UNIVERSITÉ DU QUÉBEC

COMPORTEMENT DE PONTE DES FEMELLES EIDER À DUVET (*SOMATERIA MOLLISSIMA*)

MÉMOIRE PRÉSENTÉ À L'UNIVERSITÉ DU QUÉBEC À RIMOUSKI

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Avertissement

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RÉSUMÉ

Le comportement d'incubation des femelles Eider à duvet (*Somateria mollissima*) a déjà fait l'objet de plusieurs études. Les femelles eiders passent plus de 95% de leur temps sur les nids, ce qui représente une constance d'incubation parmi les plus élevées que l'on puisse rencontrer chez les oiseaux. Cela limite le temps disponible pour se nourrir et de fait, les femelles jeûnent pendant la majeure partie des 26 jours que dure l'incubation. Le comportement de ponte et de pré-ponte est beaucoup moins connu. Pourtant c'est pendant ces deux périodes que les femelles vont devoir subvenir à une dépense énergétique élevée car elles doivent accumuler les réserves nécessaires pour faire face à la production d'une couvée et au jeûne associé à l'incubation. Cette étude s'attache ainsi à décrire leur comportement pendant ces deux périodes et à savoir quand les femelles fréquentent leur nid et ce qu'elles font lorsqu'elles s'en absentent. Pour ce faire, nous avons tout d'abord déterminé la date de ponte et d'éclosion, la taille des couvées de même que le poids des femelles au début de la reproduction. Dans un deuxième temps nous avons muni des femelles de deux types de consignateurs de données. Les premiers sont des consignateurs enregistrant la température des nids à intervalle de temps régulier (1,5 ou 3 minutes suivant les modèles) et permettant de connaître les périodes de présence et d'absence des femelles de leur nid. Les seconds sont des consignateurs de rythme cardiaque et de pression hydrostatique implantés dans la cavité abdominale des femelles et permettant d'enregistrer les activités de plongée effectuées par l'oiseau.

Les premiers consignateurs nous ont permis de montrer que le temps passé sur les nids augmentait de 6 heures 20 minutes à 23 heures 24 minutes pendant les six premiers jours de ponte et que les femelles passaient en moyenne 39% de temps de plus sur leur nid le jour que la nuit. L'augmentation du temps passé sur les nids est principalement liée au fait que les femelles s'installaient sur les nids de plus en plus tôt chaque jour (de 02 :49 au jour 1 à 22 :15 au jour 5). Cette fréquentation des nids n'induit une différence de développement embryonnaire que de 15,91 degrés-jours, correspondant à 1,2 jour de pleine incubation, ce qui ne compromet pas le synchronisme des éclosions observé chez cette espèce. Ce comportement peut s'expliquer en invoquant plusieurs sources de pression de sélection : d'une part la prédation sur les œufs par les prédateurs aériens qui expliquerait la présence des femelles le jour pour limiter l'exposition des œufs et d'autre part la prédation sur les adultes par les prédateurs terrestres et/ou la nécessité de s'alimenter qui induirait le départ des femelles la nuit.

Les seconds consignateurs ont mis en évidence que les femelles passaient beaucoup de temps à plonger, près de 3 heures 45 minutes, pendant la période pré-ponte c'est à dire entre la fin de la migration printanière les menant sur les sites de reproduction et le début de la ponte. Nous pouvons relier ce phénomène à la constitution de réserves pendant les

premiers jours suivant l'arrivée des oiseaux sur les sites de reproduction et à la croissance des ovaires et la constitution des œufs par la suite. Il est également apparu que le temps de plongée diminuait à 1heure 10 minutes au début de la ponte. Cela indique que même si les femelles diminuent beaucoup leur activité de plongée, celle-ci n'en reste pas moins substantielle et que les femelles peuvent donc combler une partie de leurs besoins avec de la nourriture récemment ingérée et pas uniquement avec les réserves accumulées. Cela remet en question les conclusions d'études antérieures qui avaient caractérisé l'Eider à duvet comme une espèce ne comptant que sur ses réserves pour subvenir à la dépense énergétique engendrée par la reproduction.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

INTRODUCTION GÉNÉRALE

LES CONTRAINTES DE REPRODUCTION CHEZ LES OISEAUX

La reproduction est une étape extrêmement exigeante chez les oiseaux car elle entraîne une dépense énergétique élevée, un investissement de temps considérable et un accroissement de la vulnérabilité des adultes vis à vis de la prédation.

La dépense énergétique quotidienne pour les femelles pendant l'ensemble de la reproduction varie suivant les espèces, mais de manière générale elle représente l'un des investissements majeurs en énergie du cycle annuel. La production des œufs représente à elle seule un coût pouvant atteindre plus de trois fois le taux métabolique de base chez la sauvagine (Ward 1996, Monaghan and Nager 1997). Cette dépense énergétique exceptionnelle peut s'accompagner d'une perte de poids dépassant le tiers de la masse des individus chez ces espèces (Afton and Paulus 1992).

L'investissement de temps est lié à l'incubation des œufs d'une part et à l'élevage des jeunes d'autre part. Cet investissement est d'autant plus important que l'incubation est longue et l'autonomie des jeunes est tardive. Ces deux facteurs évoluent globalement en sens opposés : plus les oisillons sont autonomes à l'éclosion, moins ils requièrent d'attention de la part du ou des parents mais plus le temps d'incubation des œufs est long.

Enfin, il est possible que la période de reproduction constitue une phase de vulnérabilité accrue vis à vis de la prédation pour des adultes qui doivent passer du temps à incuber et défendre les œufs et à alimenter et protéger les jeunes. D'une part, la multiplication des déplacements vers un même site pourrait en outre favoriser la détection des adultes aussi bien que des nids par les prédateurs. D'autre part, certaines espèces font l'expérience d'une mobilité réduite temporaire qui augmente encore le risque de prédation (Witter et al. 1994, Kullberg et al. 2002).

LA REPRODUCTION CHEZ L'EIDER À DUVET

L'Eider à duvet (*Somateria mollissima*) a une stratégie de reproduction qui semble l'une des plus contraignantes chez les oiseaux. Comme chez la plupart des Anatidés, les femelles sont les seules à s'occuper de la formation des nids, de l'incubation des œufs et de l'élevage des jeunes. En outre, pendant les 26 jours que dure l'incubation, les femelles eiders passent plus de 95% de leur temps sur les nids (Bolduc and Guillemette 2003, Sabourin 2003). Cette période prolongée de jeûne entraîne une perte de masse de 44 à 50% sur l'ensemble de la période de reproduction et de 23 à 36% uniquement pendant la période d'incubation (Korschgen 1977, Parker and Holm 1990, Gabrielsen et al. 1991).

Ce comportement est interprété comme une adaptation visant à minimiser le risque de prédation sur les œufs, notamment par les prédateurs aériens (Choate 1967, Milne 1976, Korschgen 1977, Thompson and Raveling 1987, Thomas 1988). La prédation représente le principal facteur agissant sur le succès de reproduction des oiseaux (Choate 1967, Cody 1971, Lima 1987, Pärt 2001). Lima (1987) envisage même que la prédation soit la source

de pression de sélection ultime s'exerçant sur la taille des couvées produites par les oiseaux. Les œufs constituent en effet une source de nourriture idéale pour bien des prédateurs aviens et mammaliens puisqu'ils assurent une source d'énergie de qualité peu coûteuse à trouver et prévisible d'une année à l'autre.

La période de ponte constitue donc une période importante du cycle des femelles eiders durant laquelle celles-ci doivent passer d'une phase d'alimentation intensive en mer à une phase de jeûne et de présence presque continue sur les nids. La manière dont se fait cette transition est mal connue et les résultats déjà existants sont contradictoires. Notamment le début de l'incubation permanente varie suivant les études (Swennen et al. 1993, Hanssen et al. 2002). D'autre part certaines études concluent que les femelles jeûnent pendant la ponte (Korschgen 1977, Parker and Holm 1990) alors que des évidences indirectes provenant d'autres études suggèrent le contraire (Franzmann 1980).

OBJECTIFS DE L'ÉTUDE

L'importance de la perte de masse est un point critique chez les femelles eiders puisqu'elle peut avoir pour conséquence l'abandon de la couvée ou dans certains cas la mort de la femelle. Le moment où se produit le début de la période de jeûne ainsi que niveau de réserves accumulées par les femelles sont donc des variables pouvant jouer un rôle très important sur le succès reproducteur inclusif des femelles, notamment dans le cas d'une espèce longévive comme l'Eider à duvet. L'objectif général de cette étude est donc de décrire le comportement des femelles pendant la période de ponte et de déterminer

comment s'effectue la transition entre la période d'alimentation intensive et la période d'incubation intensive.

Chez l'Eider à duvet, les éclosions sont relativement synchrones, en l'espace de 24 heures généralement (Afton and Paulus 1992). Pour en arriver à un tel niveau de synchronie, on peut penser que la différence de développement embryonnaire entre les embryons est assez faible et donc que les premiers œufs pondus ne sont pas incubés beaucoup plus longtemps que les derniers œufs pondus. Cela suggère que l'incubation des œufs ne débute que vers la fin de la ponte et par conséquent que les femelles ne passent pas beaucoup de temps sur leurs nids pendant la ponte ou bien qu'elles limitent la température appliquée aux œufs pendant leurs périodes de présence sur les nids. Le premier objectif s'attache donc à quantifier le temps passé sur les nids ainsi que le niveau de développement embryonnaire induit.

