION BEHAVIOR OF GREATER SNOW GEESE IN RELATION TO WEATHER CONDITIONS

RÉSUMÉ

Une relation allométrique avancée par Thompson et Raveling (1987) prédit que les oies d'une grande taille devraient passer plus de temps au nid durant l'incubation que les oies de petite taille. Pendant deux saisons de reproduction, nous avons documenté les variations journalières et saisonnières du comportement d'incubation de la Grande Oie des neiges et examiné l'effet des conditions météorologiques sur la fréquence et la durée des absences. Le comportement des oies a été établi à partir de la température d'oeufs artificiels ajoutés aux couvées. En période d'incubation, les femelles étaient présentes à leur nid 91 % du temps, ce qui est relativement faible pour une oie de grande taille. Les femelles ont quotidiennement pris 5 ou 6 absences d'une durée moyenne de 23 min chacune. Les femelles ont quitté leur nid plus souvent l'après-midi, et pour plus longtemps, que la nuit. De plus, leur présence au nid a diminué avec la progression de la période d'incubation à cause d'une augmentation de la fréquence des absences et de leur durée. Les femelles ont toutefois augmenté fortement leur présence au nid environ deux jours avant l'éclosion, y passant jusqu'à 96 % de leur temps le jour d'éclosion. Les conditions météorologiques ont influencé le comportement d'incubation de 11 des 12 femelles suivies. Ainsi, les femelles ont quitté leur nid plus souvent lorsque la vitesse du vent était faible et, dans une moindre mesure, lorsque la température ambiante et le rayonnement solaire étaient élevés, quoique la réponse de chaque femelle était variable. Bien que les femelles semblent ajuster leur comportement afin de limiter le refroidissement des oeufs, les variations journalières du risque de prédation pourraient aussi influencer le patron d'incubation.

ABSTRACT

An allometric model proposed by Thompson and Raveling (1987) anticipates that geese of higher body mass should be on their nest for longer periods during incubation than smaller geese. During two nesting seasons, we documented daily and seasonal variations in incubation behavior of Greater Snow Geese and examined the effect of weather conditions on recess frequency and duration. Incubation behavior was inferred from variations in temperature recorded by artificial eggs added to clutches. Mean nest attentiveness during the incubation period was 91 %, which is relatively low for a large body size goose. Females took 5 or 6 daily recesses which lasted about 23 min each. Recesses were more frequent, and of longer duration, in the afternoon than at night. Females were also less attentive to their nest as incubation progressed, a consequence of both an increase in recess frequency and in duration. Nest attentiveness increased abruptly about two days prior to hatching, reaching a high of 96 % on the day of hatching. Weather parameters influenced movements away from the nests in 11 of the 12 females monitored. Females took more recesses when wind velocity was low and, to a lesser extent, when air temperature and solar radiation were high, but the response was quite variable among females. Although females seem to adjust their behavior in order to limit egg cooling, daily variations in risks of predation may also influence incubation rhythm.

INTRODUCTION

Incubation is a stressful period for birds because the high level of nest attentiveness required to insure normal embryonic development reduces the time available to feed for the parents. Conditions faced by arctic-nesting geese during incubation are especially harsh. Like all Anatids, only female geese incubate and the cold arctic temperature requires an almost continuous presence of the female at the nest. In order to successfully bring their clutches to hatching, geese stay on the eggs for 89 to 99 % of the time during incubation depending on the species (see review in Afton and Paulus 1992). The energy requirements of the females during these long bouts are largely met by endogenous lipid reserves although, as incubation progresses, females may increasingly rely on energy acquired by feeding (Madsen *et al.* 1989, Murphy and Boag 1989, Reed *et al.* 1995). Females must balance the energy invested into incubation with their own survival. Harvey (1971) reported incubating female Lesser Snow Goose (*Anser caerulescens caerulescens*) dying on the nest after exhausting their endogenous reserves. Therefore, incubating females should adjust their behavior in order to maximize the chances of hatching of the embryos while minimizing their own risk of starvation.

Abiotic factors have a direct effect on heat loss of the clutch (see Chapter 2) and this should have a strong influence on the incubation behavior of females in a cold environment. Many authors have reported that incubating geese leave their nest more often and for longer periods during the afternoon, which is the warmest portion of the day (Cooper 1978, Aldrich and Raveling 1983, Thompson and Raveling 1987, Madsen *et al.* 1989, Spaans *et al.* 1993, Reed *et al.* 1995). However, few studies have shown a direct relationship between the duration or frequency of recesses and prevalent abiotic factors such as ambient temperature, rain or windspeed. In Canada Geese (*Branta canadensis*), Cooper (1978) found that recesses were longer during low wind chill but were not influenced by either air temperature or wind speed at time of recess. Krechmar and Kondratiev (1982) reported that wild Emperor Geese (*Anser canagicus*) took longer recesses when air temperature was high, but captive Emperor Geese monitored by Thompson and Raveling (1987) did not leave the nest more frequently or for longer times during periods of high air temperature or low wind speed. Incubating birds also protect their eggs from extreme conditions. For example, Lesser Snow Geese continuously stayed on their nest for 60 h during a snow storm (Krechmar and Syroechkovsky 1978). Daily rhythm in incubation behavior, however, may not solely be a consequence of daily variations in weather conditions. In Greenland White-Fronted Geese (*Anser albifrons flavirostris*), nests are widely dispersed and Stroud (1982) suggested that females initiated more recesses at night in response to a low predator activity, rather than weather conditions *per se*.

The Greater Snow Goose (*Anser caerulescens atlantica*) is a large body size goose species with one of the northernmost breeding area in the canadian Arctic. Females incubate in a cold and often unpredictable environment, with extreme weather conditions being a constant threat for the parents and the eggs. Recently, Reed *et al.* (1995) reported a relatively low level of nest attentiveness during incubation (93 %) in this species. This observation contradicts the allometric model of Thompson and Raveling (1987) according to which large body size geese should have an almost continuous incubation constancy (> 95 %) because they can store more reserves and expend less energy per unit of mass than smaller species. However, the results of Reed *et al.* (1995) were drawn from only four days of visual observation within the incubation period, without reference to weather conditions. Thus, the present study was designed to (1) examine the incubation behavior of Greater Snow Geese throughout the entire incubation period and (2) to assess the effect of weather conditions on the incubation rhythm of females in a cold environment. We predicted that incubating females would regulate their absence away from the nest in order to minimize heat loss for the developing embryos.

METHODS

Field work was carried out on Bylot Island, Northwest Territories (73 °N, 80 °W), during the summers of 1995-1996. Data were collected at two nesting sites: a glacial valley characterized by wet polygon tundra and a low-elevated plateau 30 km south of the main study site (see description in Lepage *et al.* 1996). Geese nest colonially at each site and benefit from 24-h daylight during the entire nesting period.

Incubation rhythm

Egg temperatures were obtained from the addition of artificial eggs (hereafter called EGG) in goose nests (see Chapter 2 for full description and Appendix A for picture). EGGS were made of a hollow copper shell covered by a few millimeters of plaster to adopt the shape and size of real goose eggs. A thermistor soldered to the copper provided uniform temperature reading regardless of the orientation of the EGG with respect to the incubating bird thanks to the high conductivity of copper. Each thermistor was hooked to an electronic data logger (StowAway, *Onset Computer*) which stored temperature readings.

A total of 23 EGGS were added to clutches at the laying stage: 11 in 1995 and 12 in 1996. However, predators took 9 EGGS in 1995 and two females rolled the EGGS from their nest in 1996. As a result, 12 nests were followed during most of the incubation period (10 - 24 d). Temperatures were recorded by the thermistors with an accuracy of 0.5 °C and mean values were stored continuously at an interval ranging from 0.7 min to 3.2 min according to incubation stage and year (see Chapter 2 for precise values).

As thermal inertia of the EGGS was low, an abrupt drop in temperature reading was recorded every time females left their nest. Daily recess frequency and nest attentiveness were thus inferred for each nest from the EGG temperature data. Recesses were absences lasting ≥ 6 min and were easy to recognize on graphs of EGG temperature vs. time (see Fig. 1, Chapter 2). Duration of recess was the time from the beginning of a temperature drop to the end. The validity of recess duration calculated from the EGG temperature was determined by visual observations of five nests equipped with EGGS (see Appendix B for more details). There was no significant difference between the observed recess durations and the ones estimated from the EGGS (paired *t*-test, $df = 38$, $p > 0.86$). Periods of disturbance (duration 1 - 3 h) during nest visits were eliminated from the data and the mean daily values were adjusted to a 24-h period.

Weather parameters

An automated weather station at the main study area recorded air temperature (°C), relative humidity (%) and solar radiation (W/m^2) at 2 m above ground and wind velocity (m/s) at 2.5 m every min. Mean hourly values were saved by a *Campbell Scientific* CR-10 data logger. Precipitation was measured manually with a rain gauge by taking a daily reading around 21:00 (see Chapter 2 for more details).

Statistical analyses

Variations in mean daily recess frequency, recess duration and nest attentiveness were compared among females with one-way analyses of variance (ANOVA, model II). The effect of laying date of the first egg and the total clutch size on these three behavioral variables were examined with simple regressions. To test for a daily rhythm in incubation behavior, the day was divided into 8 periods of 3-h each (00:00-03:00, 03:00-06:00, 06:00-09:00, 09:00-12:00, 12:00-15:00, 15:00-18:00, 18:00-21:00 and 21:00-00:00, EST). Each recess was assigned to one of these periods based on its midtime. Each variable was analysed with a two-way analysis of variance using individual females and periods as factors. Multiple a posteriori comparisons followed Tukey's Honestly Significant Difference tests (Kirk 1982). The relationships between day of incubation and recess frequency, recess duration and nest attentiveness were examined to see how female behavior varied as the incubation period progressed. When laying date was unknown, incubation days were backdated from hatching date assuming that incubation lasts 24 d. Forward polynomial regressions were performed to determine temporal trends using mean daily behavior of females ($n = 24$). The effect of daily weather parameters on the behavioral variables was tested using multiple stepwise regressions for each female monitored. Significant level to enter or remove a variable was fixed to 0.05. Precipitation was not entered in the analyses for female 106 because it did not rain during the period that the nest was monitored. Results are presented as mean ± *SE*.

