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SEASONAL DECLINE IN CLUTCH SIZE OF THE BARNACLE GOOSE IN SVALBARD[1]

LAILA DALHAUG, INGUNN M. TOMBRE AND
KJELL EINAR ERIKSTAD
Foundation for Nature Research and Cultural Heritage Research, Department for Arctic Ecology, c/o Tromsø Museum, N-9006 Tromsø, Norway and
University of Tromsø, Dept of Ecology/Zoology, Institute for Biology and Geology, University of Tromsø, N-9037 Tromsø, Norway

Abstract. We examined seasonal decline in clutch size in the high arctic Barnacle Goose *Branta leucopsis* in Svalbard. Females that arrived first at the breeding ground nested first, had the longest prelaying period, produced the largest clutches and also had the longest incubation period. Nevertheless, their brood size at hatching was larger than late nesters. These results do not support the nutrient reallocation hypothesis which suggests that seasonal decline in clutch size in arctic nesting geese results from the mobilization of nutrient reserves during the period before egg laying. Instead, we propose that geese which arrive late at the breeding area spend relatively less of their reserves on eggs. They do this presumably to achieve synchronous hatching with early nesting birds and/or to prevent a late breeding season which may reduce gosling survival, adult survival and/or future fecundity.

Key words: Barnacle geese; Branta leucopsis; *clutch size; breeding date; incubation period; body condition.*

INTRODUCTION

When arctic-nesting geese depart from staging areas in spring, nesting conditions may still be unfavorable on their breeding grounds and may also vary considerably among years (Barry 1962, Ely and Raveling 1984, Petersen 1992, Prop and de Vries 1993). The timing of breeding may affect individual fitness, and a number of proximate factors have been proposed to explain the timing of breeding in geese; weather conditions (e.g., Barry 1962, Mickelson 1975), age, physical condition of the laying female and available food resources (reviewed by Johnson et al. 1992). When spring thaw is late, the average clutch size in geese is reduced (Ryder 1970). Clutch sizes have been found to vary within, as well as between, seasons and a negative relationship between nesting date and clutch size has been recorded for all species studied in detail (reviewed by Rohwer 1992). Several hypotheses have been put forward to explain the seasonal decline in clutch size in geese (see Sjöberg 1994 for a recent review). The most accepted hypothesis for arctic-nesting geese is the nutrient reallocation hypothesis (NRH) (Barry 1962). This hypothesis is based on the observation that follicular atresia (vesicles resulting from degeneration of follicles) in Atlantic Brent Geese *Branta bernicla* was more common for individuals with small clutches and for those which failed to breed compared to successful females which produced large clutches (Barry 1962). Barry (1962) suggested that follicular atresia was induced by prolonged bad weather which covered the nesting areas with snow. Consequently, resorption of nutrients for maintenance while waiting for nesting conditions to be favorable becomes necessary.

The argument for small clutches in late years may also apply to the decline in clutch sizes within seasons (Ryder 1970). According to the NRH, it is assumed that all geese arrive at the same time and in similar body condition. Since bad weather and snow cover may induce competition for available nest sites, some females delay egg laying longer than others. During this delay, the females utilize stored nutrients which could otherwise have been used for egg production (Hamann et al. 1986). Therefore, according to the NRH, females laying late in the season have a longer prelaying period and produce smaller clutches compared to early layers.

Several ultimate hypotheses have also been proposed to explain seasonal decline in clutch size. The growth rate and survival of young, and thereby recruitment of young to the population, decrease as the breeding season proceeds (Sedin-

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ger and Raveling 1986, Larsson and Forslund 1991, Lindholm et al. 1994). Time could be saved by producing smaller clutches late in the season, the cost-of-delay hypothesis (Drent and Daan 1980). The balance between current reproductive effort and future breeding could also change as the season proceeds; for example, the parents' reproductive effort should be lower late in the season since late breeding is costly for the parents (Toft et al. 1986, reviewed in Rohwer 1992).

So far, there are few critical studies of the seasonal decline in clutch size in arctic-nesting geese. No data document the relationship between the date of arrival, length of the prelaying period and clutch size, which would make it possible to examine the NRH in any detail (for review see Rohwer 1992).

In this study we examined the seasonal decline in clutch size in Barnacle Geese *Branta leucopsis* breeding in Svalbard. The main purpose of the study was to describe the relationship between date of arrival at the breeding area, the length of the prelaying period and their effects on clutch size. We also present data on the length of the incubation period, egg predation during incubation and female body condition at hatching. We discuss these data in relation to the NRH and the ultimate hypotheses described to explain seasonal decline in clutch size for Barnacle Geese. We also outline an alternative explanation for how female geese allocate their body reserves to eggs and incubation in relation to the time of the season when they start nesting.

