

Brent goose *Branta bernicla bernicla* feeding behaviour during incubation, Taimyr Peninsula, Russia

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Abstract Incubating birds must balance the time and the energy invested in incubation with the energy acquisition for their survival. Many factors such as weather and predation influence this trade-off. In Arctic geese, only females incubate, and they leave the nest regularly to feed while males invest in keeping their nests and mates safe. This study conducted on Big Bird Island (Taimyr Peninsula) during the summer of 2004 examined the incubation behavior of dark-bellied brent geese *Branta bernicla bernicla* to assess the effect of date, period of day and weather conditions on the incubation and feeding behaviors of females and males. Females were at their nests only for 65% of the total time observed. This very low value, compared to other goose species, could be the result of the combined effects of good weather conditions, low predation pressure and opportunities to feed close to the nest. We found differential adjustments of male and female behaviors. Females appeared to focus on the trade-off between feeding and incubating, in relation to weather conditions, and on their own energy balance. Males appeared to respond primarily by the absence of the female from their nest.

Introduction

Incubating birds must balance the time and the energy invested in incubation with the energy necessary to their own survival. They should therefore adjust their behaviour to maximize the chances that the embryos will hatch while minimizing their own risk of starvation (Poussart et al. 2001). Keeping eggs at an optimal temperature and protecting them from predation seem the two most important actions insuring good hatching conditions, and both thermal and predation risks are increased for eggs without parental protection (Webb 1987; Poussart et al. 2000; Samelius and Alisauskas 2001). On the other hand, birds must acquire enough energy to face the costs of both self-maintenance and incubation. Few species can rely exclusively on endogenous sources of energy during the incubation period, and most birds require exogenous sources provided by feeding (Ankney and McInnes 1978; Gauthier et al. 2003). Weather conditions determine vegetation growth, but also determine the energetic costs for the birds, and ultimately even more importantly, the energy required to keep the eggs above a critical temperature (Reid et al. 2000). In addition, predation pressure can significantly impact the energetics of breeding birds by increasing the costs of protection while reducing the available foraging time (Kostin and Mooij 1995; Duriez et al. 2005). The trade-off between incubation, feeding behaviour and avoidance of predation is therefore all the more important for birds breeding in cold weather, especially the polar areas where the birds have to cope with severe climatic conditions, a very short period of food abundance and high predation at nests (Larson 1960).

As for all anatids, only the females incubate the eggs in the Arctic breeding dark-bellied brent goose *Branta bernicla bernicla*. These leave the nest regularly to feed while

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males invest in keeping their nests and mates safe, as well as allowing the females to feed as efficiently as possible (Spaans et al. 1993). Little is known about the behaviour of brent geese on their breeding grounds (but see the few studies describing the breeding and incubating ecology of this species on their breeding grounds, Summers and Underhill 1987; Spaans et al. 1993, 1998). We therefore propose that, as for other better-known geese species, the time spent incubating by females may decrease as incubation progresses (Aldrich and Raveling 1983; Reed et al. 1995; Poussart et al. 2001); change between periods of day (Spaans et al. 1993; Poussart et al. 2001); and it may be influenced by weather conditions (i.e. air temperature, wind speed or solar radiation, Poussart et al. 2000, 2001). Moreover, because of the difference between sexes and of the role of male brent geese as a “nest and mate guard” during the incubation period, the behaviour of males may be strongly influenced by the incubating behaviour of the females, and indirectly by abiotic parameters. However, few studies have described male behaviour during incubation. The results of previous studies on this species showed a decrease of male feeding time when the incubation progressed and a tendency for them to feed more when female fed less (Spaans et al. 1993). We therefore expect that, in addition to the time budget of males and females, also feeding efficiency of both sexes could be affected by abiotic factors.