D'autre part, des études antérieures ont qualifiées l'Eider à duvet d'espèce se reproduisant sur leur « capital », c'est-à-dire utilisant uniquement leurs réserves pour produire les œufs et subvenir à leurs besoins pendant la reproduction (Meijer and Drent 1999). Cette stratégie suppose que les femelles ne s'alimentent pas et économisent leur énergie pendant les périodes de ponte et d'incubation. Les méthodes utilisées pour en arriver à cette conclusion sont discutables et nous souhaitons valider l'existence de ce comportement en utilisant une méthode directe pour quantifier le temps passé à plonger. Le second objectif est donc de déterminer si les femelles s'alimentent pendant la période de ponte.

CHAPITRE 1

FEMALE BEHAVIOUR DURING EGG-LAYING IN COMMON EIDERS

Abstract. Laying is a critical period for female Common Eiders (*Somateria mollissima*) as it represents the transition between a period of intense feeding activity during pre-laying and a period of high nest attendance during incubation. Thus a number of important tactical decisions such as when to lay eggs, when to start incubating, when to stop feeding need to be made. We investigated laying behaviour in a Danish colony in April 2003-2005 by implanting temperature recorders in eider nests just after the first egg was laid. From temperature patterns, we extracted presence and recess periods of females on their nests and calculated embryonic development of each egg laid. We compared nests attendance and embryonic development patterns to predictions associated with a set of factors explaining the different aspects of females laying behaviour. We observed that nest attendance increased similarly for all females over the laying sequence irrespective to clutch size produced and was 39% higher during daylight hours than during nightlight hours. Temperatures high enough for embryonic development were applied as early as the second day of laying but did not induce an asynchrony higher than 2.5 days. These results were mostly consistent with three selective factors: nest predation, adult predation and feeding.

Key words: Common Eider, nest attendance, laying, incubation.

INTRODUCTION

Many studies have enlightened a recurrent paradox in precocial species. As hatching is relatively synchronous within a clutch (Cargill and Cooke 1981, Afton and Paulus 1992), females are not expected to incubate their eggs before clutch completion (Gill 1995). Yet they do (review in Afton and Paulus 1992), as females spend greater time on their nests as laying progresses (Caldwell and Cornwell 1975, Cooper 1978, Afton 1979a, b, 1980, Kennamer et al. 1990, Swennen et al. 1993, Wilson and Verbeek 1995, Persson and Goransson 1999, Poussart et al. 2000). Nest attendance during laying may induce temperatures above embryonic development threshold (Caldwell and Cornwell 1975, Cooper 1978, Afton 1979a, Persson and Goransson 1999, Poussart et al. 2000, Hanssen et al. 2002, Badyaev et al. 2003, Hepp 2004, Loos and Rohwer 2004) which are responsible for an asynchronous development of eggs within a clutch of up to two or three days (Cooch 1961, Caldwell and Cornwell 1975, Afton 1979a, Cargill and Cooke 1981, Kennamer et al. 1990).

Laying behaviour is a trade-off between periods of nest attendance and periods of recesses, each being related to potential costs and benefits. In Common Eider, costs of nest attendance include 1° reducing the female ability to forage (Aldrich and Raveling 1983, Flint and Grand 1999, MacCluskie and Sedinger 1999), 2° promoting hatching asynchrony and 3° increased risks of predation on the females (Charnov and Krebs 1974, Afton and Paulus 1992). Benefits include 4° ensuring egg viability (Arnold et al. 1987), 5° reducing risks of nest parasitism (Robertson et al. 1992, Geffen and Yom-Tov 2001, Yom-Tov

2001), 6° reducing risks of egg predation (Arnold et al. 1987, Persson and Goransson 1999, Stoleson and Beissinger 2001) 7° and reducing the overall time spent on the nest and the duration of the related fasting period (Hanssen et al. 2002, Hepp 2004). These factors can influence the distribution of presence and recess bouts.

The importance of these costs and benefits may vary. Some may be more important than others in the determination of the laying behaviour of female Common Eiders. Besides, their relative importance must change over the laying period as nest attendance increase from 0 to almost 100% (Kennamer et al. 1990, Wilson and Verbeek 1995, Loos and Rohwer 2004). Benefits of reducing risks of egg predation may increase as the energy invested in clutch production raise. Reversely costs may decrease as the risks of asynchrony become negligible and energy requirements for egg production decline.

In this study, our aim was first to quantify laying behaviour of females Common Eider and the asynchrony between embryos. For that purpose, we placed temperature sensors in eider nests and extracted presence-absence periods of females on their nests and temperature applied to eggs. Thus we have had access to information about laying behaviour of females and development of eggs laid. Second we focused on the patterns of timing of recesses to identify what factors may have selected the current behaviour of females breeding on a Danish colony.

METHODS

Study site

The study was carried out in April-May 2003-2005 on Christiansø (55°19'N, 15°12'E), a Danish island located in the Baltic sea 20 km east from Bornholm and 100 km south from Sweden. This inhabited island of about 22 ha shelters a colony of approximately 2,600 pairs of Common Eiders (*Somateria mollissima mollissima*). Birds nesting there are habituated to human presence. As a result females do not flee off the nest when approached at close distance. The island is covered with a mix of herbaceous, shrubs and trees but the study area is restricted to a 250 m^2 herbaceous and rocky area in the northern part of the island, where approximately 100 females nest each year.

Data collection

We walked across the study area looking for new nests every day in the afternoon, typically between 15:00 and 17:00. For each nest, we recorded initiation date and the evolution of nest occupation during five days following its discovery. At stages 6, 16 and 26 days after nest initiation, we captured females when possible, weighed them owing to a 3kg pesola scale and checked for clutch size. We repeated this protocol for all nests of the study area.

Nest temperature Sampling

In one or two-egg unattended nests, we placed a temperature-recording device made of a resin egg embedded with a temperature sensor on the top. This artificial egg was placed in the centre of the nests and fixed to the nest ground with two metal pins. Thermisters were linked by a one-meter wire to a data logger, Hobo Four-channel External (Onset Computer Corporation, Pocasset, Massachusetts). Loggers were held in a waterproof case and buried in the ground to avoid detection by birds. We programmed loggers to register nest temperatures every 1.5 or 3 min depending on whether an ambient thermister was joined to the nest thermister. We recorded data for 33 days in a row and we removed the device after hatching.

Nest attendance

From temperature patterns, we extracted presence and recess periods of females according to the method described by Sabourin (2003). Arrivals or departures of females were identified by a decrease or an increase of at least 2°C within 3 min. We only took into account recesses longer than 6 min because (1) we thought shorter interruptions would represent on-nest movements and (2) we could not clearly identify shorter interruptions with our record frequency. Recesses lasted from the first time the temperature dropped to the first time the temperature rose.

We studied variables related to nest attendance and nest absence. These variables were daily (24 h), diurnal and nocturnal nest attendance, daily number of recesses, length of

recesses and nest arrival and nest departure time. We analysed data for each day of the laying sequence and compared laying trends according to clutch size, initiation date and body mass. We categorised clutch size as small (3-4 eggs) or large (5-6 eggs) and initiation date as early (females laying prior to median nest initiation date of the colony) or late.

Nest temperature

We studied mean nest temperatures for each day of the laying sequence We also analysed temperature patterns for each nest by fitting a logistic growth curve to each temperature series. The expression for the logistic growth curve was:

$$Temperature = Min + \frac{Max - Min}{1 + (Time/k)^{Slope}}$$

Parameters Min, Max, k and Slope were estimated with Sigmaplot 9.0 (SPSS 2004) and we compared these parameters according to clutch size, initiation date and body mass as we did for nest attendance variables.

We were also interested in comparing nest temperatures during attendance bouts for each day of the laying sequence. That part of the analysis was conducted considering data from one hour after the arrival of the female on its nest until the end of an attendance bout. We decided not to take into account the first minutes of temperature rise following a recess as the rate of the rise varied from one female to another.

Embryonic development

We used data from 24 different nests for which we had reliable temperature data and for which we could determine precisely female presence and absence periods. We used the method based on the calculation of the number of "degree days" (DD) experienced by an egg over a defined amount of time. This calculation relies on two key points. First, the existence of a physiological zero temperature (PZT) below which no development occur, which for birds has been set at approximately 25-27 °C (White and Kinney 1974, Drent 1975). Second, on the fact that embryonic development speed increases with temperatures, which tends to be true for birds (Gillooly and Dodson 2000, Gillooly et al. 2002). We calculated DD according to equation:

$$DD = \frac{1}{1440} \sum_i m_i \times (\theta_i - PZT)$$

m_i is the active period length (min) and corresponds to the length of the period during which temperature is higher than PZT. θ_i is the mean temperature (Celsius degrees) experienced by the egg over an active embryonic period. Embryonic development of each egg within a nest was estimated at the end of the laying sequence which corresponded to the estimated moment when the last egg was laid. We studied differences of development between intra-clutch eggs for each nest and we compared results according to clutch size. The artificial egg we used in our study has been previously tested (Flint and MacCluskie 1995, Poussart et al. 2000) and represents a good estimate of egg temperature when incubated but warm up and cool down more rapidly than natural eggs. In our calculation of

DD we took into account only mean temperatures when females were attending their nests. That generally means intervals of several hours during which egg temperature is mainly constant. Increasing and decreasing phases only represent a little proportion of the period considered and variations between real egg temperature and artificial ones may not significantly influence our mean temperature. Besides, the difference due to faster warming rate may be compensated at the end by a faster cooling rate. For these reasons we believe our device provide reliable estimates of egg temperatures. We made our calculation on the basis of egg temperatures, which must be different from embryo temperature. However Drent (1975) described the PZT as a threshold for egg temperature and not for embryo temperature. Finally, our method is only an estimation of the embryonic development whose purpose is to allow us to draw general patterns of variation.

