Travels in a changing world flexibility and constraints in migration and breeding of the barnacle goose

Eichhorn, Götz

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Nest attentiveness in temperate and arctic-breeding barnacle geese

Götz Eichhorn
Julia Karagicheva

In barnacle geese like in most waterfowl incubation is carried out solely by the female. In contrast to eiders *Somateria molissima* and some of the larger waterfowl species (Afton and Paulus 1992) female barnacle geese cannot sustain themselves through incubation by drawing from body stores alone, but rely on additional nutrient input from feeding recesses. Incubation behaviour is expected to be regulated by body condition as well as by environmental factors, among them weather and food conditions and predation pressure (e.g., Thompson and Raveling 1987; Poussart et al. 2001; Poisbleau et al. 2007). At least some of these conditions are further expected to differ for birds from the long-distance migratory population of barnacle geese breeding in the Russian Arctic and birds from the sedentary population breeding in the Netherlands. Here we describe incubation patterns (in more detail for the Dutch birds) and compare nest attentiveness of females from these two study populations. We were further interested in how incubation behaviour relates to the different use of body stores found for females from these populations (ch. 7 this thesis).

Methods

Temperate-breeding barnacle geese from the North Sea population were studied in the Netherlands at Hellegatsplaten (51°42'N, 4°20'E), one of the largest colonies in the Delta area in the southwest of the country. Arctic-breeding barnacle geese from the Barents Sea population were studied in a colony on the northwest coast of Kolokolkova Bay, near the abandoned settlement of Tobseda, northern Russia (68°35'N, 52°20'E). Details on these study populations and study sites can be found in the introduction of this thesis.

To monitor incubation behaviour of females from the Dutch population a temperature probe (5 mm in diameter, 10 to 20 mm long) was installed in the bottom of the nest cup between the eggs, so that it pointed upwards with the end at level of the upper egg surface. Data were recorded at 30 sec intervals and logged

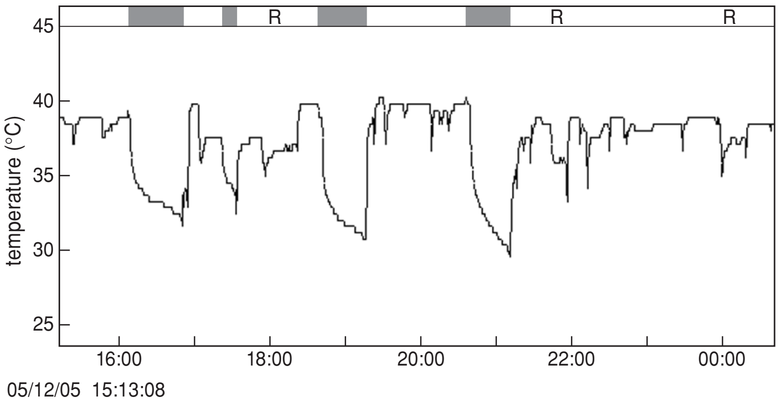

Figure BoxC.1. Example of temperature readings measured at 30 sec intervals with probes installed in the nest of incubating female barnacle geese from the Dutch study population. Four recesses (between 16:00 and 24:00) can be detected (marked by bars; R= resettling on the clutch without leaving nest).

onto HOBO loggers (Onset Computer Corporation, model H08-008-04 or H08-031-08). With this method 14 nests were monitored on 4 to 18 days (average 10 days) during incubation in 2005 (12 nests hatched, 2 females abandoned the nest before, likely due to human interference). Incubation and recess bouts were read from temperature graphs displayed by the software programme BoxCar Pro 4 (see Fig. BoxC.1 for an example). The interpretation of graphs was calibrated by comparing temperature logger data with simultaneous direct observations. Displacement of the probe by the bird happened in a number of nests for part of the measurement period resulting in irregular temperature graphs. Such periods as well as readings around the time of hatching were discarded. On days when geese left the nest due to human interference (e.g., during weekly data download) the data of that whole day were discarded. For data from the Dutch population we included only data that comprised complete 24 hour periods to calculate the following three parameters: *daily recess frequency* (i.e., number of recesses per 24 hours), *recess duration* (which was averaged per female before calculation of the mean over all females per day) and *total daily recess time*.

Data on females from the Russian population were gathered by direct observation (Karagicheva and Gurtovaya in prep.). Individual nests were scanned using binoculars and a 30–40x telescope at frequent intervals (usually every 10–15 minutes) and female presence/absence on the nest was noted. In total 42 nests were monitored in 2004 and 2005 from a permanent hide erected on a dune overlooking the colony. All nests were marked by flagged stakes visible from the hide. Single observational bouts lasted from 6 to 48 hours and covered all periods of the day and stages of incubation. Laying dates, clutch size and hatching success were determined by nest checks every 1–2 days.