RESULTS

General incubation pattern

Females took on average 5 or 6 recesses per day (Table 5). Mean recess duration was 23 min, although median duration was only 17.5 min, which suggests that most recesses were of short duration with a few long ones (see Appendix D). Nest attentiveness during the whole incubation period was 91 %. Daily recess frequency, recess duration and nest attentiveness differed among females (recess frequency $F = 5.3$, $df = 11, 210$; recess duration $F = 12.2$, $df = 11, 204$; nest attentiveness $F = 16.8$, $df = 11, 210$; all $p < 0.01$) but variations were larger within females than among them (recess frequency 53.8 %; recess duration 61.5 %; nest attentiveness 81.2 %). Female 114 was clearly an outlier: she took more recesses and of longer duration than all other females monitored while having the highest average egg temperature during incubation (without recesses; Table 2). Consequently, her nest attentiveness was very low (Table 5). If we exclude this female, daily recess frequency among the other 11 females averaged 5.1, their duration 21.5 min and nest attentiveness was 92.4 % (Table 5).

Recess frequency, recess duration and nest attentiveness were not related with laying date ($r^2 = 0.02$, $p > 0.65$; $r^2 = 0.23$, $p > 0.10$; $r^2 = 0.11$, $p > 0.30$, respectively) nor with clutch size ($r^2 = 0.25$, $p > 0.05$; $r^2 = 0.26$, $p > 0.05$; $r^2 = 0.29$, $p > 0.05$; all $df = 11$). Thus, female behavior did not vary in any way with respect to the onset of laying or the number of eggs laid.

Daily rhythm

Incubation behavior varied significantly throughout the day and showed a clear daily cycle (Fig. 5). Females took more than twice as many recesses in late afternoon (0.99 / 3 h; 15:00 - 18:00) than at night (0.38 / 3 h; 00:00 - 06:00; $F = 16.6$, $df = 7, 77$, $p < 0.01$), and recesses were longer in late afternoon (25 min) than at night (20 min; $F = 7.1$, $df = 7, 77$ $p < 0.01$). As a result, nest attentiveness was highest at night (95 %) and lowest during late afternoon (86 %; $F = 18.7$, $df = 7, 77$, $p < 0.01$). Females differed in their incubation behavior ($F \geq 6.3$, $df = 11, 77$ $p < 0.01$ for all 3 variables) but examination of the daily pattern of individual females showed that they all adopted the same daily cycle for the three behavioral variables studied. Some females, however, consistently took more recesses or of longer duration than others.

Table 5. Laying date, clutch size (total laid and final at hatching), daily recess frequency and nest attentiveness, and recess duration of 12 female Greater Snow Goose. Mean ± *SE*.

Female	Laying date (June)	Clutch size total	Clutch size final	Recess frequency (n / d)	Nest attentiveness (%)	*N* (Days)	Recess duration (min)	*N* (Recesses)
14	12	7	7	3.9 ± 0.5	95.3 ± 0.7	23	17.3 ± 0.7	87
15	10	5	2	5.2 ± 0.6	92.8 ± 0.8	22	19.2 ± 0.6	112
103	13	4	3	4.9 ± 0.5	93.4 ± 0.7	24	19.8 ± 0.6	113
106	15	3	3	7.1 ± 0.7	90.1 ± 0.9	10	20.0 ± 0.9	69
107	14	4	3	5.0 ± 0.5	91.1 ± 0.9	17	25.7 ± 1.0	82
108	17	4	4	3.9 ± 0.4	95.2 ± 0.7	15	17.8 ± 0.9	57
114	18	2	2	8.0 ± 0.6	79.6 ± 1.8	13	36.6 ± 1.4	102
115	16	3	3	6.1 ± 0.6	91.0 ± 1.0	24	21.2 ± 0.6	140
118	17	3	2	5.6 ± 0.5	91.2 ± 0.8	19	22.9 ± 0.8	103
331	17	5	4	5.6 ± 0.4	90.0 ± 0.8	22	25.6 ± 1.0	119
363	19	3	3	3.1 ± 0.4	95.1 ± 0.9	15	22.6 ± 1.5	46
365	14	5	5	5.2 ± 0.4	91.4 ± 0.8	18	24.0 ± 0.8	90
Mean ± *SE*	15 ± 0.8	4 ± 0.4	3.4 ± 0.4	5.6 ± 0.4	91.4 ± 1.2	12	22.7 ± 1.5	12
Without 114	15 ± 0.8	4 ± 0.4	3.5 ± 0.4	5.1 ± 0.3	92.4 ± 0.6	11	21.5 ± 0.9	11

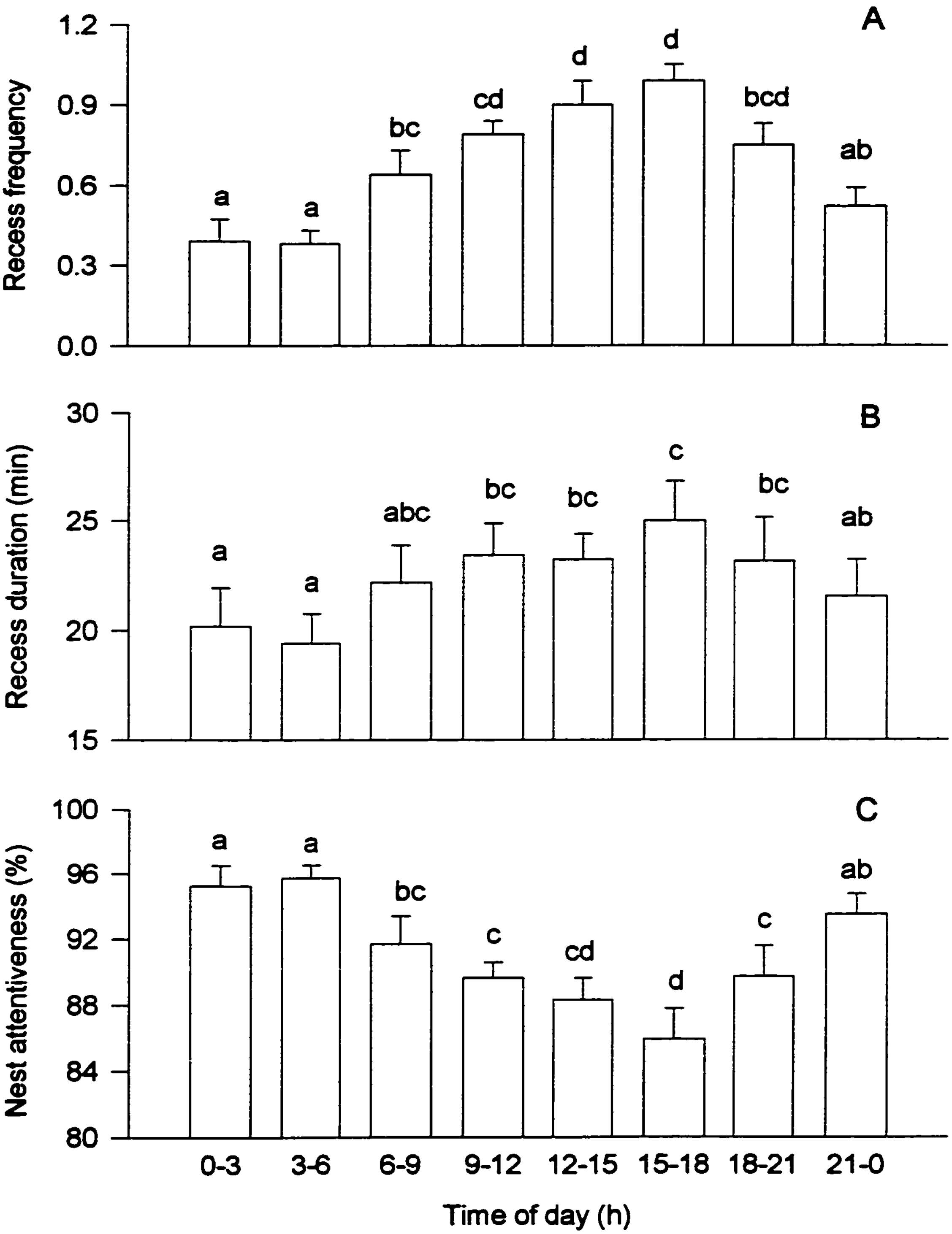

Figure 5. Relationship between recess frequency (A), recess duration (B) and nest attentiveness (C) of incubating female Greater Snow Goose ($n = 12$) and time of day. Mean (± *SE*) with different letters within each graph are significantly different (Tukey HSD, $p < 0.05$).

Incubation stage

Female behavior changed during the incubation period (Fig. 6). Recess frequency showed a gradual increase from less than four recesses on the first day of incubation to a maximum of seven recesses on day 19, followed by a sudden decrease to about two recesses on the day of hatching. A similar pattern was found for recess duration although variations were smaller. Duration increased from about 20 min on the first day of incubation to 24 min at mid-incubation and decreased thereafter to about 19 min at hatching. The net effect of these changes is reflected in daily nest attentiveness which declined for the first 17 d of incubation from 95 % to a low of 89 %, and then abruptly rose to a high of 96 % on the day of hatching.

Weather conditions and incubation rhythm

Incubating females were monitored for a period of 25 d in 1995 (15 June to 9 July) and 28 d in 1996 (18 June to 15 July). Prevailing weather conditions during this period (hourly means) in 1995 and 1996 were: mean ambient air temperature of 4.6 (range: 0.4 to 9.6) and 5.7 °C (-2.5 to 13.8); mean wind velocities of 3.5 (0.1 to 10.8) and 2.6 m/s (0 to 10.2); mean solar radiation of 210 (0 to 740) and 290 W/m^2 (0 to 700); mean relative humidity of 86.5 (54.6 to 94.7) and 83.5 % (58.5 to 92.2); total precipitation of 29 (maximal daily value: 12) and 18 mm (max: 7.5) of rain.