In this study, we examined the incubation behaviour of dark-bellied brent geese to assess (1) the effect of date, period of day and weather conditions on the incubation and feeding behaviours of females and (2) the effect of date, period of day, weather conditions and female incubating behaviour on the time budget and feeding behaviour of the paired male. We expected differential adjustment of male and female behaviour with females being focused on the trade-off between feeding and incubating, in relation to weather conditions and their own energy balance. In contrast, males should be constrained by the behaviour of their mate (primarily by the absence of the female from the nest when feeding). Subsequently, they should be affected indirectly by the local climate, as this can influence female behavioural decisions. Because this study took place after the snow thawed and with 24 h sunlight, we did not expect an important effect of date and period of day on both male and female behaviours. As egg cooling rates may be affected by weather conditions in geese (Poussart et al. 2000), we predicted that incubating females would reduce their absences from the nest and adopt a more efficient feeding behaviour in bad weather conditions compared with good ones. In parallel, males should forage and rest less efficiently while increasing their vigilance behaviour when their females were outside the nests.

Methods

Study population and study area

Dark-bellied brent geese winter mainly along the coasts of France, the United Kingdom and the Netherlands, and stage from March until late May mainly in the Wadden Sea, from the northern Netherlands to Denmark (Ebbinge et al. 1999). They breed in colonies scattered in the Russian high Arctic, mainly along the coasts of the Taïmyr Peninsula from 73 to 79°N, and from 75 to 122°E (Syroechkovski and Zockler 1997). The spring migration is fairly synchronous and most of the population arrives the second week of June, with egg laying usually underway within a week (Clausen 1997; Spaans et al. 1998).

Our study area was one of the Bird Islands located in the Pyasina delta, about 250 km ENE of Dickson, Taïmyr, Russia (74°07'N, 86°36'E). This small, flat island is called “Big Bird Island”; it is 4 m above sea level and is about 950 m long and 500 m wide (16 ha). A small observation hut overlooked most of the island. The tundra vegetation on the island is dominated by mosses, lichens and grasses (Spaans et al. 1998). Each summer, depending on the abundance of Siberian lemmings *Lemmus sibiricus* and collared lemmings *Dicrostonyx torquatus*, up to one hundred pairs of brent geese nest in “Big Bird Island” (Spaans et al. 1998). In general (including our observation period in 2004) the Taïmyr gull *Larus (argentatus) taimyrensis* is the only predator present in this island (Spaans et al. 1998). No Arctic fox *Alopex lagopus* or snowy owl *Nyctea scandiaca* were seen on Big Bird Island in the summer of 2004.

We were present on the island from the 6th to the 16th July 2004. The arrival date of geese at the colony is not known for 2004. Based on previous observations geese arrive between June 10 and 20 and start nesting very soon after their arrival (Spaans et al. 1998). During the incubating period in 2004, we observed a maximum of 143 brent geese at the same time on the island ($n = 90$ counts, $\min = 72$ geese, $\text{mean} = 106 \pm 2$ (SE) geese).

Behavioural observations

Behavioural observations were conducted throughout the 24-h day, as there was sunlight throughout this period. Geese mainly stayed within their nesting territories and could be observed continuously. We studied time budgets during incubation by using the focal sampling method (Altmann 1974). Using a telescope, we followed ten different nesting pairs within 500 m of the hut. These were chosen for their easy identification and location of both pair members while they foraged, even in poor light conditions. Daily observations averaged 16 h (mainly between 1000 and 2000 hour local time).