METHOD AND STUDY AREA

The study was carried out in 1993 in a colony near Ny-Ålesund, in the Kongsfjord area on the NW coast of Svalbard. The colony (ca. 240 breeding pairs) studied was on an island (Storholmen 78°55′N, 12°15′E) of 30 ha. Almost 70% of the adults in the study area have color rings with individual letter codes, and some are of known breeding age.

Birds were identified daily as they arrived in the Kongsfjorden area. The colony was visited every day during the egg laying and hatching periods. Birds which were observed for the first time during egg laying were excluded from the prelaying period analysis. Females laying more than once (renesters), and all nests containing fewer than three eggs, were excluded from all analyses. The following data were collected for each pair: date of arrival to the breeding area, date of egg laying (determined by extrapolation using the number of eggs found in a nest and assuming that one egg is laid per day), length of the prelaying period (number of days between arrival and egg laying), clutch size, length of the incubation period (defined as the number of days between the last egg laid and the first egg hatched) and the female body condition at hatching. The females were caught at the nest at the end of incubation (one to three days before hatching) using a noose on the end of a fishing rod. The geese were weighed and measurements of skull (head including bill) and wing length were taken. Then body size was calculated using a principal component analysis (PCA). The first principal component (PC1) explained 68.8% of the standardized variance in the two characters. The female's body condition was defined as the residuals from a body mass vs. PC1 regression. The total explained variance in the female body mass due to size was 35% ($r^2 = 0.35$, df = 16, $P = 0.001$).

The statistical analyses were carried out using the SAS statistical package (SAS Institute 1990). All values are given as means ± SE. The significance level is set at $P < 0.05$.

RESULTS

DATE OF ARRIVAL AND START OF EGG LAYING

There was a considerable variation in arrival dates among females to the breeding ground. Early arriving females started egg laying first; the first egg laying date was 4 June (Fig. 1a). These females also had the longest prelaying period (Fig. 1b). Females arriving at the breeding ground when other females already had started egg laying waited approximately three days before they laid their first egg (Fig. 1b). For these females the laying date was determined by the date of arrival.

CLUTCH SIZE AND LAYING DATE

Clutch size decreased significantly with laying date (Fig. 2). Egg loss to predators (based on loss of single eggs) was very low (7.6%, n = 397). Accordingly, mean brood size at hatching (3.32 ± 0.08, n = 110) was only slightly less than mean clutch size produced (3.56 ± 0.06, n = 123), but differed significantly (t = 2.39, df = 231, P < 0.01). Therefore, females laying large clutches early in the season are also those which produce the largest number of goslings at hatching.

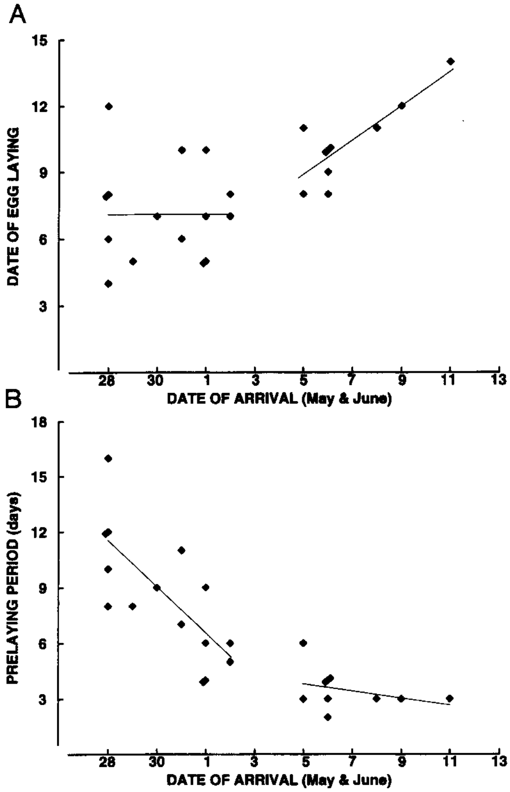

FIGURE 1. The relationship between A) date of egg laying and the date of arrival at the breeding grounds, and B) length of the prelaying period and the date of arrival at the breeding grounds in a Barnacle Goose population in Kongsfjorden, Svalbard (a. Early arriving geese: $R^2 = 0.001$, df = 14, $P = 0.91$, $y = 8.30 - 0.04x$, Late arriving geese: $R^2 = 0.70$, df = 9, $P = 0.003$, $y = 0.79x - 19.63$, b. Early arriving geese: $R^2 = 0, 55$, df = 14, $P = 0.002$, $y = 46.47x - 1.25$, Late arriving geese, $R^2 = 0.14$, df = 9, $P = 0.29$, $y = 11.38 - 0.21x$.

LAYING DATE AND CLUTCH SIZE IN RELATION TO FEMALE AGE

There was no indication from this study area that the age of the breeding females had any significant effect on laying date and clutch size. First-breeders (2 years old) had the same mean laying date (9.69 ± 0.81 in June) as females 5 years old or more (9.41 ± 0.57 in June) ($t = 0.29$, df = 28, $P = 0.77$). Furthermore, there were no differences in the mean clutch sizes of the two age groups (young geese: 3.23 ± 0.25, $n = 13$, old geese: 3.64 ± 0.20, $n = 17$, $t = -1.26$, df = 28, $P = 0.21$).