The incubation behavior of all females but number 106 was affected by prevailing weather conditions. Weather variables explained between 23 and 70 % of the variation in incubation behavior depending on the female (Tables 6 to 8). Generally, weather conditions explained more variation in recess frequency and nest attentiveness than in recess duration, and for a greater number of females. Five of the 12 females took more recesses when wind velocity was lower but one female (331) showed an opposite trend (Table 6). Three females also took more recesses when air temperature was warmer and one female under conditions of high solar radiation. Recesses were shorter when it rained for two females and when wind velocity was high for two females, although the effect of wind was in the opposite direction for another female (108; Table 7). Recesses were also longer for one female under high solar radiation and for another one when air temperature was high. Females sat for longer periods of time on their nest when wind velocity was high (5 females) and on rainy days (1 female), but diminished their attentiveness when solar radiation (3 females) and air temperature (3 females) were high (Table 8).

When data from all the nests were combined, precipitation and humidity had no effect on the incubation behavior (Table 9). However, it should be noted that even though it rained on 11 of the 25 d when females 14 and 15 were monitored in 1995, rain fell on only five of the 28 d during the 1996 nesting season. Other weather variables explained a significant but small amount of variation in incubation behavior of females. High air temperatures were associated with longer recesses and especially lower nest attentiveness. Under high solar radiation, nest attentiveness decreased because females left the nest more often and for longer periods of time. Finally, nest attentiveness increased under strong wind.

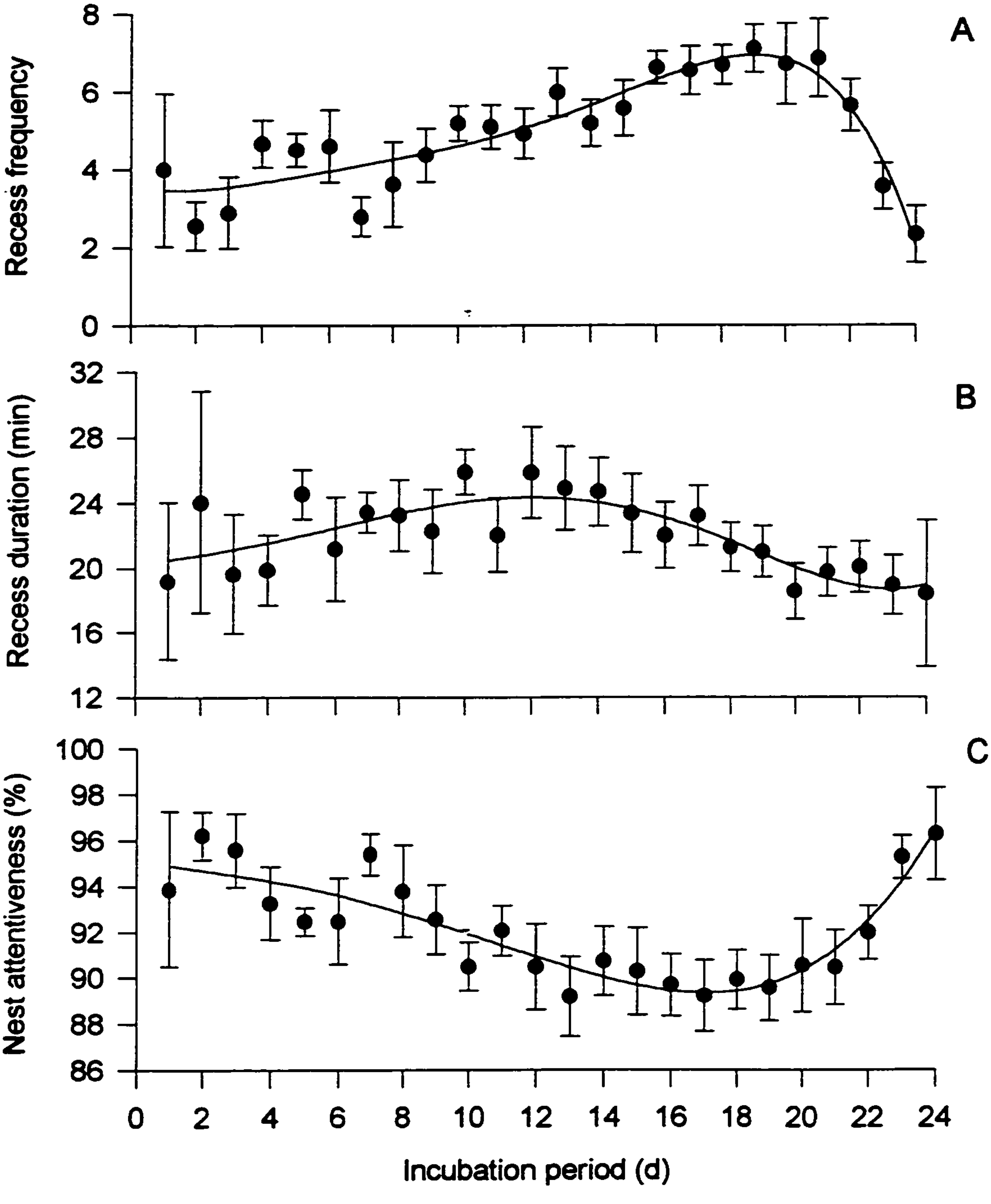

Figure 6. Relationship between daily recess frequency (A), recess duration (B) and nest attentiveness (C) of incubating female Greater Snow Goose and days into the incubation period. Each circle (mean ± *SE*) is the average value of 4 to 12 females. Curves are best of fit ($n = 24$) and were all significant ($p < 0.01$): recess frequency ($Y = 3.7 + 1.3686E\text{-}4X^4 - 5.8834E\text{-}6X^5$, $r^2 = 0.83$), recess duration ($Y = 19.4 + 0.60X - 1.8892E\text{-}4X^4 + 5.9622E\text{-}6X^5$, $r^2 = 0.63$) and nest attentiveness ($Y = 95.1 - 0.21X + 0.0114X^2 - 3.775E\text{-}3X^3 + 1.5700E\text{-}4X^4$, $r^2 = 0.82$).

Table 6. Relationship between daily recess frequency and daily weather conditions in individual female Greater Snow Goose. The sign and partial r^2 of variables which were significant, or almost significant, in the stepwise multiple regression model are shown ([ ] $p < 0.10$, *$p < 0.05$, **$p < 0.01$).

Female	Partial r^2					Total r^2	N
	Precipitation	Humidity	Solar radiation	Air temperature	Wind velocity		(Days)
14	-	-	(+) [0.14]	-	(-) [0.16]	ns	23
15	(-) [0.09]	-	(+) 0.33**	-	(-) 0.22**	0.55	22
103	-	-	-	(+) 0.13*	(-) 0.52**	0.65	24
106	-	-	-	-	-	ns	10
107	-	-	-	-	(-) 0.30*	0.30	17
108	-	-	-	-	-	ns	15
114	-	-	-	-	(-) 0.59**	0.59	13
115	-	-	-	(+) 0.49**	-	0.49	24
118	-	-	-	-	-	ns	19
331	-	(-) [0.11]	-	-	(+) 0.36**	0.36	22
363	-	-	-	-	(-) 0.48**	0.48	15
365	-	-	-	(+) 0.23*	-	0.23	18

Table 7. Relationship between daily recess duration and daily weather conditions in individual female Greater Snow Goose. The sign and partial r^2 of variables which were significant, or almost significant, in the stepwise multiple regression model are shown ([ ] $p < 0.10$, *$p < 0.05$, **$p < 0.01$).

Female	Partial r^2					Total r^2	N (Days)
	Precipitation	Humidity	Solar radiation	Air temperature	Wind velocity		
14	(-) 0.26*	-	-	(+) 0.17*	-	0.43	23
15	-	-	-	-	-	ns	22
103	-	-	-	-	-	ns	24
106	-	-	-	-	-	ns	10
107	-	-	-	-	(-) 0.47**	0.47	17
108	(-) 0.26*	(+) [0.14]	-	(+) [0.12]	(+) 0.32*	0.58	15
114	-	-	-	-	-	ns	13
115	-	-	(+) 0.32**	(+) [0.10]	-	0.32	24
118	-	-	-	-	(-) 0.38**	0.38	19
331	-	-	-	-	-	ns	22
363	-	-	-	-	(-) [0.27]	ns	15
365	-	-	-	-	-	ns	18

Table 8. Relationship between daily nest attentiveness and daily weather conditions in individual female Greater Snow Goose. The sign and partial r^2 of variables which were significant, or almost significant, in the stepwise multiple regression model are shown ([ ] $p < 0.10$, *$p < 0.05$, **$p < 0.01$).

Female	Partial r^2					Total r^2	N
	Precipitation	Humidity	Solar radiation	Air temperature	Wind velocity		(Days)
14	(+) [0.17]	-	-	-	-	ns	23
15	(+) 0.11*	-	(-) 0.34**	-	(+) 0.24**	0.69	22
103	-	-	-	(-) 0.11*	(+) 0.52**	0.63	24
106	-	-	(-) [0.36]	-	-	ns	10
107	-	-	-	-	(+) 0.59**	0.59	17
108	-	-	-	-	-	ns	15
114	-	-	(-) 0.19*	-	(+) 0.51**	0.70	13
115	-	-	(-) 0.11*	(-) 0.48**	-	0.59	24
118	-	(+) [0.06]	-	-	(+) 0.62**	0.62	19
331	-	-	-	-	-	ns	22
363	-	-	-	(-) 0.49**	-	0.49	15
365	-	-	-	-	(+) [0.22]	ns	18

Table 9. Relationship between daily incubation behavior of Greater Snow Geese and weather conditions, all nests combined (n = 222 d). The sign and partial r^2 of variables which were significant in the stepwise multiple regression ($^*p < 0.05$, $^{**}p < 0.01$) are shown. Precipitation and relative humidity were not significant for any of the incubation behavior variables.