On the breeding areas, young geese of the previous year were already separated from their parents (Black and Owen 1989; Lambeck 1990). The sexes were identified before the start of observations by their behaviour; the sex difference was obvious when the female was on the nest and the male in the territory. When a female was not on the nest, she was usually identifiable as feeding very actively close to its nest. We continued each observation until the female returned to the nest in order to be sure of our sex determination. We recorded behaviour differently according to the sex of the bird. For females, we noted both the times they left their nest and when they returned when possible. When both times were recorded, we calculated the duration of the recess period. For males, we carried out 10 min observation periods, distinguishing whether the female was on the nest or not. Behavioural categories were as follows: feeding (head below horizontal, either grazing, grubbing or seeking food), alert (head up, standing still on land), walking (head up, moving on land), resting/immobile (without any specific activity and/or with head tucked in feathers, either standing or sitting), preening (all comfort movements) and social interactions (with conspecifics or other avian species, specially red-breasted geese *Branta ruficollis*). Preening and social interactions were not analysed in this study as they were considered secondary behaviours, representing only a minor proportion of the behaviour and only weakly affected by the female behaviour.

For both sexes, we recorded individual pecking rates (time for 50 pecks including “head-up” behaviours), feeding efficiencies (time for 50 pecks excluding all behaviours other than feeding) and stepping rates (time for 50 steps when the geese were feeding) which were all converted to number of pecks or steps/min.

Meteorological data

The sun was always above the horizon during the summer, hence daily meteorological variations are moderate. We divided the day into three 8-h periods. In the middle of each 8-h period (800, 1600 and 2400 hour local time), we recorded the temperature (in degrees Celsius), the wind speed (in kilometres per hour) and the cloud cover (from 0 when there was no cloud to 8 when the sky was totally covered). Nests were located within 500 m from the point where we took meteorological parameters.

Because three meteorological parameters significantly covaried (temperature vs. cloud: Pearson correlation test, $r = -0.52$, $P = 0.002$, temperature vs. wind: $r = -0.31$, $P = 0.076$, cloud vs. wind: $r = 0.38$, $P = 0.030$), we could not test for their separate effects on behaviour within the same statistical model. We therefore used the first principal component score (PC1, subsequently called “weather”) from a principal component analysis (PCA, SYSTAT 7.0,

Wilkinson 1997) of the three meteorological measurements as an index of the general weather conditions during each 8-h periods ($n = 33$). This “weather” compound variable showed a negative correlation with temperature (loading = -0.799) and a positive correlation with cloud (loading = 0.833) and wind speed (loading = 0.855), i.e. on windy days often with cloudy skies, temperature were always low. PC1 had an Eigen value of 1.815 and explained 60.49% of the variation.

Statistical analyses

To analyse the effect of time of day, we used the same 8-h blocks as for weather variables, and considered three periods of day (morning from 400 to 1200, afternoon from 1200 to 2000 and night from 2000 to 400 the next day) as a categorical variable in the analyses.

The analysis of male behavioural data resulting from focal sampling were however potentially flawed as the measures were likely to be correlated (the sum of all behaviours adds up to 100%) and we thus performed a PCA on arcsine-transformed proportions of time for the four behaviours. The first two axes accounted for 82% of variance (Table 1); with all original variables being highly correlated with the first or the second component (all $> |0.75|$, see Table 1). We thus used the scores on PC1 to perform analyses on the foraging behaviours (feeding + walking) and on PC2 to perform analyses on resting versus alert behaviours.

Peck and step measurements were \log_{10} -transformed, whereas all other parameters followed a normal distribution without other transformation, allowing for parametric tests (Sokal and Rohlf 1995). We used General Linear Mixed Models (GLMM, SAS software, SAS Institute 1997) to explore effect of date, period of day and weather (all fixed factors) on different behaviours of both sexes, with focal bird as a random factor, to account for the repeated measures made on the same individuals. For the males, we also tested if the fact that their female partners were or not on

Table 1 Results of the principal component analysis performed on four behavioural parameters recorded during focal observations of male brent geese ($n = 66$). See “Methods” for further details