We estimated laying interval and mean laying hour of each egg in a clutch owing to attendance pattern. From daily nest attendance intervals, we calculated the smallest and largest potential laying intervals. Small intervals corresponded to intervals between the last time the female was on her nest on day n and the first time she was back on day n+1. They were the smallest period that could separate the laying of two consecutive eggs in the nest. Large intervals corresponded to intervals between the first time she was on her nest on day n and the last time she was on it on day n+1 and were the longest period that could separate the laying of two consecutive eggs. We repeated this method for all eggs to get a set of small intervals and a set of large intervals. We considered that laying interval for our sample to be between the longest small interval and the shortest large interval.

Given this mean laying interval, we estimated eggs laying time. We added the laying interval to the attendance period of day n to obtain the potential laying period of day n+1. Each time the attendance period of day n+1 was shorter than our estimated laying period we were able to restrict its limits. We finally estimated the laying time as the mid point of the resulting potential laying period of each egg within a clutch.

Statistical analysis

We conducted two kinds of analyses on nest attendance and nest temperature data. First, we analysed variations of these two variables over the laying sequence. For these analyses, the sample unit was one day of a laying female and the null-hypothesis tested was that all females spent the same amount of time on their nests each day of the laying sequence or applied the same temperatures to their eggs. We tested our null hypothesis using analyses of covariance (ANCOVA) with female as a factor and the day of the laying sequence as a covariate to study relationships between time spent on nest or temperature applied on nest and time during laying. Then we investigated relationships between those variables and body mass, clutch size and laying date (expressed in Julian dates) by introducing those parameters as factors and the day of the laying sequence as a covariate. We restricted to the first six days after nest initiation to avoid integrating the incubation phase in our analysis.

Second, we conducted analyses on nest attendance and nest temperature patterns. For these analyses the sample unit was a laying female. We tested for a difference of time spent on nest during the last day of laying in relation to clutch size using a t-test and for a

difference of time spent on nest according to the daily period (night or daylight) using a paired t-test. We also compared parameters of logistic growth curves analyses led on temperature data according to body mass, clutch size and laying date using multi-way analyses of variance (ANOVA). Slopes of the curves were log-transformed to normalise data.

We calculated embryonic development of each egg within a nest but our analyses focused only on the total asynchrony of development between the first and the last egg laid. The sample unit was thus a nest of a laying female and we tested the null-hypothesis that all nests had a similar asynchrony of development at the end of the laying presence. We conducted multi-way analyses of variance with body mass, clutch size and laying date as explicative variables.

Tests were performed with Systat 9.0 (SPSS 1999). Non-parametric tests were used when conditions of parametric tests (normality, equality of variances of the residuals) were not met. All results are given as mean ± standard error.

RESULTS

Nest attendance

Time spent on nest increased significantly over the laying sequence from 378 ± 45 minutes on day 1 to 1404 ± 8 minutes on day 6 (ANCOVA, $F=716.32$, $n=48$, $df=1$, $P<0.001$; Fig. 1) and the rate of increase varied significantly with the female (ANCOVA,

F=4.84, n=48, df=43, P<0.001). However, we found no detectable relationship either with clutch size or initiation date or any interaction (ANCOVA, n=48, df=1, P>0.05).
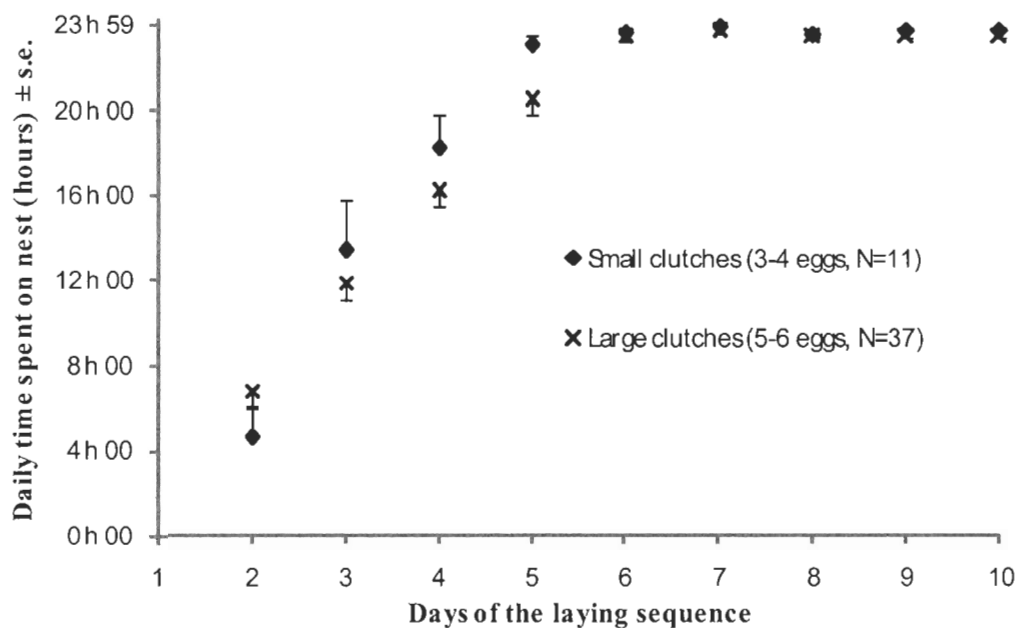
Figure 1. Daily time spent on nest according to clutch size.

Female spent more than 95% of the time on nests after 5.3 ± 0.1 days in the laying sequence on average and we found a significant relation with clutch size class (4.6 ± 0.3 days, n=11 for 3-4 egg clutches; 5.4 ± 0.1 days, n=37 for 5-6 egg clutches; Student test, t=2.83, n=48, df=47, P=0.007).

The number of recess bouts also decreased significantly with the day of the laying sequence (from 1.7 ± 0.1 recess on day 2 to 0.9 ± 0.1 on day 6; ANCOVA, F=14.47, n=48, df=1, P<0.001) and the rate of decrease also varied with the female (ANCOVA, F=2.39, n=48, df=43, P<0.001). There was a significant influence of clutch size class on the rate of

decrease (-0.04 ± 0.03 recess.day^{-1}, n=10 for 3-4 egg clutches and -0.17 ± 0.02 recess.day^{-1}, n=37; ANCOVA, F=4.96, n=48, df=1, P=0.031). Females producing smaller clutches took fewer recesses at the beginning of laying and thus experienced a rate of decrease lower than females producing larger clutches. We found no significant influence of laying date and interactions between clutch size, laying date and day in the sequence (ANCOVA, n=48, df=1, P>0.05). Mean length of recesses decreased over the laying sequence.