	Partial r^2		
	Solar radiation	Air temperature	Wind velocity
Recess frequency	(+) 0.02*	-	-
Recess duration	(+) 0.09**	(+) 0.04**	-
Nest attentiveness	(-) 0.06**	(-) 0.18**	(+) 0.03**

DISCUSSION

General incubation behavior

The average incubation behavior reported here agrees with the values obtained by Reed *et al.* (1995) who previously monitored Snow Goose behavior during only 4 d at the same study site in 1991. Mean nest attentiveness (91.4 % here vs. 93 % in Reed *et al.* 1995) and recess frequency (5.6 vs. 6.1 recesses / d) were very similar although recess duration was longer (23 vs. 16 min) in our study. The latter difference could partly be a consequence of difference in methods used as ours could not detect recesses of very short duration (< 6 min). However, this bias is probably slight as such brief recesses are rare (Appendix B; Reed *et al.* 1995). The 1996 nesting season was delayed because snow-melt took place about two weeks later than usual (Lepage *et al.* 1996, personal observation). As a result, plant growth was delayed by almost two weeks compared to previous years (Gauthier *et al.* 1995; unpubl. data). Because females devote most of their time to feeding during recesses (Reed *et al.* 1995), they may have been forced to search for food or feed for prolonged periods of time in 1996 compared to 1991.

Our results support those of Reed *et al.* (1995) and dissipate any doubts associated with the short observation period in their work. Both studies show that female Greater Snow Goose have a relatively low nest attentiveness for a large body size goose. Although they certainly use endogenous lipid reserves during incubation, female Greater Snow Goose spend a significant amount of time feeding during this period and the time spent off the nest increases throughout incubation. Body mass of birds at the end of incubation suggests that endogenous lipid reserves are not totally depleted and that females are still in good condition (Reed *et al.* 1995). Hence, Greater Snow Geese do not conform to the allometric model proposed by Thompson and Raveling (1987) based on energetic constraints which predicts a positive relationship between goose body mass and nest attentiveness. According to this model, a bird the size of a Greater Snow Goose should spend well over 95 % of the time on the eggs during incubation which is clearly not the case. The risks of predation, the capacity of the birds to defend their nest, the investment of energy in the eggs which in part determines the endogenous reserves remaining to incubate the clutch, and the availability of food around the nests are other factors that may also affect the total nest attentiveness of females.

Canada Geese (Aldrich and Raveling 1983), Dark-Bellied Brent Geese (*Branta bernicla bernicla*; Spaans *et al.* 1993) and Greater Snow Geese (Reed *et al.* 1995; this study) have all been shown to leave the nest more often and for longer periods as incubation progresses (but not Emperor Geese, Thompson and Raveling 1987). Females could decrease their nest attentiveness over time because air and ground temperature increases, thereby reducing egg cooling rates during recesses. However, it is unlikely that this explanation applies to geese nesting on Bylot Island. Temperature at 2 cm below ground only rose by 0.2 °C from mid-June to mid-July. Furthermore, although air temperature increased by about 7 °C during the same period, egg cooling rates were not affected by air temperature (Chapter 2). An alternative explanation for the decrease in attentiveness could be that egg cooling rate during a recess decreases over time as growing embryos produce more heat (Turner 1990). Finally, it is also possible that females take more feeding bouts with the progression of the incubation as a response to decreasing lipid reserves.

A few days prior to hatching, young start to vocalize in the eggs, and later make clicking sounds as they start breaking the inner shell membranes. These auditory cues probably contributed to the increasing level of nest attentiveness by female Snow Goose, a common phenomenon in geese (Cooper 1978, Thompson and Raveling 1987, Madsen *et al.* 1989, Reed *et al.* 1995, but see Aldrich and Raveling 1983). High nest attentiveness during hatching would provide the young with the heat and humidity necessary for optimal hatching, as well as ensuring them an early imprinting on their mother.

Incubation rhythm according to time of day and weather conditions

Female Greater Snow Goose were more often away from their nest and for longer periods of time in the afternoon compared to the night, a commonly observed behavior in geese (Cooper 1978, Thompson and Raveling 1987, Madsen *et al.* 1989, Spaans *et al.* 1993, Reed *et al.* 1995) and in other arctic-nesting species (*e.g.* White-Rumped Sandpiper *Caladris fuscicollis*, Cantar and Montgomerie 1985). This daily cycle was present even though Greater Snow Geese were exposed to continuous 24-h daylight throughout the incubation period. However, it seems unlikely that this activity cycle was a consequence of an internal circadian rhythm as neither pre-laying nor brood-rearing Snow Geese showed a clear daily cycle in their time budget under conditions of continuous daylight (Giroux *et al.* 1986, Gauthier and Tardif 1991).

As eggs readily cool down when not attended, incubating birds may adjust their recesses in order to limit egg cooling rates and thereby maintain egg temperature within the critical thermal range for optimal embryonic development. This hypothesis was put forward by Aldrich and Raveling (1983) to explain why captive Canada Geese took more recesses in the afternoon, when ambient temperature was highest, than in the morning and at night. Such behavior is widespread in waterfowl as many other species have also been found to take longer recesses when air temperature is high (Mallard Ducks *Anas platyrhynchos*, Caldwell and Cornwell 1975; Northern Shovelers *Anas clypeata*, Afton 1980; Black Ducks *Anas rubripes*, Ringelman *et al.* 1982; Common Goldeneyes *Bucephala clangula*, Mallory and Weatherhead 1993; but not White-Winged Scoters *Melanitta fusca*, Brown and Fredrickson 1987; Emperor Geese, Thompson and Raveling 1987). Snow Goose movements away from the nest were mostly influenced by wind velocity, and to a lesser extent by air temperature and solar radiation. As the two latter variables reach their highest values during the middle of the day, it could explain the daily incubation rhythm of females. However, cooling rates of Greater Snow Goose eggs were found to be smaller when wind velocity was low and, to a lesser extent when solar radiation was high, while ambient air temperature had no significant effect (Chapter 2). As wind velocity does not show a clear daily cycle even though it tends to be strongest during the afternoon, our results only provide weak support to the hypothesis that daily incubation rhythm of females is a consequence of daily variation in factors affecting egg cooling rate during recesses.

Precipitation, and to a lesser extent relative humidity, have been shown to prevent incubating females from leaving their nest, although they do not follow a daily cyclic pattern (Afton 1980, Hawkins 1986, Brown and Fredrickson 1987, but see Ringelman *et al.* 1982). These variables were not significant in our study. However, it is possible that rain was not abundant enough on the study area during the 1996 nesting season to induce a detectable effect on the female behavior as it was sunny on 23 of the 28 d that nests were monitored.

It is also important to point out that females varied greatly in their response to prevailing weather conditions. This is not surprising as the microenvironment of each nest most probably modulated the effect of some weather parameters studied. For example, nests 115 and 118 were on a gentle slope facing the NorthWest, which could have reduced the radiative heat gain of the eggs during female recesses. Also, nest 331 was about 1 m East of a big rock, which could have reduced convective heat loss when the wind was coming from the West, the prevailing wind direction. Interestingly, it was this female whose behavior was in opposite direction to other females in response to wind (Table 6). Differences in nest microenvironment could therefore explain the large inter-individual differences in the effect of various weather variables on the incubation behavior of females, and moreover, why weather variables were not good predictors of behavior when all nests were combined (*i.e.* some effects were opposite in different females).

An alternative hypothesis to explain the daily cycle in incubation behavior might be differential predation risks with respect to the time of day. Predation is a major cause of nest failure in geese (Summers and Underhill 1987, Kostin and Mooij 1995, but see Harvey 1971) and unattended nests may be more vulnerable to predation (Inglis 1977). However, few authors have actually reported that predation pressure was a factor affecting incubation rhythm *per se* (Stroud 1982). Arctic Foxes (*Alopex lagopus*) are the dominant egg predators on our study area (Tremblay *et al.* 1997) and they were regularly observed at the goose colonies during both summers. Other predators include birds such as Gulls (*Larus* spp.), Jeagers (*Stercorarius* spp.) and the Common Raven (*Corvus corax*). The active period of these two groups of predators is very different: fox activity is largely concentrated at night whereas birds tend to be more active during the day (95 % of attacks by foxes on goose nests were observed between 19:00 and 03:00 vs. 15 % by birds; Joël Bêty, unpubl. data). Snow Geese defend their clutch from potential predators such as foxes. Recesses by incubating females are most often taken very close to the nest (< 20 m; Reed *et al.* 1995) and feeding couples run back to their nest when a fox is detected in the colony. Female are then reluctant to leave the nest for at least one hour after this mammal had been active at the colony (Reed *et al.* 1995, personal observation). Therefore, geese may adjust their incubation rhythm in reaction to the presence of predators such as foxes and this may be an important factor to account for higher nest attentiveness of geese at night.

In conclusion, incubation behavior of female Greater Snow Goose does not follow the allometric model proposed by Thompson and Raveling (1987). The relatively low nest attentiveness of Greater Snow Geese compared to other species of geese may be explained by other factors than strictly energetic considerations. Females mainly adjusted their incubation behavior in response to wind velocity, and, although this factor influenced egg cooling rates, predator activity may also play a role in the daily incubation rhythm.

CHAPITRE 4

HATCHING ASYNCHRONY IN GREATER SNOW GOOSE CLUTCHES: IS IT REALLY IMPORTANT ?

RÉSUMÉ

Le patron d'éclosion a été étudié chez la Grande Oie des neiges pour évaluer l'étendue dans l'éclosion des jeunes et voir comment ceci peut influencer leur survie. Bien que chaque oeuf prend environ 1,5 d pour éclore, l'écart d'éclosion à l'intérieur d'une même couvée était < 24 h dans la majorité des nids suivis (85 %). Aucune relation n'a été décelée entre le degré d'asynchronie d'éclosion des oeufs et la date d'éclosion ou la taille de couvée à l'éclosion. Il y a eu abandon d'oeufs et de jeunes dans 20 % des couvées mais dans la plupart des cas, l'éclosion des oeufs n'avait pas encore débutée. Le plus petit oeuf des couvées, considéré comme le dernier oeuf pondu, a été le dernier à éclore dans la moitié des couvées suivies. Puisque la relation entre la ponte du dernier oeuf et son ordre d'éclosion est faible, et que l'incubation chez la Grande Oie des neiges n'est initiée qu'une fois la ponte terminée, le dernier oeuf pondu ne semble pas désavantagé par rapport aux autres de la couvée.