	PC1	PC2	PC3	PC4
Eigenvalues	1.851	1.429	0.613	0.108
Proportion of variance (%)	46.27	35.716	15.325	2.689
Cumulative proportion (%)	46.27	81.986	97.311	100
Behaviours				
Feeding	-0.917	-0.083	-0.338	0.195
Resting	0.468	0.853	0.125	0.193
Walking	-0.754	0.113	0.647	-0.005
Alert	0.473	-0.825	0.253	0.179

nest (fixed factor) affected their own behaviour. We started with the maximal model (i.e. all explanatory variables and their interactions), and compared it with submodels from which we sequentially deleted non-significant terms until we obtained the most parsimonious model only containing significant variables. The model selection procedure was performed using Akaike's Information Criterion (AIC), selecting the lowest AIC value. We considered two models to be significantly different when difference between AIC was greater than 2 (Burnham and Anderson 1998). Values are presented as means \pm standard error.

Results

Time budget and feeding rate of females

On average, females fed for 21.8 ± 8.9 min ($n = 89$) and spent 39.9 ± 21.1 min on their nest ($n = 35$). This means that females fed once per hour and 24 times a day. Recess duration and time spent on nest between two recesses were both independent of date (respectively, $F_{1,76} = 0.24$, $P = 0.627$ and $F_{1,27} = 0.44$, $P = 0.513$) and period of day (respectively, $F_{2,77} = 0.64$, $P = 0.530$ and $F_{2,27} = 0.70$, $P = 0.506$). Recess durations were dependent on weather ($F_{1,79} = 6.91$, $P = 0.010$, $t = -2.63$, Fig. 1); whereas time spent on nest between two recesses was independent of these climatic conditions ($F_{1,24} = 0.02$, $P = 0.903$). When the weather was bad, females had shorter recesses, even though the time elapsed between two consecutive recesses was unchanged, leading to shorter daily recess duration. Recess durations were neither dependent on previous or next time on nest (respectively, $F_{1,21} = 1.24$, $P = 0.277$ and $F_{1,18} = 0.79$, $P = 0.385$) and times on nest were independent of previous or next recess duration ($F_{1,19} = 3.02$, $P = 0.098$ and $F_{1,22} = 1.36$, $P = 0.255$).

When females were feeding, they never or very rarely raised their heads, and showed similar "pecking rates" and "feeding efficiencies" (Fig. 2). Females generally had higher pecking rates when the weather was cold, cloudy and windy ($F_{1,212} = 17.63$, $P < 0.001$) as well as in the morning ($F_{2,212} = 8.10$, $P < 0.001$; 153 ± 9 pecks/min from 400 to 1200 hour, 149 ± 4 pecks/min from 1200 to 2000 hour and 139 ± 5 pecks/min from 2000 to 400 hour). This was modulated by date, as the slope of the peck rate–weather relationship decreased with date but remained positive (weather \times date interaction: $F_{1,212} = 17.62$, $P < 0.001$). This is likely to be due to the fact that the variance of weather decreased with date, with a tendency for it to be milder. Stepping rates showed similar patterns, with females walking quickly in bad weather ($F_{1,207} = 18.29$, $P < 0.001$) although less markedly as date progressed (weather \times date interaction: $F_{1,207} = 18.29$, $P < 0.001$).

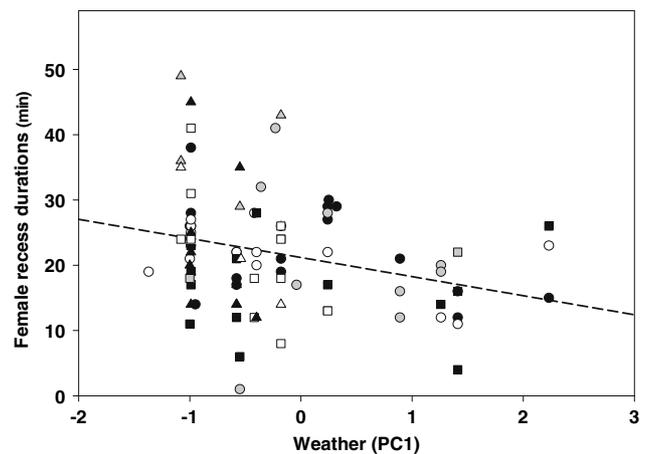


Fig. 1 Relationship between weather conditions during incubation and the duration of female recess events. PC1 = -0.799 Temperature + 0.833 Cloud cover + 0.855 Wind speed. Each symbol represents a different nest. The line symbolises the linear regression for all data. Equation: Female recess duration = -2.6841 PC1 + 21.7365