Diurnal nest attendance (81 ± 3%) was significantly higher than nocturnal attendance (43 ± 3%) over the laying sequence (Wilcoxon test, Z=11.866, n=233, P<0.001; Fig. 2). Decrease of recess duration was mainly due to a decrease of arrival time from 02:49 (± 00:52) on day 1 to 22:15 (± 00:20) on day 5 (Fig. 2). Mean departure time was more stable over the laying phase varying from 20:04 (± 00:39) on day 1 to 22:06 (± 00:25) on day 6.
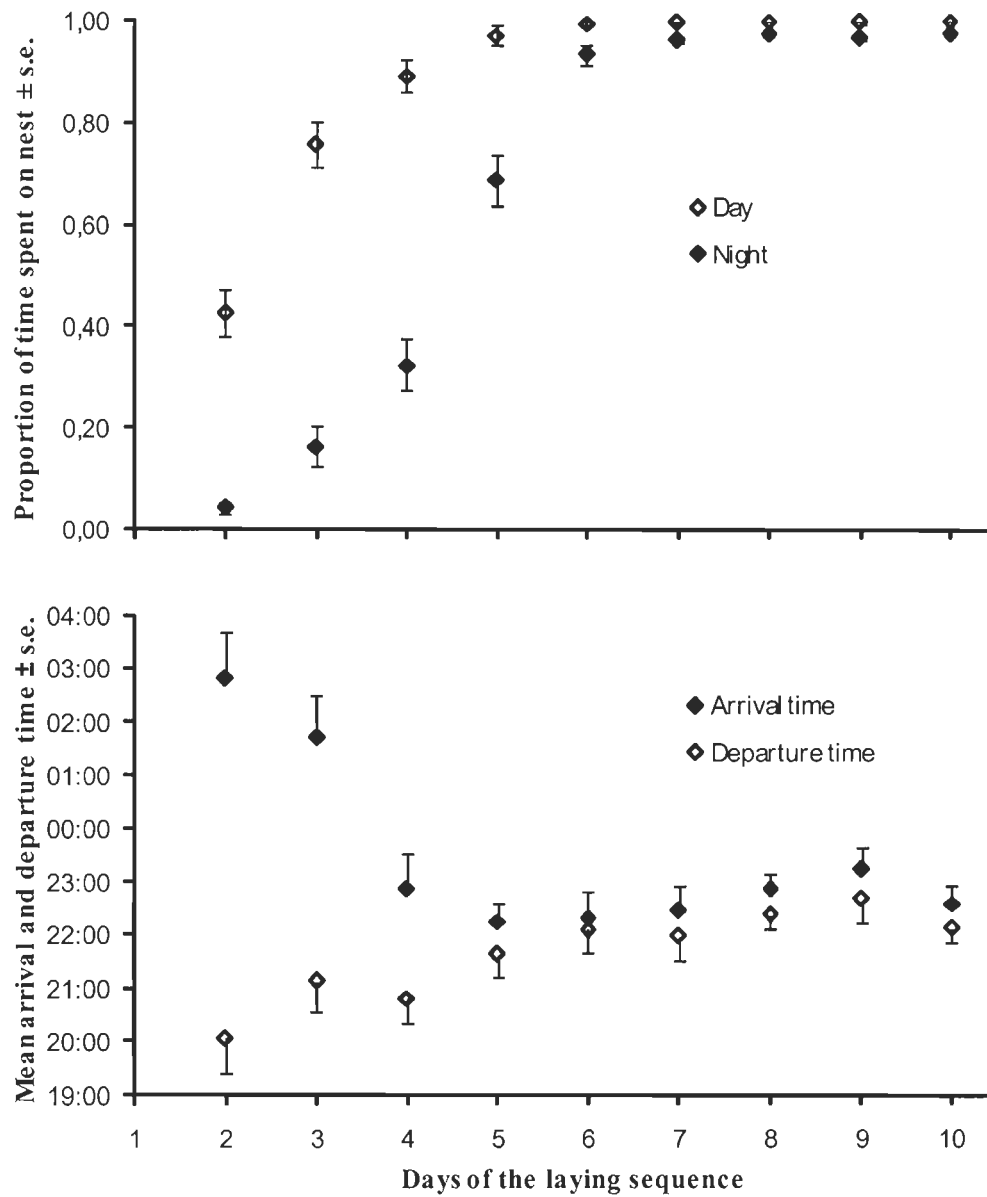
Figure 2. Proportion of time spent on nest and mean daily arrival and departure time in relation to laying sequence. Discrimination between diurnal and nocturnal hours is based on sunrise and sunset hours and values are expressed in local time. N=48.

Nest temperatures

Daily mean nest temperatures increased significantly from 12.8 ± 0.8 °C on day 1 to 35.5 ± 0.5°C on day 10 (ANCOVA, F=974.24, n=48, df=1, P<0.001). We found a significant influence of females on the rate of increase of nest temperatures (ANCOVA, F=6.48, n=48, df=43, P<0.001) but no influence of clutch size, laying date or interactions between factors (ANCOVA, n=48, df=1, P>0.05).

Nest temperatures data varied through time accordingly to a general S-shape pattern for all individuals. Slopes of the curves decreased significantly from small to large clutches (ANOVA, F=4571.4, n=61, df=1, P=0.009) whereas K, minimum and maximum of the curves did not change. This means that for both classes of clutches, the ascending phase began approximately at the same time but with a different slope. The difference in the temperature pattern between small and large clutches was therefore mainly due to a difference in the increase rate of the temperature but not to the time this increase started.

Small clutches reached the curves plateau (typically a variation less than 1°C over 1000 min) 0.8 days before large clutches (4.7 ± 0.2 days after thermister introduction vs. 5.5 ± 0.1 days; ANOVA, F=458.5, n=61, df=1, P=0.030) but we found no difference at the time the 27°C threshold was reached (3.2 ± 0.2 days vs. 3.7 ± 0.1 days). Laying date had no influence on those two variables. The temperature required for embryonic development is reached as early as the second egg is laid in the majority of nests.

Nest temperatures during attendance bouts increased significantly over the laying phase (Friedman test, F=63.96, n=18, df=4, P<0.001). Typically nest asymptotic temperatures rose from 28.8 ± 1.8°C on day 1 to 37.3 ± 0.6°C on day 6 of laying or incubation.

Embryonic development

Minimum upper limit of laying interval was 27.0 hours and maximum lower limit was 26.5 hours. We thus considered those two values as the estimating span for the laying interval and we used 27.0 hours to estimate the laying time of eggs.

Considering that interval, we estimated the mean laying time of all eggs: 9:57 on day 1 for egg 1; 12:57 on day 2 for egg 2; 15:57 on day 3 for egg 3; 18:57 on day 4 for egg 4; 21:57 on day 5 for egg 5 and 00:57 on day 7 for egg 6.

Since temperatures high enough for embryonic development were applied as early as the second day of laying, we observed a difference of development between almost all eggs laid within a clutch. The difference of synchrony averaged 15.91 (± 1.96) degree-days, which corresponds to approximately 1.2 days of permanent full incubation at a temperature of 40°C. It rose to a maximum of 32.97 degree-days, which means 2.5 days of "full" incubation. The difference between two consecutive eggs increased over the laying phase and the difference between the first and the last egg laid increased significantly (Sheirer-Ray-Hare test, F=12.908, n=24, df=1, P=0.002) with clutch size (Fig. 3) but not with laying

date. Clutch size and asynchrony were correlated (Pearson, r=0.779, n=24, df=22, P<0.001).
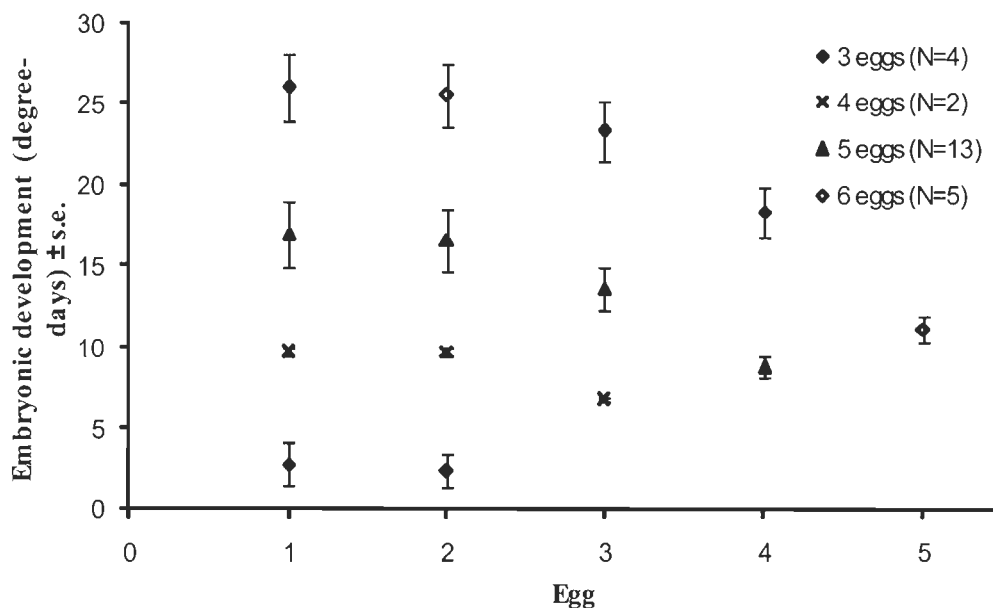
Figure 3. Embryonic development of eggs laid expressed as degree-days at the end of laying according to clutch size.

DISCUSSION

Female Common Eiders laid eggs mostly during the day and took recesses at nights. They progressively increased time spent on nest over the laying sequence by reducing nocturnal recess duration and by starting attending nests earlier in the day. They reached permanent nest attendance approximately the fifth day after laying onset. In the following section, we confronted those findings to behavioural predictions related to costs and benefits of nest attendance.

First, in Prairie Ducks, hatchability of eggs decreases when not attended for several days (Arnold et al. 1987), which was interpreted as a decrease of egg viability in unattended nests. To maintain egg viability, females would start to spend time on their nests before clutch completion to maintain egg viability. Besides as embryos are very sensitive to high temperatures and egg-viability decline more steadily when exposed to such conditions (Webb 1987, Stoleson and Beissinger 1999), we would expect females to spend time on their nests during hot daylight hours to prevent them from over-heating. Predominant diurnal nest attendance of females is consistent with these predictions. However clutch size in Common Eider varies between three and six eggs and we found a laying interval of 27 hours, close to what have previously been reported for that species (Watson et al. 1993). Consequently, depending on clutch size, the laying period lasts between 2.2 and 5.6 days. The pattern of egg viability decline varies according to species. It starts after only 3 days of unattendance in Parrotlets and House Sparrow (Viega 1992, Stoleson and Beissinger 1999) but after 5-10 days in a waterfowl species such as arctic breeding Prairie Ducks (Arnold et al. 1987, Arnold 1993). The longest laying period in Common Eider is close to 5 days, a period of time for which no decline has been observed in Prairie Ducks. Viability declines with high ambient temperatures (Stoleson and Beissinger 1999), but Common Eiders on Christiansø did not breed under hot conditions. Temperatures oscillated typically between 2°C at night and 15°C during the day. Nest temperatures always dropped to ambient temperatures during females recesses indicating that eggs were not over-heating when unattended. We thus rejected the idea that egg-viability plays a significant role in the selection of the laying behaviour.