ABSTRACT

Hatching pattern in Greater Snow Goose clutches was investigated to evaluate the magnitude of asynchrony in hatching and to see how it may affect the fate of newly hatched goslings. Although each egg takes about 1.5 d to hatch, the hatching interval within clutches was < 24 h in 85 % of the nests observed. The degree of hatching asynchrony within clutches was not related to either hatching date or final clutch size at hatching. Eggs or young were abandoned in 20 % of the clutches monitored but most of those eggs had not yet initiated hatching. The smallest egg in each clutch, considered to be the last-laid egg, was the last one to hatch in half of the clutches. As the relationship between the last-laid egg and its hatching order was weak and incubation in Greater Snow Geese is only initiated once the clutch is completed, last-laid eggs did not seem at a disadvantage compared to the other eggs in the clutch.

INTRODUCTION

Altricial birds often start incubating before the end of the laying period, which causes a developmental asynchrony among eggs of the same clutch (Stoleson and Beissinger 1995). Thus, the hatching sequence in those species often follows the laying order. On the contrary, in precocial species like ducks and geese, hatching of the eggs in a clutch should be synchronized as parents leave the nest with newly hatched young soon after their emergence (< 24 h). However, some authors have reported a certain degree of hatching asynchrony in ducks and geese, primarily for the last-laid egg of a clutch which tends to hatch last (Swennen et *al.* 1993). In Lesser Snow Geese (*Anser caerulescens caerulescens*), Cargill and Cooke (1981) even reported a close correspondence between laying and hatching sequences which suggests that females start incubating well before clutch completion. An early onset of incubation could be a strategy of the female to reduce the period of exposure of the clutch to predators (Arnold *et al.* 1987) or to advance hatching (Nilsson and Svensson 1993) if reproductive success declines seasonally (Lindholm *et al.* 1994, Lepage 1997). However, this may be a costly strategy in precocial birds because it will increase hatching asynchrony. Late-hatching embryos have a high risk of being abandoned by females who generally leave the nest for brood-rearing areas as soon as the first goslings are dry (Williams *et al.* 1993). We examined the level of intraclutch hatching asynchrony in Greater Snow Goose (*Anser caerulescens atlantica*) clutches, its relationship with the laying sequence and its consequence on the survival of embryos.

METHODS

Field methods

Field work was carried out during the summers of 1995-1996 at the Bylot Island Snow Goose colony (73 °N, 80 °W). The study area (see description in Lepage *et al.* 1996) was searched during the laying stage and nests found were identified with individually marked wooden stakes. Eggs were numbered with a felt pen, assigning numbers according to the reverse order of dirtiness if more than one new egg was present (assuming that the cleanest egg was the last-laid). Eggs were also measured along the longest and shortest axis to the nearest 0.1 mm using a dial caliper. In many nests, the exact laying sequence was unknown because the interval between visits at the same nest was too long.

Marked nests were visited daily at hatch and the exact hatching stages of each egg was identified using the following categories:

0 = No sign of hatching
1 = Chick can be heard tapping through the unbroken shell
2 = Single crack but no hole
3 = Several cracks (star) but still no apparent hole
4 = Egg pipped, hole < 1 cm
5 = Egg pipped, hole > 1 cm
6 = Wet chick out or almost out of the shell
7 = Dry chick

The time of each visit was noted. Nests were checked again after families had left the nest to record abandoned eggs or dead chicks. Unhatched eggs were broken to verify embryonic development.

Data analyses

We estimated the time taken by embryos to hatch, defined as the time required to go from stage 2 (first crack) to 7 (dry chick). This was determined based on the hatching stage of individual eggs at each visit and the time elapsed between two visits assuming that each hatching stage had an equal length. Stage 1 was excluded because it was more difficult to determine in the field and casual observations suggested that it could be longer than the other stages. For each nest, we calculated an index of hatching asynchrony defined as the difference in hatching stages between the most and the less advanced viable eggs in the hatching sequence on any particular visit. The index of asynchrony was related with hatching date via a simple regression and the effect of final clutch size at hatching was examined with a one-way analysis of variance (ANOVA).

Because complete laying sequences were unknown for many nests, egg size was used to infer the last-laid egg of a clutch. In waterfowl, the last-laid egg is almost invariably the smallest (Flint and Sedinger 1992, Robertson and Cooke 1993, Williams *et al.* 1993). Egg volume was determined according to: $V = 0.51 * \text{Length} * \text{Breadth}^2$ (Hoyt 1979). We retained only clutches in which 3, 4 and 5 eggs hatched because they were the most common. We tested the null hypothesis that the smallest egg had the same probability of hatching last compared to the other eggs of a clutch with Chi-square tests. Also, we checked if abandoned eggs were the smallest of the clutch and if the observed ratio differed from the one expected by chance only with Chi-square tests. Results are presented as mean ± *SE*.

RESULTS

The duration of hatching was determined for 249 eggs in 97 nests visited at least twice during the hatching process. The average duration of each hatching stage was 7.4 ± 0.2 h (range: 2.8 - 23.7 h). This gives an estimate of 37 h for the whole duration of hatching (from appearance of the first crack to a dry chick), which shows that clutches took more than a day to hatch. Our index of hatching asynchrony, which estimates the dispersion of hatching among eggs within a clutch, ranged from 0 to 5 stages, with a mean of 2.1 ± 0.1 stages, or 15.5 h ($n = 128$ clutches). Hence, the difference between the first and the last egg to hatch was < 24 h in 85 % of the monitored clutches. The index of hatching asynchrony was not related with hatching date ($r^2 = 0.02$, $df = 127$, $p > 0.85$) nor with final clutch size at hatching ($F = 1.6$, $df = 3, 124$, $p > 0.20$).

Abandoned eggs and young occurred in 20 % of the clutches (26 / 128) as follows: 1 egg in 21 clutches, 2 or 3 eggs in 3 clutches and 1 young in 2 clutches. The developmental stage of the eggs is unknown in 18 of these cases, but 8 eggs contained fully developped young and two eggs had no sign of embryonic development. Most of the abandoned eggs (23 / 28) never initiated hatching (*i.e.* never reached stage 2) and the two eggs most advanced in the hatching process reached stage 5.

Smallest eggs were the last ones to hatch in 50 % of the monitored clutches (61 / 123), a ratio which differs from the one expected by chance for all clutch size (Table 10). Thus, smallest eggs hatched last more often than others. The abandoned egg was the smallest one in 31 % of the clutches (5 / 16) in which only one egg was left behind and in which every egg of the clutch was measured. However, this ratio was not different from the one expected by chance ($\chi^2 = 4$, $df = 3$, $p > 0.50$).

Table 10. Expected proportion and observed frequencies in abandoned eggs of the smallest egg being the last egg to hatch vs. not being the last egg to hatch in a clutch. The null hypothesis assumes that the probability of the smallest egg to hatch last is equal to the other eggs.

Clutch size	Expected proportion	Observed frequencies	Chi-square value	*df*	*p*
3	1 : 2 (33 %)	33 : 25 (57 %)	15.33	1	< 0.01
4	1 : 3 (25 %)	18 : 25 (42 %)	5.94	1	< 0.02
5	1 : 4 (20 %)	10 : 12 (45 %)	11.00	1	< 0.01
Total	-	61 : 62 (50 %)	32.27	3	< 0.01

DISCUSSION

Most nests monitored (85 %) had all their young hatching less than 24 h apart, which suggests a low level of hatching asynchrony in Greater Snow Goose clutches. Such synchrony is essential in precocial species like geese because newly hatched goslings stay < 24 h at the nest before the parents lead them to nearby feeding areas (Williams *et al.* 1993). This may also explain why the degree of asynchrony within clutches was not related to either hatching date or final clutch size at hatching. The absence of seasonal effects on hatching asynchrony does not support the hypothesis that late-nesting females could start incubating earlier in the laying sequence than early-nesting ones to advance hatching and thereby benefit of better conditions for the growth of their elder goslings (Lindholm *et al.* 1994, Lepage 1997). However, intraclutch hatching asynchrony was variable among clutches, and this makes any seasonal effect hard to dissociate from individual differences. It also appears that the higher number of eggs implied in the process of hatching in a larger clutch has no effect on hatching asynchrony. Vocal communication among embryos in the latter stages of incubation may help synchronize hatching (Vince 1964) and thus cancel out a possible effect of clutch size (Davies and Cooke 1983).

Hatching sequence in waterfowl nests has sometimes been shown to follow laying order (Syroechkovsky 1975, Cargill and Cooke 1981) but not always (Cooper and Hickin 1972, Swennen *et al.* 1993). Our study only provides weak support for this conclusion. Although the smallest egg, which is almost always the last one laid in geese (Flint and Sedinger 1992, Williams *et al.* 1993), had a higher probability of hatching last, final eggs were not the last ones to hatch in half of the clutches we monitored. The relationship between laying and hatching sequences observed in some studies was attributed to a developmental asynchrony between the first and last eggs of a clutch caused by the onset of incubation before termination of laying. We showed that although nest attentiveness by female Greater Snow Goose increased during laying, egg temperature was still well below the one reached during the incubation period, when embryos develop (see Chapter 2). Hence, the near absence of embryonic development during laying could explain why last-laid eggs were often not the last one to hatch in our study.