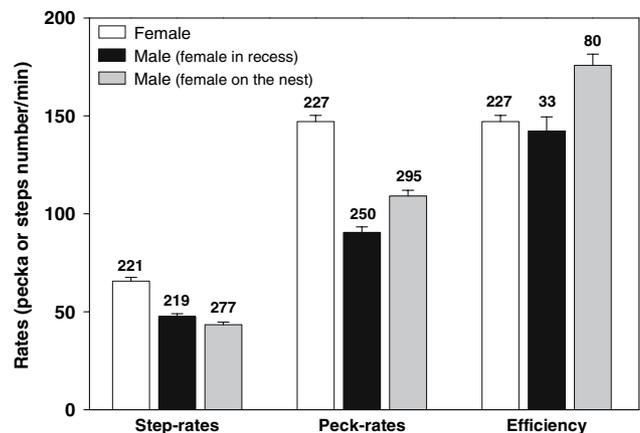


Fig. 2 Pecking rate, stepping rates and feeding efficiency of brent geese during the incubation period. Mean \pm standard error

Time budget and feeding rates of males

The most important behaviour for males during incubation was being alert, then feeding and resting (corresponding to 90% of their time budget whether their females were on the nests or not, Fig. 3). Foraging behaviours feeding + walking did not change according to the date and period of the day ($F_{1,51} = 2.52$, $P = 0.119$ and $F_{2,52} = 2.29$, $P = 0.112$, respectively). Foraging time varied significantly according to whether the female was on the nest or not, and according to weather conditions (see Table 2). When the female was on the nest, the male foraged more, especially during poor weather conditions (lower temperature, more wind and more clouds). Conversely, when the female was foraging, the male foraged less during bad weather. The relationship between resting and vigilance did not change according to

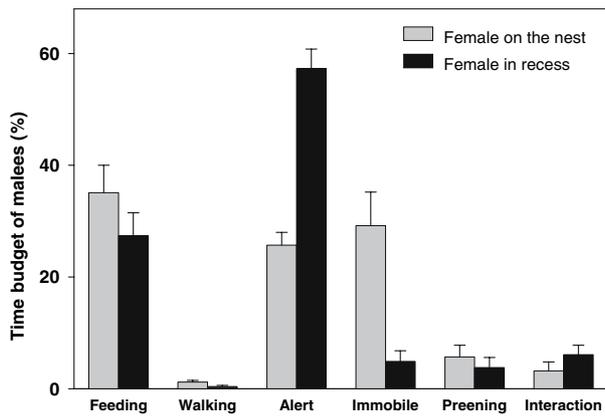


Fig. 3 Proportion of time that male spent in each six principal behaviours during incubation. $N = 66$ focal periods. Mean \pm standard error

Table 2 Results of linear mixed-models fitted by maximum likelihood on scores of the first and second principal components of the PCA on behaviours of male brent geese, with denominator degrees of freedom (DF), F -values, and P -values for the terms in ANOVA models and with parameter estimates (i.e. fixed effects estimates), approximate standard error (SE), ratios between the estimates and their standard errors (T -value), and P -values from a t distribution for the fixed effect table