Second, intra-specific parasitism is found in many waterfowl species such as the Common Eider (Robertson et al. 1992, Geffen and Yom-Tov 2001, Yom-Tov 2001). This may be costly for females since first it increases the number of eggs incubated and second it can induce hatching asynchrony between the two sets of eggs. Parasitism may be a selective pressure acting on females laying behaviour (Kennamer et al. 1990, Persson and Goransson 1999) and we expect that females would spend time on their nests when the risk of parasitism is highest, which is during the laying of the first eggs of the. Our results are inconsistent with these expectations as we observed a low nest attendance during the first days of laying. Besides parasitism seems not to be very costly in that species (Robertson et al. 1992) and that Hepp (2004) as well as Persson and Göransson (1999) have already rejected the impact of parasitism on birds laying behaviour.

Third, egg predation is a major cause of reproduction failure in birds (Choate 1967, Cody 1971, Lima 1987, Pärt 2001). One strategy developed by birds to fight against that threat is to stay on their nests to defend eggs or to avoid their detection by predators. We expected that our females would stay on their nests during daylight to limit egg exposure to aerial predation (Arnold et al. 1987, Persson and Goransson 1999, Stoleson and Beissinger 2001, Bolduc and Guillemette 2003). This is consistent with the predominant diurnal nest attendance that we observed. Egg predation by avian species, for instance large gulls, is predominant at daylight since most predators are diurnal. Christiansø shelters a colony of about 10000 Herring Gulls (*Larus argentatus*) which feeds partly on eider eggs (personal observations). Female eiders rely on behavioural strategies to minimise egg detection and egg consumption by predators (covering early-laid eggs with nest material, depositing

faeces on eggs). Despite these adaptations, eggs are depredated when unattended which suggest that the best strategy for females is to stay on their nests. Moreover, the fast of female eiders during reproduction has been interpreted as an adaptation to limit egg exposure to predators (Afton and Paulus 1992).

Indeed Female Common Eiders are known to fast over laying and incubation periods (Korschgen 1977, Drent and Daan 1980, Bolduc and Guillemette 2003). Mass loss over the reproduction is one of the most extreme encountered in birds (Korschgen 1977, Parker and Holm 1990, Gabrielsen et al. 1991, Bolduc and Guillemette 2003). The duration of laying and incubation periods is a predominant factor acting on potential adult survival rate. The shorter the reproduction is the better for females. In that situation, females would attend nests and begin to incubate the first eggs to shorten the fasting period as in Wood Ducks (Hepp 2004). This supposes the existence of mechanisms promoting hatching synchrony. Despite that mechanisms such as embryos communication (Persson and Andersson 1999, Nicolai et al. 2004), egg size reduction (Drent 1975, Arnold 1991, Robertson 1995a, Hanssen et al. 2002, Massaro et al. 2002, Nicolai et al. 2004), metabolic acceleration (MacCluskie et al. 1997), and a reduction of maturity at hatching (Slattery and Alisauskas 1995) seem to exist, the strong nest attendance pattern of females during laying is inconsistent with the predictions, as we would not have expected any particular trend in the attendance pattern.

Fourth, nest attendance and the high temperature induced can start early incubation of the first laid eggs within a clutch (Caldwell and Cornwell 1975, Cooper 1978, Afton 1979a,

Persson and Goransson 1999, Poussart et al. 2000, Hanssen et al. 2002, Badyaev et al. 2003, Hepp 2004, Loos and Rohwer 2004). This could be detrimental as the asynchrony of development can lead to an asynchronous hatching of all eggs and the abandonment of the last ones (Cooch 1961, Caldwell and Cornwell 1975, Afton 1979a, Cargill and Cooke 1981, Kennamer et al. 1990). Thus we expected that females would take recesses to limit the embryonic development of eggs and would attend the nest only while laying an egg and leave it the rest of the time irrespective of the period of the day. Nest attendance would thus be negligible until the last eggs are laid. The strong nest attendance pattern is also inconsistent with that factor. Asynchrony of eggs development reached a maximum of 2.5 days in case of a six-eggs clutch, which is lower than four days found by Davies and Cooke (1983) in Lesser Snow Goose above which the asynchrony can not be compensated. However, asymptotic temperatures of nests when females are attending eggs increased over the laying sequence and we believe that females could limit temperature rise when necessary. If females were simply trying to limit asynchrony, they could stay on their nests longer and reduce temperatures applied, or at least stay near the nests. This strategy would be less risky for eggs. Further, we did not found strong differences in laying behaviour between clutch sizes, which means that females laying small clutches did not increase nest attendance faster. If embryonic synchrony was a major selective pressure acting on females laying behaviour, females laying only tree or four eggs should have started "full" incubation before others as asynchrony can not increase after the last egg is laid.

Fifth, in several species of ducks, nocturnal attentiveness onset is delayed to limit vulnerability of ground-nesting ducks to mammalian predators (Afton and Paulus 1992).

Adult predation by terrestrial mammals is a potential cause of mortality in Common Eider (Choate 1967) and a factor influencing nest site selection (Quilan and Lenhausen 1982, Robertson 1995b). This is also an important factor for long-lived species (Erikstad et al. 1998) as females must trade off hatching success with their own survival (Aldrich and Raveling 1983). Thus females should minimise time spent on the nest and delay incubation onset if there is a risk of predation while on the nest (Charnov and Krebs 1974). Nocturnal nest unattendance observed is consistent with these predictions. Common Eiders have relatively short wings compared to the size of their body which results in a very high wing-loading (Guillemette 1994, Guillemette and Ouellet 2005b). During pre-laying, females accumulate reserves, body mass reaches its higher annual level and wing-loading becomes critical to the point where they experience a period of temporary flightlessness (Guillemette and Ouellet 2005b). This condition is likely to increase predation risk on themselves and Guillemette and Ouellet (2005a) debated whether it represents a cost of reproduction. Eider females would thus go off their nests at night when mammalian predators are mostly active and their detection harder, to limit their exposure (Audet et al. 2002).

This could also explain why females increased laying attendance as laying progressed. As body mass increases during follicular growth, specific lift decreases below 9.8 N.kg^{-1} (Guillemette and Ouellet 2005a), which is the threshold for take-off capability. As females lay eggs, they lose weight, approximately 40 g.day^{-1} (Franzmann 1980) and specific lift increased to pass over 9.8 N.kg^{-1} after six days of laying. Consequently females would then leave their nests during the first days of laying to avoid risk of

predation by predators on themselves and as they lose weight they become less vulnerable to mammalian predation and increase time spent on nest.

Yet, mammalian predators are absent from Christiansø so we could challenge this hypothesis. Behavioural changes are generally highly reversible (Relyea 2003, Gabriel et al. 2005) and behavioural adaptations developed to face predation must have disappeared as females are not confronted to adult predators. Nevertheless lags can occur between the disappearance of a behaviour and the disappearance of its cause, for instance when individuals do not have complete information about their environment or when they face predators on wintering or staging grounds (Gabriel et al. 2005). This situation can cause prey to perform anticipated behaviours to face for situations not currently encountered.

Sixth, other waterfowl species such as Spectacled Eiders (Flint and Grand 1999), Northern Shoveler (MacCluskie and Sedinger 1999) and Canada Goose (Aldrich and Raveling 1983) leave their nest during daylight hours, presumably to search for food. For some species that relies on reserves stored during breeding, food accumulation can be a critical aspect of reproduction. In this case, adults would leave their nests during daylight hours while laying to complete reserve storage or maintain body reserves. Nest unattendance at night seems inconsistent with that proposition. Laying is the transition period between pre-laying which is an energy demanding phase supported by an hyperphagic behaviour and incubation during which females fast throughout 26 days (Chapitre 2, Korschgen 1977, Parker and Holm 1990). The laying phase could thus be useful to complete the reserves necessary for fasting if females are able to feed during the

nights. Foraging activity of females during nightlight hours is substantial during pre-laying and remained stable during laying to become predominant over daylight foraging activity (Chapitre 2). Consequently we speculate that benefits resulting from feeding and from nest predation could interact and force females to stay on their nests during daylight and leave them at nights to feed.

Increase of nest attendance interpretation is complex. Female could spend more time on their nests as they recover full take-off capabilities. However, not only do females leave the nest but they also spend time feeding during recesses. Daylight foraging activity decreases during laying (Rigou and Guillemette unpublished data), which is a factor of major importance accounting for the increase of nest attendance over the laying sequence. Consequently we could envisage that the increase of clutch value resulting of the increase on the number of eggs laid and the energy invested could explain the increase of nest attendance. On the other hand, nightlight foraging activity is stable during pre-laying and laying and decrease only the day the last egg is laid. Foraging activity is substantial until the end of laying and can be important to sustain energy requirements of egg production. Decrease of energy requirements could thus interact with adult predation and increase of clutch value to account for the increase of nest attendance.