Average start of incubation in the sample of 14 females from the Dutch population was 30 April. For birds from the Russian study site start of incubation peaked on 9 June in 2005 for the colony as a whole. These dates were either back-calculated from hatching date or, alternatively, from dates of egg-laying assuming commencement of incubation at the 3rd egg-stage (for clutches of 3 to 5 eggs) or 4th egg-stage (for clutches larger than 5 eggs) and 33 hours laying interval (Alisauskas and Ankney 1992a; Schubert and Cooke 1993). Incubation in barnacle geese lasts for approximately 25 (24–26) days (Dalhaug et al. 1996; own obs.). To give an indication of the ambient temperatures experienced by females from both populations during incubation we plotted data of daily maximum, mean and minimum temperatures for a period of 30 days starting from the abovementioned average dates of incubation initiation. At the Russian field site temperature was measured adjacent to the colony. Data provided from the Royal Netherlands Meteorological Institute (KNMI) for the weather station in Vlissingen (51° 27' N, 03° 36' E) were taken as representative for the Dutch breeding site. Temperature sensors at both sites were installed at 2 m and 1.5 m above ground, respectively, and protected from sun radiation. An estimate of the lower critical temperature in the barnacle goose was calculated after Calder and King (1974) yielding 4°C (for 1660 g body mass at mid incubation). However, Stahl (2001) reported a value of 12°C for this species, and we assume the true value within the range of these two estimates.

Results

Incubating females from the Dutch colony left the nest on average 2.6 times per day for a mean period of 30 minutes per recess; the accumulated recess time per day was 78 min translating to a nest attentiveness of nearly 95% (Table BoxC.1). When related to day of incubation recess frequency showed no clear trend for most of the incubation period, but decreased over the last three days of incubation, whereas duration of recesses remained stable over the same period. Recess bouts appeared to be shorter during the first six days of incubation (Fig. BoxC.2).

Daily recess time of females from the Arctic Russian colony was higher than for Dutch birds for most of the incubation period (Fig. BoxC.3) and averaging 157 min over 26 days of incubation (equating to a nest attentiveness of 89%). As in Dutch breeders Russian birds reduced their time off the nest over the last three days of incubation. Thus, daily recess time was reasonably stable over the first 22 days of

Table BoxC.1. Incubation rhythm in the barnacle goose from a Dutch colony.

	Mean ± SE	n	Range
Daily recess frequency	2.6 ± 0.1	138	0 - 6
Recess duration [min]	30.3 ± 1.3	134	9 - 99
Daily recess time [min]	77.6 ± 3.7	138	0 - 214
Daily nest attentiveness [%]	94.6 ± 0.3	138	85.1 - 100

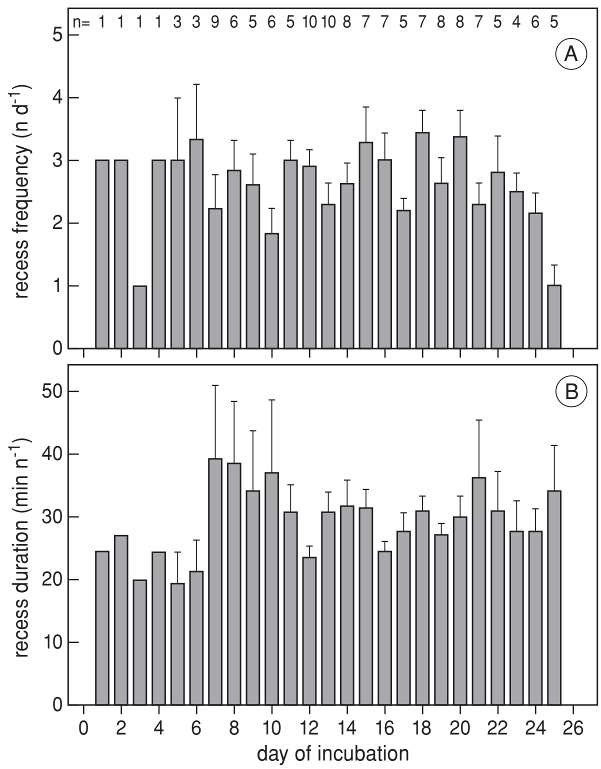

Figure BoxC.2. Pattern of daily incubation recesses for female barnacle geese from a Dutch breeding population. A) Mean ± SE recess frequency and B) recess duration calculated from daily means of individual females. Number of females monitored per day is given at the top (n = 138 bird-days in total).

incubation averaging 80 min and 177 min in Dutch and Russian birds, respectively. Despite the paucity of our observations on the Dutch birds, actual daily feeding time differs even more than the recess times indicate. The proportion of time spent feeding during a recess (head below horizontal and grazing or seeking for food) amounted to 64 ± 4% (mean ± SE, n = 11) and 77 ± 2% (n = 34) for Dutch (in 2005) and Russian (2003 and 2004 combined) breeders, respectively. Thus, estimated average daily feeding time for Dutch incubating females (50 min) would be only 40% as long as compared to their Russian conspecifics (121 min).