Factors	DF	F	Estimate	SE	T	P
PC1: foraging behaviours						
Intercept	8		-0.1432	0.1947	-0.74	0.4831
Weather	54	0.31	-0.3250	0.1424	-2.28	0.5797
Female nesting	54	2.00	0.3328	0.2352	1.41	0.1628
Weather \times Female nesting	54	7.27	0.5359	0.1988	2.70	0.0093
PC2: Alert vs. resting behaviours						
Intercept	8		0.7267	0.1348	5.39	0.0007
Weather	55	4.76	-0.1742	0.0798	-2.18	0.0334
Female nesting	55	52.81	-1.3488	0.1856	-7.27	< 0.0001

date and period of the day either ($F_{1,54} = 0.94$, $P = 0.336$ and $F_{2,52} = 0.69$, $P = 0.507$, respectively) but it differed significantly if the female was on the nest or not, and according to weather conditions (see Table 2). If the female was away from the nest, the male was significantly more alert and rested less than when the female was on the nest. The level of vigilance increased when the weather became worse, whether the female was on the nest or off it.

The main source of variation in pecking rates appeared to be the breeding activity of the female, being higher when the female was on the nest ($F_{1,528} = 6.29$, $P = 0.012$, Fig. 2); although pecking rates also increased with date ($F_{1,528} = 4.78$, $P = 0.029$) and especially when the female was on the nest (interaction: $F_{1,528} = 6.29$, $P = 0.012$). Male stepping rates seemed more influenced by date ($F_{1,476} =$

15.45, $P < 0.001$) and time of day ($F_{1,476} = 4.09$, $P = 0.017$), increasing with date and during the day. When females were brooding, male stepping rates varied more with period of day (interaction: $F_{1,476} = 4.04$, $P = 0.018$). Overall, males increased their feeding efficiency when females were on the nest (Fig. 2). Male feeding efficiency also varied with period of day, with a slight decrease in efficiency with day period, which was more significant while the female was on the nest (interaction: $F_{1,97} = 6.15$, $P = 0.003$).

Discussion

Female incubating behaviour

Females were at their nests for only 65% of the total time observed, which is very little compared to previous studies of other small geese species, which incubate for about 93% of the day, the remaining time being spent in several short feeding recesses (Reed et al. 1995). Larger geese species spend even more time on the nest (97–99%, up to 99.2% for white-fronted geese *Anser albifrons albifrons*, Spaans et al. 1999) and take fewer but longer recesses during which less than half of the time is devoted to feeding (Reed et al. 1995). The present results are also generally lower than the values obtained by Spaans et al. (i.e. 90.4%, Spaans et al. 1993) for the same species on the Taïmyr Peninsula. These authors, like other workers studying other geese species, noted a decrease in nest attendance (i.e. an increase in recess frequency and duration) as incubation progressed (Aldrich and Raveling 1983; Reed et al. 1995; Poussart et al. 2001), resulting in more foraging time for the female. Our study was performed for 10 days during the second half of the incubation period (24.5 days, Spaans et al. 1993). During this period, Spaans et al. (1993) found daily recess times up to 336 min a day (corresponding to around 77% of the time on the nest) for the two studied females on the island. Nevertheless, we observed no significant variation of the recess behaviour according to date and period of day probably because our analysis simultaneously integrated weather conditions (here a highly significant factor), which often also fluctuate with date and period of day (Poussart et al. 2001). Females decreased feeding time in bad weather conditions as predicted. Incubating females therefore appear to adjust their recesses to limit egg cooling and insure that the egg temperature does not fall much below the optimal thermal range for embryonic development (35–40°C, Webb 1987). An alternative hypothesis to explain the absence of daily cycles in incubation behaviour may be the absence of fox predation on Big Bird Island. Because the active period of this predator is largely concentrated in the nocturnal hours, even when sunlight is permanent, geese

may adjust their incubation cycle when they breed within fox areas and this factor alone could explain the higher nest attentiveness of geese at night than in the daytime in most studies (Poussart et al. 2001). Finally, the very low nest attendance by nesting brent geese compared with other geese species may be also explained by a combination of (1) low predation pressure (no foxes and mainly gulls in Big Bird Island during this study), (2) opportunities to feed close to the nest as this would allow the pair to watch the nest for potential attacks by egg predators while off the nest and (3) benign weather conditions during the summer of 2003 (average temperature during the study period was around 14°C compared to 10°C for the same periods between 1977 and 1990, Spaans et al. 1993).