Despite a low level of hatching asynchrony, many clutches had eggs left behind by the parents. Developmental stage of many of these eggs was unknown, but several were viable eggs as they contained fully grown young, and sterile eggs are not very common (Williams *et al.* 1993). Only 31 % of the abandoned eggs were the smallest of the clutch. If we assume that smallest eggs are the last-laid ones, this result does not agree with Williams *et al.* (1993) findings that last-laid eggs in geese have lower chances of producing a fledging than eggs in the middle of the laying sequence largely because of abandonment at the nest. However, most of the abandoned eggs in our study never initiated hatching, suggesting that they had a much delayed embryonic development in comparison to the other eggs of the clutch. Intraspecific nest parasitism affects a low but variable proportion of Snow Goose clutches (Lank *et al.* 1990). As these eggs are often laid after the onset of incubation by the host, it is possible that some of the eggs left behind came from a female other than the incubating parent. Human presence in the colony during hatching may have caused some families to leave the nest sooner than if otherwise undisturbed, which could explain some of the abandonment. However, since most of the abandoned eggs would have taken at least an extra day to hatch, it is likely that they would have been left behind, regardless of any possible disturbance at the nest.

In conclusion, hatching asynchrony within clutches appears to be low in Greater Snow Goose clutches even though the hatching process lasts about 1.5 d. Some eggs were abandoned in 20 % of the clutches monitored but, in most cases, this did not appear to be a consequence of asynchronous hatching caused by an early onset of incubation by the female. Other factors such as nest parasitism could be involved.

CHAPITRE 5

CONCLUSION GÉNÉRALE

Les limites et les avantages de la méthode utilisée

La présente étude visait à documenter le comportement de nidification de la Grande Oie des neiges de la ponte à l'éclosion, à déterminer le régime thermique des oeufs pendant toute la période d'incubation et à établir leurs conséquences sur la synchronie d'éclosion. La période de nidification a été étudiée chez plusieurs espèces d'oies, bien que peu de chercheurs ont utilisé, comme nous, la température des oeufs pour en déduire le comportement des femelles. Une saison de terrain difficile en 1995, marquée par un faible effort de reproduction des oies sur le site d'étude et un niveau de prédation très élevé, a exigé des modifications au protocole expérimental initial et une seconde année de terrain. Tous les objectifs ont alors été atteints.

L'aspect le plus décevant de la technique initiale a été sans contredit la perte de matériel sur le terrain en 1995. Le choix de ne pas attacher les faux oeufs contenant les thermomètres devait favoriser leur acceptation par les femelles couveuses. Mais, une telle précaution a peut-être été excessive car, bien que les mouvements de rotation des faux oeufs étaient restreints par le système d'ancrage utilisé en 1996, la majorité des femelles les ont quand même acceptés dans leur couvée (rejet par deux femelles).

L'utilisation de la température des oeufs pour en déduire le patron d'incubation des oies s'est avérée une méthode fiable, confirmée par la relation étroite entre la durée des absences évaluée par les faux oeufs et celle déterminée par l'observation visuelle des femelles au nid (Annexe B). L'identification des absences sur les graphiques de la température des faux oeufs en fonction du temps a par ailleurs été facilitée par la faible inertie thermique des boîtiers en cuivre des faux oeufs (Fig. 1; Chapitre 2). De plus, l'utilisation d'enregistreurs numériques avec une mémoire étendue (capacité de 32 000 valeurs dans l'intervalle de temps spécifié) nous a permis d'obtenir une quantité appréciable de données pendant plusieurs jours consécutifs tout en minimisant le dérangement des femelles. Bien que lors des absences parentales, les températures enregistrées par les faux oeufs diffèrent de celles des oeufs d'oie, à cause de leur propriétés conductives et inertielles différentes, la calibration des faux oeufs a permis d'ajuster les données afin que les chutes de température et les taux de refroidissement en l'absence des femelles réflètent plus étroitement ceux subis par les oeufs d'oies.

Plus d'une centaine de nids ont également été suivis durant l'éclosion. Il aurait été très intéressant de mettre en relation l'examen détaillé des séquences d'éclosion que nous avons fait avec les séquences de ponte respectives. Ceci était malheureusement impossible à cause d'un manque d'information au niveau des données de ponte. Il a donc fallu recourir à une autre méthode pour obtenir de l'information partielle sur les séquences de ponte, soit le volume des oeufs puisque le dernier oeuf pondu est presque toujours le plus petit de la couvée. Quoique cette méthode peut occasionner un léger biais, la taille du premier oeuf pondu de la couvée pouvant parfois s'approcher de celle du dernier (Williams *et al.* 1993), ce biais n'a pas pu être mesuré ni corrigé.

Les résultats

Malgré le peu de nids suivis durant la ponte, les résultats nous ont permis de mieux connaître le patron de présence au nid des femelles en parallèle avec la température des oeufs. Une présence croissante des femelles de la Grande Oie des neiges sur leurs oeufs démontre que l'incubation débute progressivement. Cependant, la température relativement basse des oeufs durant la ponte suggère que le développement embryonnaire commence seulement lorsque toute la couvée a été pondue. Cette présence sur les oeufs pourrait être une réponse des femelles à une motivation grandissante à incuber, provoquée par un changement hormonal, pour protéger les oeufs contre les prédateurs ou pour les maintenir au-dessus de la température de congélation afin d'en assurer leur viabilité. Il a déjà été noté que les oies passent assez de temps au nid durant la ponte. Il avait alors été conclu que ce comportement occasionnait un certain développement embryonnaire dans les oeufs (Cooper 1978), susceptible d'entraîner ainsi une certaine asynchronie dans l'éclosion des oeufs à l'intérieur d'une même couvée (Cargill et Cooke 1981). Mes résultats semblent donc contredire cette hypothèse. Cependant, la température des oeufs durant la ponte a été rarement mesurée (Krechmar et Syroechkovsky 1978, Flint *et al.* 1994).

Le faible écart dans l'éclosion des jeunes d'une couvée appuie les données obtenues durant la ponte selon lesquelles le développement embryonnaire à l'intérieur d'une même couvée est uniforme, ou presque. Celui-ci pourrait donc expliquer la faible relation observée entre le dernier oeuf pondu (*i.e.* le plus petit) et l'émergence du dernier jeune d'une couvée. Chez les espèces nidifuges comme les oies, une synchronie à l'éclosion est capitale pour la survie des jeunes puisque les parents doivent les amener vers des sites d'alimentation et d'élevage peu de temps après leur émergence (< 24 h). Néanmoins, il y a eu l'abandon d'un oeuf ou d'un jeune dans 20 % des nids. Bien que dans plusieurs des cas la croissance des embryons était complète ou presque, l'oeuf abandonné n'avait souvent pas encore débuté le processus d'éclosion. Ainsi, le développement embryonnaire tardif de ces oeufs suggère que certains pourraient avoir été ajoutés au nid une fois l'incubation amorcée (*i.e.* par parasitisme intraspécifique).

Les 12 femelles suivies ont adopté un rythme d'incubation similaire à celui observé par Reed *et al.* (1995) lors de leur étude répartie sur quatre jours d'incubation au même site en 1991. La présence au nid des femelles est cependant inférieure à celle anticipée par la relation allométrique avancée par Thompson et Raveling (1987). Reed *et al.* (1995) ont associé cette faible assiduité à de basses réserves énergétiques disponibles pour l'incubation suite à une longue migration. Les femelles dépendraient alors considérablement de la nourriture obtenue sur le site de nidification pour répondre à leurs besoins énergétiques durant l'incubation.

Le patron de réchauffement des oeufs par les femelles a un effet immédiat sur le développement des embryons et sur la protection des oeufs. Ainsi, les absences du nid sont habituellement de courte durée (23 min) et elles sont plus souvent prises l'après-midi que la nuit, lorsque le milieu ambient est plus chaud. De plus, plusieurs femelles ont quitté leur nid moins souvent lorsque la vitesse du vent était élevée, un paramètre qui influence le taux de refroidissement des oeufs. Les oeufs sont incubés à une moyenne de 37 °C et leur température ne chute que d'environ 3 °C lorsque l'oie s'absente du nid. Les absences semblent donc être prises lorsque les conditions n'occasionnent pas un trop grand refroidissement des oeufs, ce qui permet de maintenir ces derniers dans un environnement thermique favorisant leur développement embryonnaire. Toutefois, le rythme journalier d'activité des femelles pourrait également être influencé par les périodes de présence des prédateurs. Lors des absences, les femelles s'alimentent à proximité de leur nid (< 20 m; Reed *et al.* 1995) et elles reviennent toujours sur leur couvée lorsqu'il y a un prédateur dans la colonie. Les oies sont aussi plus actives loin du nid le jour, à l'inverse de leur prédateur principal d'oeufs, le renard arctique (Tremblay *et al.* 1997), qui est surtout actif la nuit.

La durée des absences à l'intérieur d'une journée varie très peu pendant la période d'incubation, ce qui suggère que la durée observée pourrait représenter le temps nécessaire pour remplir complètement le jabot. Les besoins alimentaires grandissant avec la progression de l'incubation seraient alors comblés par un plus grand nombre d'absences. Une augmentation du temps consacré à l'alimentation pourrait être une réponse à la diminution de réserves lipidiques endogènes.

Implications de la recherche

La présente recherche a mis en lumière plusieurs aspects du comportement des femelles de la Grande Oie des neiges, de la ponte à l'éclosion. Toutefois, certains de nos résultats contredisent ceux obtenus par d'autres chercheurs. De plus, l'absence de développement embryonnaire durant la ponte devrait être vérifiée et confirmée avec un plus grand échantillon. Il reste encore plusieurs phénomènes à mieux comprendre, comme par exemple le rôle exact de la présence des prédateurs sur le comportement des femelles à leur nid.

ANNEXE A

Figure 7- Picture showing, from left to right, (1) an electronic data logger (StowAway, *Onset Computer*), (2) a waterproof plastic tube in which data loggers were placed, (3) a finished EGG, and (4) a hollow copper shell (open), revealing the thermistor wire and the metal wire to hold the EGG to the ground and to reinforce the sensor wire.