Discussion

Studies on Canada geese *Branta canadensis moffitti* (Aldrich and Raveling 1983), greater snow geese *Anser caerulescens atlanticus* (Poussart et al. 2001) and black brent *Branta bernicla nigricans* (Eichholz and Sedinger 1999) reported an increase in daily recess time as incubation progressed, whereas studies on emperor geese *Anser canagicus* (Thompson and Raveling 1987), brent geese *Branta b. bernicla* (Spaans et

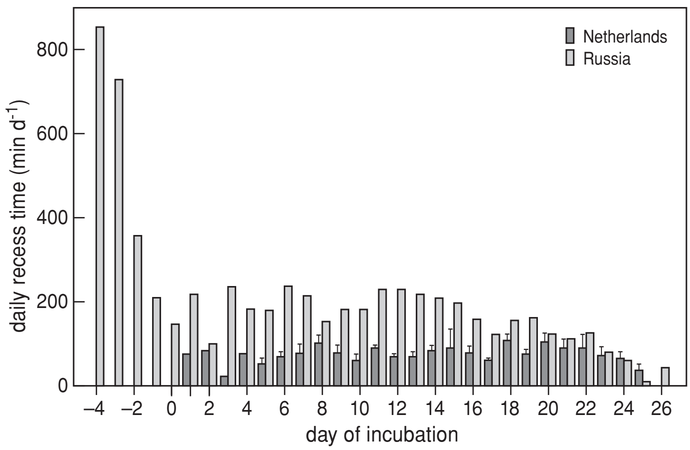

Figure BoxC.3. Average daily recess time per day of incubation for female barnacle geese from a colony in the Netherlands and Arctic Russia. For Dutch birds standard errors are given based on the sample of birds monitored with help of temperature loggers installed in the nest (n per day given in Fig. 1A). For Russian birds only averages are shown from direct scan sampling procedures of 42 nests in 2004 and 2005 combined.

al. 2007) and barnacle geese (this study) did not find such a trend. However, all studies observed increased nest attendance during the last few days of incubation. Weather conditions and predation pressure have been suggested as important environmental factors regulating incubation behaviour in geese (Aldrich and Raveling 1983; Thompson and Raveling 1987; Poussart et al. 2001; Poisbleau et al. 2007). Weather and food conditions generally improve over the season and may stimulate absence from the nest. In contrary, unprofitable feeding conditions may cause unexpected high nest attentiveness (Jonsson et al. 2007).

Barnacle geese from the Dutch colony enjoy milder temperatures than geese breeding in the Russian Arctic (Fig. BoxC.4) thereby likely reducing costs for both maintaining body temperature and reheating the clutch after incubation recesses. Feeding conditions, as judged by the nitrogen content of food plants, appeared to be comparable for Dutch and Russian barnacle geese (ch. 6 this thesis), and predation pressure on unattended clutches seemed to be actually lower in the Dutch colonies (own obs.). Thus, the above cited environmental factors can hardly explain the higher nest attendance of geese from the Dutch colony. The finding of a higher nest attentiveness in temperate compared to arctic-nesting barnacle geese is supported by other studies. Tombre and Erikstad (1996) reported for barnacle geese from the Spitsbergen population an average daily recess time of 151 minutes (N = 76 nests observed at Ny-Ålesund) with 7.2 recesses per day lasting 21.5 minutes on average. This daily nest attendance of 89.5% contrasts with 94.8% found for free-flying barnacle geese breeding at the Wildfowl Trust's reserve at Slimbridge, UK (Lessells et al. 1979; Afton and Paulus 1992).

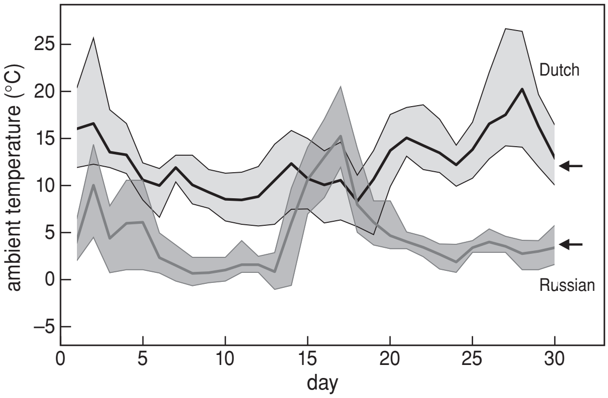

Figure BoxC.4. Daily maximum, mean and minimum temperatures measured at the Dutch and Russian study sites in 2005 for a period of 30 days starting from the respective mean dates of start of incubation (30 April and 9 June). The arrows at the right mark two estimates of the lower critical temperature (see methods for details).

Apart from external factors females adjust incubation behaviour in relation to the state of body stores (see discussion in ch. 7). They may balance their stores in order to not exhaust them completely until hatch. Female Spitsbergen barnacle geese with experimentally prolonged incubation (extra 5 d by clutch swap) although sacrificing body condition did not increase recess time in late incubation (Tombre and Erikstad 1996). However, with an estimated 32 g fat residue at hatch and a daily fat loss of 10 g the Russian female barnacle geese are apparently unable to incubate for another 5 days unless they notably increase their food uptake (ch. 7).

In conclusion, temperate barnacle geese commence incubation with more body stores allowing them to reduce feeding time compared to arctic conspecifics (see also Table 7.5 in ch. 7). Apparently, nest attentiveness is maximised as permitted by the amount of body stores, even under actually benign environmental conditions (including relaxed predation pressure in the absence of foxes).