Our study is descriptive as we did not conduct manipulative experiments on laying behaviour. Consequently we do not intend to give definitive conclusions about the role played by each factor we envisaged. We simply compared the prediction linked to costs and benefits of nest attendance to the laying behaviour we observed on that specific colony and

we proposed an overview of the ones that may influence behaviour of females Common Eider laying in Denmark and of the ones that may not. It turned out that risks of nest predation risks of adult predation and necessity to feed could explain laying behaviour (Table 1). Risks of adult predation and necessity to feed may be mutually exclusive as they both account for night time recesses, but we were unable to determine the one that was predominant.

Tableau 1. Predictions and conclusions related to ten selective factors envisaged to explain laying behaviour of female Common Eiders. Conclusion figures mean the degree of reliance in the factor for explaining laying behaviour.

Selective factor	Origin	Predictions	Results	Conclusion
Egg-viability	Arnold *et al.* 1987	Laying period of at least 5-10 days	Short laying period	0
Parsitism	Kennamer *et al.* 1990	High nest attendance at the beginning of laying	Low nest attendance at the beginning of laying	0
Nest-predation	Arnold *et al.* 1987	Daylight attendance	Attendance mainly during daylight periods	3
Energy-saving	Hannsen *et al.* 2002	No strong attendance pattern	Strong attendance pattern in favor of daylight periods	0
Embryonic-synchrony	Kennamer *et al.* 1990	No strong attendance pattern, Females recesses near the nests, Onset of incubation earlier for small clutches	Strong attendance pattern, Females away from the nests, Weak difference of onset of incubation between clutch size categories	0
Adult-predation	Charnov and Krebs 1974	Night-time recesses; Increase of nest attendance during laying	Night-time mainly spent off nest; Increase of nest attendance during laying	2
Feeding	This study	Daylight recesses, Feeding activity	Recesses mainly during nightlight periods, Feeding activity	1
Increasing-clutch-value	Erikstad *et al.* 1998	Increase of nest attendance during laying	Increase of nest attendance during laying	2
Decreasing-risk-of-asynchrony	This study	Increase of nest attendance during laying and strong influence of embryonic-synchrony hypothesis	Increase of nest attendance during laying but weak influence of embryonic-synchrony hypothesis	0
Decreasing-energy-requirements	Drobney 1980	Increase of nest attendance during laying and strong influence of feeding hypothesis	Increase of nest attendance during laying but questionable influence of feeding hypothesis	1

CHAPITRE 2

FORAGING EFFORT BEFORE AND DURING LAYING IN COMMON EIDERS: EVIDENCE THAT FEMALES ARE NOT CAPITAL LAYERS

Abstract. To face energetic demand related to reproduction, female birds need either to build-up reserves before breeding and/or to feed while producing eggs, laying and incubating. In 2004, we monitored foraging and flight activity of five female Common Eiders (*Somateria mollissima*) for a full year using implanted data loggers. The pre-laying period, defined as the interval between the end of spring migration and laying of the first egg, extended over 11 to 27 days and represented a period of intense foraging activity as females spent a daily average of 159.6 ± 16.0 min diving, compared to an annual average of 91.4 ± 37.8 min. This foraging activity decreased during the laying period as time spent diving averaged 69.8 ± 7.4 min. In contrast to previous speculations considering that female eiders did not feed while laying and that egg material was coming from body reserves, females were showing hyperphagic behaviour during follicular growth suggesting that they directly diverted food intakes for egg production and egg laying. Furthermore, since some females were on the breeding grounds before the beginning of follicular growth and were hyperphagic, it suggests that some individuals were completing body reserves after spring migration.

Key-words: Common Eider, capital breeders, income breeders, foraging, laying

INTRODUCTION

There is ample evidence that birds can buffer daily energy requirements through regulation of body mass. While breeding, birds face energy and nutrient requirements for the production of the clutch (Sotherland and Rahn 1987) and in mono-parental species, females need to solve the conflicting demands of incubating the eggs and feeding. That is probably why some waterfowl species developed the ability to build-up endogenous reserves for latter use during incubation.

Drent and Daan (1980) introduced the concept of capital and income breeding to discriminate between birds that rely on their body condition to initiate breeding (capital breeders) and birds that rely on the rate of nutrient accumulation (income breeders). Thomas (1988) and Stearns (1989) expanded the definitions of capital and income breeders. A capital breeder is a bird that relies on reserves accumulated and an income breeder is a bird that relies on food intakes to face the energy demand of reproduction. The origin of food resources used for reproduction becomes the key-point to discriminate capital and income breeders (Jönsson 1997).

Jönsson (1997) reviewed the costs and benefits associated with being a capital breeder. It is beneficial when breeding is associated with (1) food scarcity, (2) high food demand, (3) unpredictability of food resources or demands, (4) high egg predation risk when leaving the nest to forage or (5) when nesting duties limit time available for foraging activities. On the other hand, being a capital breeder is detrimental since (1) it increases the energetic costs of locomotion (flight and foraging), (2) it induces cost of conversion and

catabolism of nutrients as well as costs of maintenance of new tissues and (3) it increases adult predation risks.

Female Common Eiders are often considered as the archetype of capital breeders (Meijer and Drent 1999) as they are thought to rely exclusively on endogenous reserves during breeding (Korschgen 1977, Parker and Holm 1990, Swennen et al. 1993), although direct evidence is lacking. However, being a capital breeder may incur substantial costs. Pelletier (2006) used various models to estimate flight cost in winter and found that results converge to 20 × basal metabolic rate (BMR) in this species. Body mass increases by 37% in females from winter to pre-laying (Guillemette 1994, Guillemette and Ouellet 2005b) resulting to extreme wing loading and low flight muscles ratio, even leading to episodes of flightlessness under still air condition (Guillemette and Ouellet 2005b). In a second study, Guillemette and Ouellet (2005a) proposed that such a condition would be associated with a cost of reproduction since aerial, terrestrial and aquatic predators of Common Eiders are more likely to be successful during pre-laying. Altogether, this indicates that the interpretation of the breeding strategy of that species is more complex than previously thought.

In this paper, we investigated the timing of foraging effort of females in relation to their breeding status to check whether egg formation and egg laying were accompanied by a low feeding activity, which would strongly support the hypothesis that Common Eider is a capital breeder. Common Eiders are diving benthic predators feeding on blue mussels (*Mytilus edulis*), an abundant and predictable food resource (Guillemette and Himmelman

1996, Larsen and Guillemette 2000). We studied foraging effort in relation to the start of laying and incubation by monitoring continuously the diving behaviour of females of known laying dates. We used data loggers implanted in the body cavity of females for a full year to record flight and diving schedules (Guillemette et al. 2007, Pelletier et al. 2007) and identify (1) time of arrival on the breeding grounds, (2) duration of pre-laying period, (3) dive depth, (4) time spent diving and (5) time spent on the bottom in relation to laying dates. We show that females upon arrival on breeding grounds exhibit a high feeding activity (hyperphagia), which decrease during laying and finally become negligible during incubation. These findings are discussed in relation to the capital/income conceptual framework.

METHODS

Study area

The study was carried out in 2004-2005 on female Common Eiders (*Somateria mollissima mollissima*) breeding on Christiansø (55°19'N, 15°12'E), a Danish island located in the Baltic sea 20 km east from Bornholm and 100 km south from Sweden. This inhabited island of about 22 ha shelters an eider colony of approximately 2600 nests. There, the slope of the littoral zone is steep and diving depth increases rapidly with distance from the shore.

Experimental device and implantation

In April 2004, 10 females were implanted with DLs (Data Loggers) that recorded heart rate (2 Hz) and hydrostatic pressure (diving depth; 2 Hz). DLs were 36 mm long, 28

mm wide, 11 mm thick and weighted 25 g after encapsulation in paraffin wax for waterproofing and a silicone coating for biocompatibility. During implantation, birds were anaesthetised with isoflurane and the sterilized DL was inserted into the abdominal cavity via midline incision in the skin and body wall (Guillemette et al. 2002). To prevent infection, a long-acting antibiotic (*LA Terramycin,* Pfizer, New York) was also injected intramuscularly. One year later (April 2005), we recaptured implanted females and removed DLs according to the same procedure. The implantation and removal time were less than 45 min. DLs accounted for 1.2 % of the bird's body mass at implantation (1735 ± 176 g, $n = 10$) and previous studies could not detect any negative impact on reproductive success and survival (Guillemette et al. 2002, Guillemette unpublished data). Eight females came back on the colony the following year of which five DLs had data covering a full annual cycle.

Breeding biology

In April 2005, we monitored breeding biology of females nesting on the experimental plot including the birds implanted with data loggers. We walked across the study area looking for new nests every day in the afternoon, typically between 15:00 and 17:00. For each nest, we recorded initiation date and the evolution of nest occupation during five days following its discovery. From those observations, we could define the laying period as the time interval between the day the first egg and last egg were laid as determined by Rigou (Chapter 1).