ANNEXE B

Visual observation of incubating females with EGGS in their nest allowed us to verify the validity of recess frequency and duration data calculated from the recordings of EGG temperature. During 54 h of observation between 28 June and 7 July 1996, we witnessed 40 recesses from five different females. The relationship between recess duration measured from the EGGS and directly observed are presented on Fig. 8. Statistics were performed excluding one outlying point: during this recess, the EGG temperature showed a gradual stepwise cooling trend instead of a clear rapid drop in temperature as in the other cases. On two additional occasions, the EGG temperature showed a temperature drop suggesting an absence by the female even if it went unnoticed to the observer. This could have been a misidentified female as many more females were present around the observed one, or a female standing up above her clutch in a way that was not detected due to distance.

A paired *t*-test showed that there was no significant difference between the observed recess duration and the one calculated from the EGGS ($t = -0.17$, $df = 38$, $p > 0.86$). The relationship between the two measurements was highly significant (Fig. 8; $r^2 = 0.62$, $p < 0.01$), although the slope of the relationship differed from 1 ($b = 0.78$, [0.58 - 0.98] 95 % CI of slope). Consequently, the EGGS overestimated recess duration when the female was absent for < 23.6 min. Recess durations used were those evaluated from the EGGS temperature, without any correction factor.

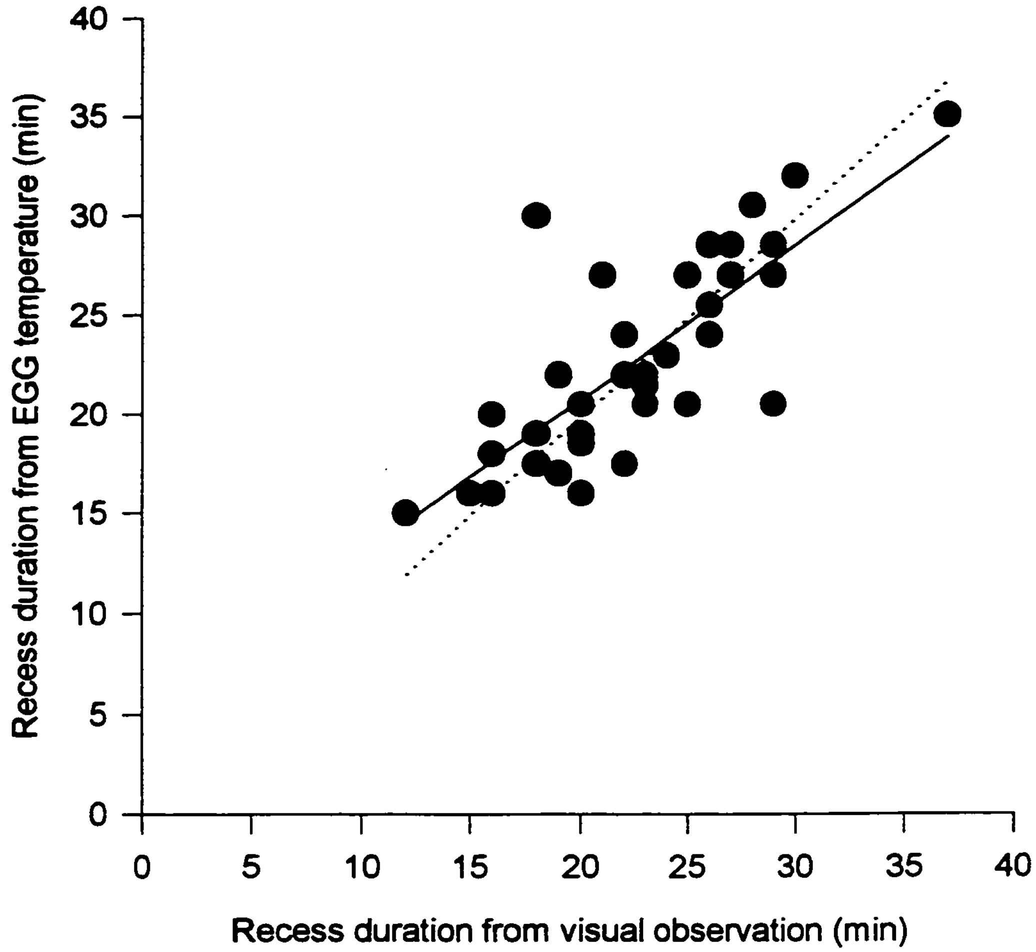

Figure 8. Relationship between recess duration determined by EGG temperature and direct observation of goose attentiveness at the nest, Y = 0.78X + 5.21. The stippled line is the predicted line of equality between the two methods (slope = 1).

ANNEXE C

Mathematical model to obtain cooling rates of goose egg

Artificial eggs were built from material with thermal properties that differed from those of real goose eggs. It was therefore necessary to apply a correction factor to transform cooling rates of the artificial eggs during the absence of females into values which would more adequately reflect those of real goose eggs.

Three freshly laid goose eggs (mass of 111, 118 and 120 g) were fitted with a thermistor inserted near their centre. Temperature values were recorded every 1.6 min with an accuracy of 0.5 °C and stored in a electronic data logger (StowAway, *Onset Computer*). Real and artificial eggs ($n = 3$) were simultaneously exposed to six sessions of cooling and heating. All eggs were placed in an oven at 37 °C until equilibrium was reached (4 h) and were then transferred to a closed box which was put in an environment of about 4 °C for another 4 h (Fig. 9). The operation was reversed for heating experiments. This allowed us to calculate time constants, defined here as the time necessary for each egg tested to reach 63.2 % of temperature change between the initial temperature and the one at equilibrium. Cooling experiments yielded time constants of 33.2 ± 10.3 (*SD*) min for artificial eggs and 66.7 ± 5.2 min for real eggs while the heating experiments gave time constants of 32.7 ± 2.2 min and 51.9 ± 5.4 min, respectively.

These time constants were incorporated into an exponential model to transform the final temperature obtained with artificial eggs during each recess into the value expected for a real egg. This corrected temperature was used to calculate (1) the difference in temperature between initial and final temperature (temperature drop), (2) the average egg cooling rates (°C/min), and (3) the instantaneous egg cooling rates [(°C/h)/°C] during female absences. The first and last temperature recordings by the artificial eggs were excluded from the calculation of recess duration in the formula involving cooling rates. The model was as follows:

$$T_f = T_i - \frac{\Delta T_e}{1 - e^{(-Lr/ke)}/1 - e^{(-Lr/kg)}} \tag{1}$$

$$R_a = \frac{T_f - T_i}{L_c} \tag{2}$$

$$R_i = \frac{R_a \times 60}{\Delta T_a} \tag{3}$$

where:

k_e = Time constant of artificial eggs (min)

k_g = Time constant of goose eggs (min)

L_r = Total recess duration (min)

L_c = Recess duration (excluding initial and final temperature recordings; min)

R_a = Average egg cooling rate (°C/min)

R_i = Instantaneous egg cooling rate [(°C/h)/°C]

ΔT_a = Difference between artificial egg and ambient temperature at departure of female from the nest (°C)

ΔT_e = Difference between the initial and final temperature measured by artificial eggs during the female absence (°C)

T_f = Corrected final temperature of artificial eggs during the female recess (°C)

T_i = Initial (*i.e.* incubating) temperature of artificial eggs (considered to be equal to the temperature of real goose eggs, °C)

Example of calculation

Applying the previous formula to the data in Table 11 would yield the following values:

$$T_f = 37.0 - \frac{37.0 - 27.2}{\dfrac{1 - e^{(-40.0/33.2)}}{1 - e^{(-40.0/66.7)}}} = 30.7^\circ C \tag{1}$$

$$R_a = \frac{30.7 - 36.6}{36.8} = -0.16^\circ C/\text{min} \tag{2}$$

$$R_i = \frac{-0.16 \times 60}{36.6 - 6.9} = -0.32(^\circ C/h)/^\circ C \tag{3}$$