Male time budget

The most important behaviour for a male during incubation was being alert while his female was feeding, and feeding while his female was on the nest. This result confirms that geese have distinct roles during nesting, with female geese incubating and male geese detecting and deterring predators and conspecifics (Samelius and Alisauskas 2001). This is further supported by the absence of an effect of date and period of day on the behaviour of both sexes. This supports the prediction concerning male behavioural investment in reproductive success in anatids, for which male investment allowing an increase of the female feeding time also increases breeding success. This was mostly documented during spring staging, when the main benefit of increased feeding time for females is an improvement of their fat reserves (Davis 2002; Guillemain et al. 2003; Frafjord 2004). At the nesting sites, the vigilance activity of the male will benefit the pair's breeding success. An increased feeding efficiency for the female should help compensate for fasting while on the nest, possibly allowing for longer incubating periods and consequently an improved temperature maintenance of the eggs. The vigilance behaviour of the male would also help prevent nest predation while the female forages. These male behaviours were also modulated by weather conditions: when the female was on the nest, the male foraged more when weather conditions became worse as the female foraged; the male foraged less in bad weather and his level of vigilance increased with the weather worsening, in both female positions. These adaptations could reflect the trade-off between energetic requirements and the need to protect the nest from avian predators, both potentially increase in bad weather conditions. During bad weather, the male could safely satisfy its own increased energetic demands by increasing his feeding time if the female was on the nest. Nevertheless, if the female was feeding, the male increased its vigilance behaviour and hence decreased his feeding time as his ability to detect

predator decreased with the reduction in visibility associated with grazing. This synchronisation was also observed by Spaans et al. (1993) who reported the same pattern as that described here for two males and females.

Male and female feeding rates

In Arctic geese, the females of some goose species (e.g. white-fronted geese) never feed during the incubation period and use recess periods only to drink and bathe. All the energy required during incubation is therefore derived from the catabolism of endogenous stores (Spaans et al. 1999). In brent geese as for most geese species, females have to feed during incubation. During a recess, by remaining close to the nest and devoting most of their time to feeding with a rapid peck rate, they minimized energy expenditure and maximized food intake (Reed et al. 1995). For comparison, female greater snow geese *Anser caerulescens atlanticus* in similar conditions fed at a rate of 153 ± 8 pecks/min ($n = 9$ females, Reed et al. 1995) compared to 147 ± 3 pecks/min in this present study. Nevertheless, comparing our findings with other studies is made difficult by species differences and by the greater variation of pecking and stepping rates in different biotic and abiotic conditions (see for example Prop (2004) for variation caused by food type; Durant et al. (2003) by vegetation height; and Righi and Gauthier (2002) by parasite load). It is thus more relevant to compare these rates between sexes according to weather conditions, and in the case of males, according to female incubation behaviour. In brent geese, females increased pecking and stepping rates and thus fed more actively in bad weather conditions. This reduced the time away from the nest (i.e. egg cooling) while maximizing food intake (i.e. its own energetic requirements and those necessary to keep the eggs at an optimal temperature). Males foraged more actively while the female was incubating. Moreover, females fed and pecked and walked more quickly than the male during the same period. This reflects the males' greater vigilance when the female was not on the nest (Lamprecht 1986). Nevertheless, our results showed that males could also be very efficient in their feeding behaviour when the female was protecting the nest.

To conclude, the feeding pattern of female brent geese during incubation appears to be optimised for both energy saving as well as for avoiding predation. By contrast, male behaviour, in addition to being adjusted to the behaviour of the female, also appeared to respond to an increased predation risk, particularly in bad weather conditions.

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