Flight and Dive behaviour

We used a purposed-designed software to summarise data and quantify dive and flight behaviour. Flight behaviour was identified using the drastic increase and sustained heart rate characteristic of birds using flapping flight (Pelletier et al. 2007). This method allows the exhaustive recording of all flights performed by a bird during a full year and allows the identification of all migration periods of each individual. Hence we could determine the end of spring migration as the day when daily flight time decrease abruptly (see an example in Guillemette et al. 2007) and the date of initiation of laying from observations on land. We define the pre-laying period as the time interval between the end of spring migration and the day the first egg was laid. In our study, we only used the information about spring migration to determine time of arrival on the breeding grounds.

Dives were recorded when the bird was completely submerged (0.5 m). Dive profiles of female Common Eiders are characterised by a flat pattern of time spent on the bottom since they are essentially benthic predators (Guillemette et al. 2004). Hence for each dive, we record depth, bottom and diving time (bottom time + travelling time). For each day and bird we summed all dives performed during 24 h to obtain the daily time spent diving, a procedure that we also used for bottom time.

Data analysis

Because the DLs were recording data continuously, our method was exhaustive and allowed us to identify every dive for each female. On the other, hand our sample of

experimental females (N=5) was small. Thus no inferential statistics were used. Diving patterns are analysed in regards to the breeding stage of females i.e. pre-laying, laying and incubation period (ten-days period following laying). Results are given as mean ± standard deviation.

RESULTS

The pre-laying period of the five females averaged 16.6 ± 6.3 days (11-27 days) and clutch size averaged 4.8 ± 1.1 eggs. For most females, daily time spent diving (DTSD) was high (mean = 139.1 ± 41.2 min, Fig. 4) upon arrival on the breeding grounds (the first three days after migration), which is 52% higher than the annual average (91.4 ± 37.8 min). DTSD increased during the first days of presence on the breeding grounds to reach a maximum of 225.3 ± 81.2 min about ten days before laying the first egg. Then DTSD decreased steadily until the start of laying and ultimately until incubation. Female YO behaved slightly differently. As its pre-laying period was longer, the increasing phase started earlier and reached its peak as early as the 17th day before laying. Then it maintained a substantial foraging effort during the following two weeks.
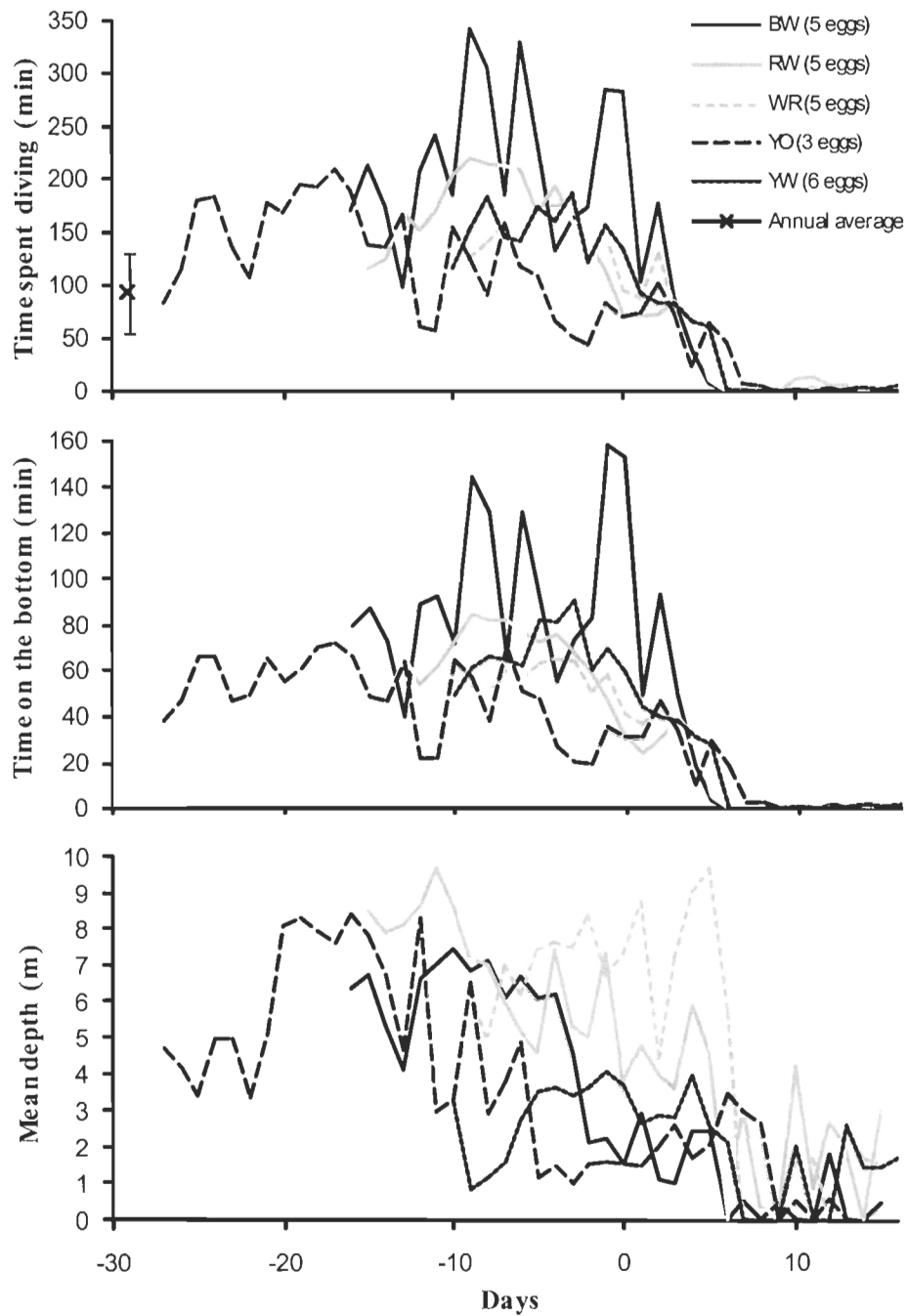
Figure 4. Daily time spent diving (a), time spent on the bottom (b) and daily average depth (c) of foraging dives for five female Common Eiders during pre-laying, laying and incubation. The annual average of the daily time spent diving (± 95% confidence interval) for the five females is shown in a). Day 1 corresponds to the laying of egg 1. Figures between parentheses are the clutch size.

Daily time spent diving during the whole pre-laying period averaged 159.6 ± 35.8 min (129-218 min), which corresponds to 224.9 ± 30.1 dives per day in average (170-306 dives). It decreased to 70.0 ± 16.5 min (44-83 min) and 142.2 ± 50.2 dives (79-195 dives) during laying and 4.2 ± 3.1 min (1-8 min) and 7.5 ± 6.8 dives (3-19 dives) during incubation. Time spent on the bottom is more representative of the time available for prey ingestion (Guillemette et al. 2004) and varied similarly to time spent diving (Fig.4). We observed a general decrease in daily diving depth for all females from the pre-laying (5.1 ± 1.7 m, range 2.7-6.9 m) to laying (3.6 ± 2.2 m, range 1.6-7.1 m) and incubation periods (2.1 ± 0.4 m, range 1.6-2.7 m), attesting that birds searched for food closer to the shore as females began full incubation. Foraging activity occurred during nightlight hours as well as during daylight hours. During pre-laying, time spent diving (TSD) averaged 66 ± 25 min (33-111 min) during nightlight hours and 89 ± 15 min (61-108 min) during daylight hours. During laying, daylight foraging activity decreased steadily as TSD averaged 25 ± 15 min (7-43 min) whereas nightlight foraging activity remained more stable as TSD was 50 ± 8 min (43-62 min) in average.

DISCUSSION

Pre-laying period

Guillemette (2001) studied foraging performance of Common Eider during the pre-laying period. He investigated females foraging activity compared to their male

counterparts assuming that the latter were under energy balance. Females preparing to breed had a daily diving time of 169 min compared to 111 min for males and he concluded that female eiders experienced hyperphagia before breeding onset. In this study, we found a very similar average of 160 min of daily diving time during pre-laying, which is 76 % higher than the annual average (Fig. 4). Clearly these pre-laying females were hyperphagic. However whether this phenomenon of hyperphagia on the breeding grounds is related to improvement of body condition or follicular growth is open to debate.