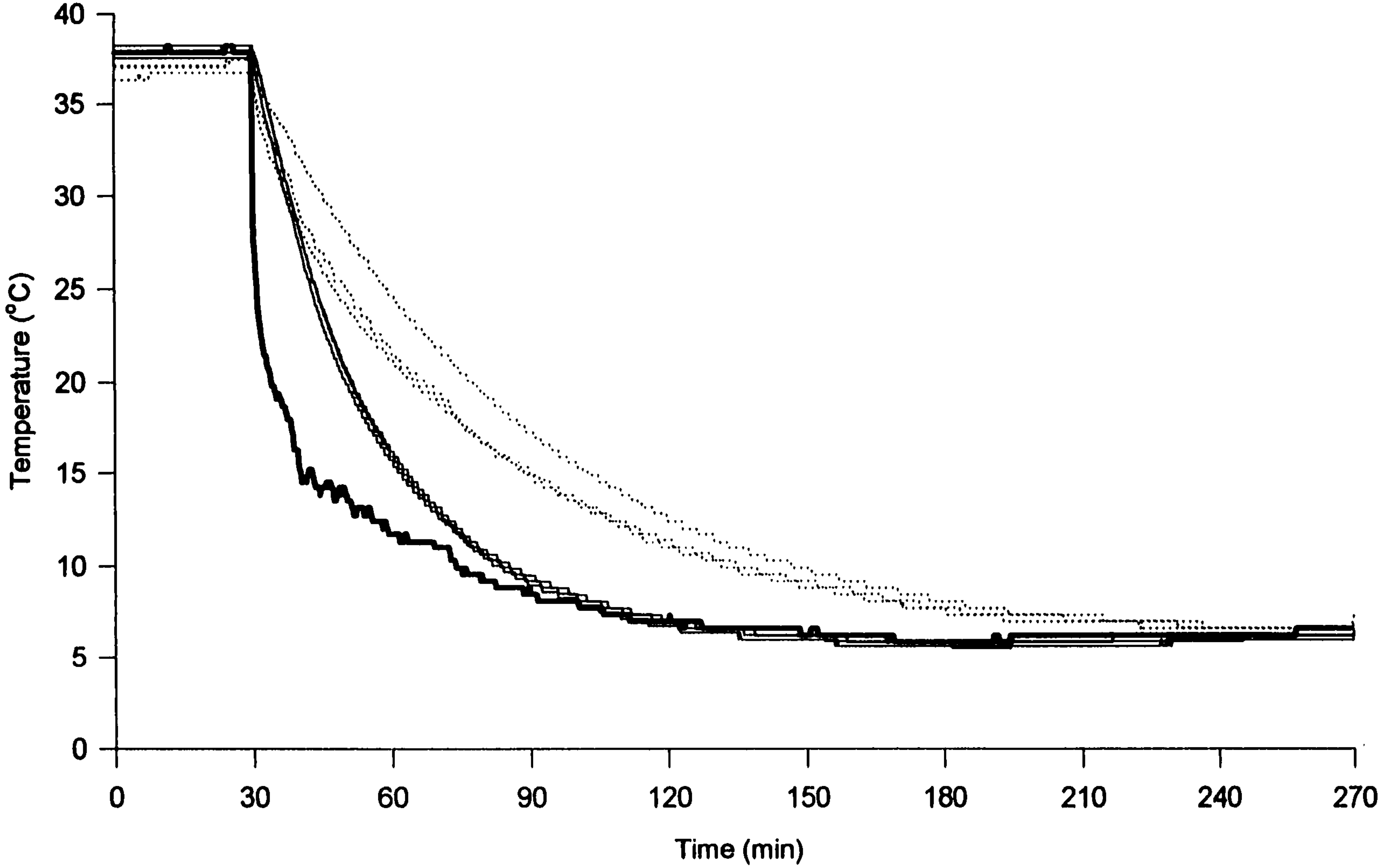

Figure 9. Example of cooling experiment, showing temperature near the eggs inside the box containing the eggs (bold line) along with goose egg (dotted lines) and artificial egg (solid lines) temperatures. Ambient air temperature outside the box was about 4 °C.

Table 11. Example of the time course of the temperature of an artificial egg during a recess of 40 min. The time shown excludes the initial and final temperature readings for the calculation of cooling rate. Air temperature during the recess was 6.9 °C.

Time (min)	Temperature (°C)
-	37.0
0.0	36.6
1.6	35.8
3.2	35.4
4.8	34.6
6.4	34.2
8.0	33.8
9.6	33.5
11.2	33.1
12.8	32.7
14.4	32.3
16.0	31.9
17.6	31.6
19.2	31.2
20.8	30.8
22.4	30.4
24.0	30.1
25.6	29.7
27.2	29.3
28.8	29.0
30.4	28.6
32.0	28.6
33.6	28.2
35.2	27.9
36.8	27.5
-	27.2

ANNEXE D

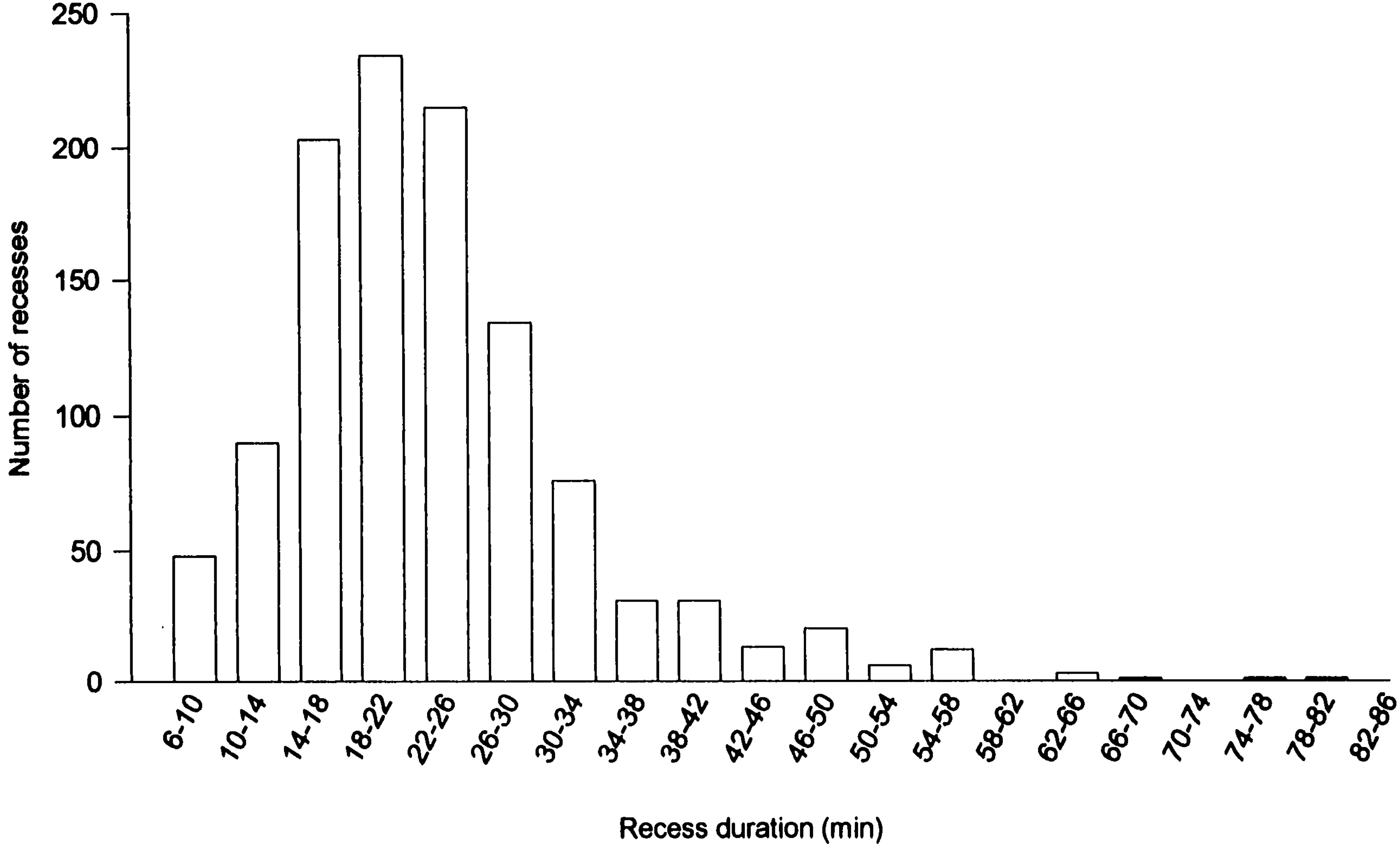

Figure 10. Distribution of every recess, except one of 98.5 min, taken by the 12 female Greater Snow Goose followed during the incubation period (n = 1119).

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IMAGE EVALUATION
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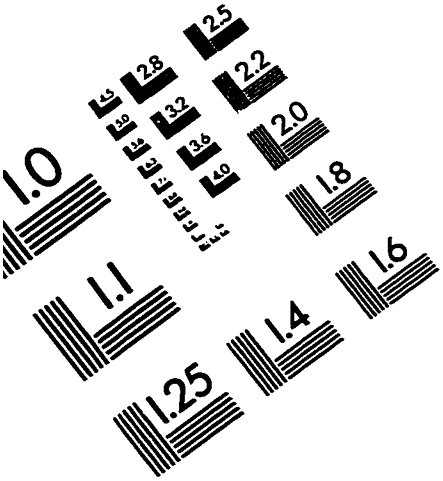

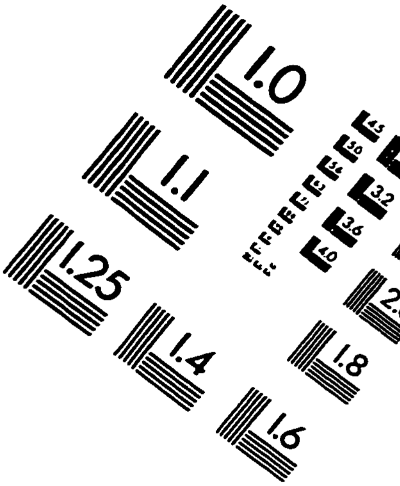

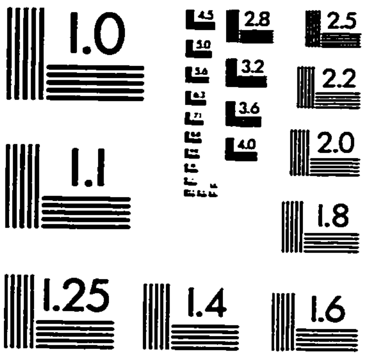

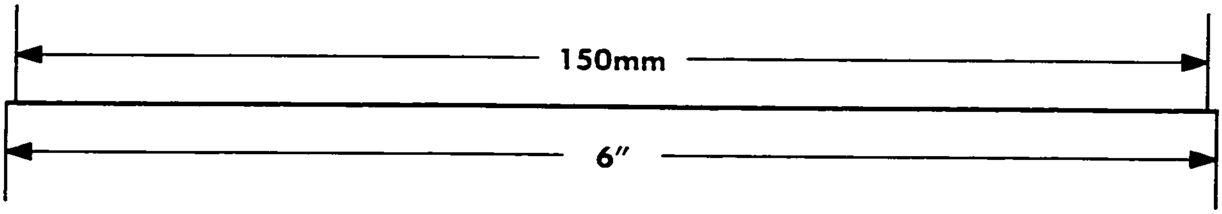

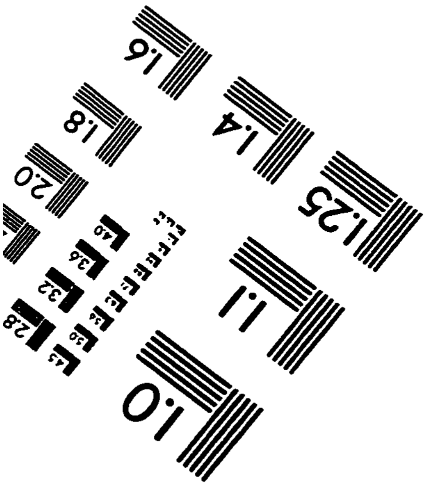

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