Rapid follicular growth seems to last seven days in Eurasian Kestrel (*Falco tunninculus*, Meijer et al. 1989) and nine days in European Starling (*Sturnus vulgaris*, Challenger et al. 2001). In waterfowl species, it lasts four days in Northern Pintail (*Anas acuta*), five days in Lesser Scaup (*Aythya affinis*), American Wigeon (*Anas americana*, Esler 1994) and Greater Scaup (*Aythya marila*, Gorman 2005), seven days in Wood Ducks (Drobney 1980). In Common Eider the duration of the follicular growth period seems to last between 6 and 9 days (Robertson 1995a). We considered a conservative eight days period as the duration of egg development in Common Eider. All five females completed rapid follicular growth on the breeding grounds given that the shortest pre-laying period was 11 days for female YW. Foraging activity during the days of follicular growth averaged 153 min, indicating that the five females fed intensively while developing ova. Such an observation does not preclude, however, the possibility that females were allocating body reserves already accumulated on the wintering grounds to ovarian growth. Recently, Guillemette and Ouellet (2005b) analysed body and organ mass of female eiders at different stages of the ovarian development from another Danish colony. They could not

detect any change in somatic body mass when they compared females at the beginning and at the end of follicular growth. Similarly body protein and body fat did not vary significantly during follicular growth, despite the fact that gizzard mass was inversely related to ovarian mass. This suggests that follicular growth is not due to a reallocation of body reserves but rather must be sustained by directly diverted exogenous nutrients.

Moreover, all individuals arrived on the breeding grounds 2-18 days (mean = 8.6 ± 2.8 days) before rapid follicular growth began, considering a conservative duration of 9 days for rapid follicular growth. Therefore we suggest that the pre-laying period, as defined in this study, is also used to improve body condition (somatic mass). The inter-individual variation observed may be due to either a difference of body condition at arrival on breeding grounds either to a difference of reserve accumulation speed (Meijer et al. 1989).

Laying and incubation period

Daily time spent diving decreased steadily during laying and become negligible at onset of incubation. Nevertheless, during laying, the five experimental females spent 70 min diving each day which is slightly below the annual average of 91 min.

These findings are corroborated by Rigou (Chapitre 1) who used nest temperatures loggers to quantify nest attendance of female eiders nesting on Christiansø. He found that time spent off nests decrease from 1117 minutes on the first day of laying to 36 minutes on day six and averaged 495 minutes over that period, thus indicating that much time is available to perform other activities while off nest.

Franzmann (1980) studied body mass change over the course of the laying period on the Christiansø colony and weighted females at different stages of laying. Mean daily mass loss calculated on a sample of 11 females was 40 g.day^{-1}. The mass of a freshly laid egg in Common Eider varies between 95 and 131 g (unpublished data). Since eider females lay approximately one egg every day (Swennen et al. 1993, Watson et al. 1993, Rigou and Guillemette in prep.), we would expect a body mass decrease of at least 95 g if they were not feeding. Results from Franzmann strongly suggest that females are feeding during laying and support the finding of the present study.

Foraging effort of our experimental females became negligible at incubation onset which confirms previous studies, which suggested that female Common Eiders do not feed while incubating (Korschgen 1977, Parker and Holm 1990, Bolduc and Guillemette 2003) and consequently must rely exclusively on endogenous reserves for their maintenance and egg incubation.

In conclusion, we propose that reproduction (clutch production and maintenance of the female) in this species to be sustained by body reserves accumulated before and after spring migration and by food locally ingested and diverted immediately to ovarian growth. Conclusions about the breeding strategy of Common Eiders within the capital-income conceptual framework are difficult due to the lack of consensus and constancy on the acceptance of definitions used. In the one hand, Klaassen *et al* (2001) concluded that species of Arctic waders were income breeders since egg materials were entirely diverted

from food locally ingested on the breeding grounds. On the other hand, Meijer and Drent (1999) claimed that the Common Eider is a capital breeder despite that it is well known that females forage actively around their breeding grounds. Those two papers lead to two opposite conclusions with similar evidence, which illustrate the difficulties associated to the currently unclear concept.

Nevertheless, the duration of the pre-laying period was variable and thus the reliance upon the different food resources (pre or post migratory) must differ between females. For instance, we determined that the period devoted to improvement of body condition on the breeding grounds varied between 3 to 20 days. Thus some females must start the accumulation of reserves before spring migration. In contrast, Guillemette (2001) found that females *S.m.borealis* preparing for spring migration do not exhibit an hyperphagic foraging activity suggesting that they do not intensively build-up endogenous reserves before departure for spring migration. Hence the contribution of the pre-migrating and post-migrating food resources can vary between individuals as well as between populations. We thus speculate that breeding strategy of Common Eider must belong to a continuum at both the individual and the population levels.

CONCLUSION

La reproduction est une période exigeante du cycle annuel des animaux qui doivent assumer leurs propres besoins nutritionnels et simultanément le développement de leur progéniture. La reproduction chez les oiseaux entraîne une contrainte supplémentaire dans la mesure où le nid est souvent distant des aires d'alimentation, ce qui implique chez les espèces monoparentales une augmentation de la probabilité de prédation des œufs lors des activités d'alimentation.

Les femelles Eiders à duvet passent presque exclusivement les 26 jours d'incubation sur leur nid à jeûner. Une stratégie si extrême implique l'existence d'adaptations comportementales préalables au niveau de la période pré-ponte et de la ponte. En effet, les femelles s'alimentent intensivement pendant la période s'étalant de l'arrivée sur les aires de reproduction jusqu'au début de la ponte. La durée de cette période de temps est très variable d'une femelle à l'autre, mais permet dans tous les cas aux femelles d'accumuler des réserves dans un premier temps et de soutenir la demande énergétique liée à la croissance folliculaire dans un second. Toutefois, l'augmentation de masse induite entraîne une diminution temporaire de la capacité de vol pendant la fin de la croissance folliculaire et le début de la ponte, qui peut être dommageable en termes de survie. Les résultats présentés dans ce mémoire suggèrent que les femelles adaptent donc leur comportement pendant la ponte en fréquentant les nids le jour de façon à limiter l'exposition des œufs à la prédation par les prédateurs aériens et en les quittant la nuit pour limiter leur propre exposition à la prédation terrestre. Même si ces périodes d'absence des nids correspondent

à des périodes nocturnes où la détection de nourriture est nécessairement plus difficile, on observe que les femelles profitent de ces absences pour soutenir une activité alimentaire non négligeable. Avec la progression de la ponte, la constance d'incubation augmente dû au retour des femelles de plus en plus tôt sur les nids la nuit et atteint un plateau environ cinq jours après la ponte du premier œuf. A partir de là, les femelles fréquentent très intensivement leur nid et l'activité alimentaire devient négligeable.

Si l'hypothèse de la prédation par les mammifères explique à elle seule les résultats observés dans cette étude et a de ce fait été privilégiée, l'hypothèse d'alimentation qui stipule que les femelles devraient s'absenter des nids pour s'alimenter ne peut néanmoins pas être écartée. Il est difficile avec nos seuls résultats de discriminer ces deux hypothèses pour expliquer un tel comportement. Peut-être qu'une étude expérimentale pourrait aider à déterminer si les femelles partent des nids pour fuir un prédateur potentiel ou pour s'alimenter. Par exemple on pourrait apporter de la nourriture aux femelles sur les nids; si les femelles continuent à quitter les nids malgré cet apport, il serait possible de conclure que les femelles cherchent avant tout à limiter leur propre exposition à la prédation. Toutefois, une telle expérience ne serait concluante qu'à la condition que les femelles s'alimentent efficacement sur la nourriture distribuée artificiellement.

D'autre part, le suivi des activités de plongée nous permet de connaître l'intensité de l'activité alimentaire pendant les différentes phases de la reproduction, mais ne nous permet pas de suivre l'évolution de la demande énergétique subie par les femelles de cette colonie.

Des études antérieures suggèrent que la demande énergétique est élevée chez les oiseaux pendant la ponte et l'incubation. Les consignateurs de données utilisés dans le second chapitre de cette étude permettent à la fois de suivre le comportement de plongée des femelles et leur rythme cardiaque et il est possible d'estimer la demande énergétique des oiseaux à partir de ce dernier paramètre. On peut donc envisager d'étudier le rythme cardiaque des femelles au cours des périodes pré-ponte, de ponte et d'incubation pour documenter l'évolution de la dépense énergétique au courant de la reproduction.

Enfin, nous ne connaissons pas la contribution des différentes ressources utilisées dans la production des œufs et l'incubation. Le temps passé en plongée est important pendant la production des œufs mais on peut se demander s'il est suffisant ou si les réserves préalablement accumulées doivent être mobilisées. Peut-être que des analyses d'isotopes stables pratiquées sur les œufs produits et sur des femelles en cours d'incubation pourraient permettre de quantifier l'importance des différentes ressources utilisées par les femelles durant la reproduction. La méthode utilisée pourrait être similaire à celle utilisée par Gauthier *et al.* (2003) sur la Grande Oie des Neiges consistant à caractériser la signature isotopique de différents tissus de femelles en fin de migration, de différentes sources de nourriture consommées sur les aires de reproduction et d'œufs produits et à suivre l'évolution de la signature isotopique de ces tissus au cours de la période pré-ponte, de la ponte et de l'incubation. Elle nous permettrait ainsi d'évaluer l'importance des sources de nourriture ingérées autour des aires de reproduction dans la constitution des réserves. Une telle méthode implique de prélever des oiseaux durant les différentes étapes de la reproduction et n'est sans doute pas facilement applicable dans le cas de la sous-espèce

mollissima dans la mer Baltique où les sources de nourriture (moules bleues) sont similaires avant et après la migration avec des signatures isotopiques probablement similaires. Peut-être que cette méthode serait applicable avec des populations se nourrissent de proies diverses au courant du printemps.

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