CLUTCH SIZE AND INCUBATION PERIOD

In addition to smaller clutches, late nesting females also had a shorter incubation period than early nesters (Fig. 3). There was no correlation between the length of the incubation period and clutch size ($r^2 = 0.005$, df = 68, $P = 0.6$), and there was a positive trend for late-laying females to be in slightly better body condition at hatching ($r^2 = 0.17$, df = 16, $P = 0.11$).

DISCUSSION

The Barnacle Geese which arrived first at the breeding ground started egg laying first. They had the longest prelaying period, but produced larger clutches than late arrivers. Females which produced the largest clutches early in the season also had a longer incubation period. These, however, hatched a larger number of goslings. These results do not support the NRH. According to this hypothesis, females with a long prelaying period should use more body reserves for maintenance while waiting to nest and therefore have less reserves to spend on egg production than those with a shorter prelaying period (Barry 1962, Ryder 1970, Rohwer 1992). In this study, however, females with the longest prelaying period produced larger clutches than females with a short prelaying period.

Late arriving females waited approximately three days before they laid their first egg, presumably a minimum of time needed before egg laying could start. Closely related species to the Barnacle Goose have a rapid follicle growth (RFG) of approximately 10–13 days (reviewed in Alisauskas and Ankney 1992). Therefore, the Barnacle Geese in Ny-Ålesund have probably already started the RFG before they arrive at their breeding grounds since most females have a prelaying period shorter than 12 days.

A number of studies on geese have shown that young females produce smaller clutches than old-

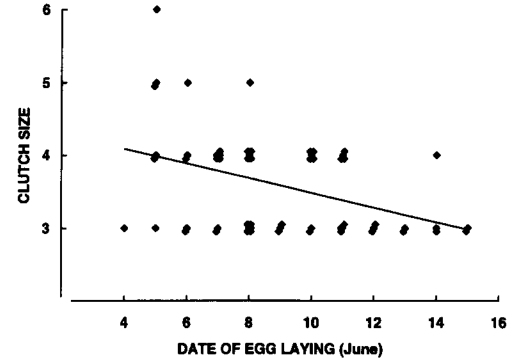

FIGURE 2. Clutch size in relation to the date of first egg laying ($y = 4.49 - 0.10x$, $R^2 = 0.17$, df = 60, $P = 0.001$).

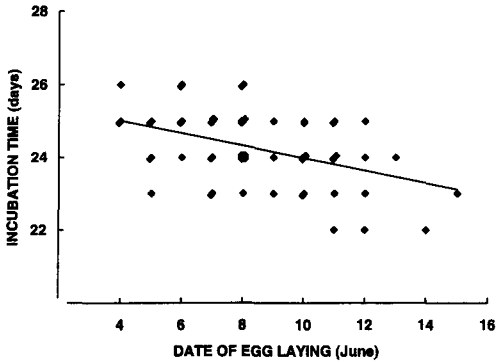

FIGURE 3. The length of the incubation period in relation to date of egg laying in a Barnacle Goose population breeding in Kongsfjorden, Spitsbergen 1993 ($y = 25.76 - 0.18x$, $R^2 = 0.21$, df = 68, $P = 0.0001$).

er geese (Brakhage 1965, Cooper 1978, Finney and Cooke 1978, Owen 1980, Raveling 1981). Such an effect has also been documented in Barnacle Geese (Forslund and Larsson 1992) where individuals of two and three years produced smaller clutches and young compared to birds of four or more years of age. However, there is no evidence in this study suggesting that female age had any impact on clutch size or laying date.

In this study, clutch size decreased with laying date. However, clutch size was not related to extra costs caused by an increased prelaying period. So far we know nothing about how the length of the prelaying period affects the body reserves of breeding females. Most likely, females arriving first must use more reserves for maintenance compared to those arriving later (e.g., Ryder 1970). It is even more likely that geese arriving late are in better body condition at the start of egg laying since they have a short prelaying period. Furthermore, a significant positive correlation has been recorded between female body condition upon arrival and date of arrival for the Barnacle Geese in Ny-Ålesund (I. M. Tombre et al., unpubl. data). Accordingly, early nesters which produce the largest clutches use relatively more of their reserves on eggs than those arriving later. This argument is also consistent with the observation that females producing clutches late in the season have similar, or slightly better, body condition at hatching compared to early nesting females. The length of the incubation period was not related to clutch size, suggesting no differences in costs of incubating clutches of different sizes.

Studies of Snow Geese (Cooke et al. 1984) and also Barnacle Geese from Svalbard (Prop and de Vries 1993) have shown that early nesters are observed with more young than late nesters in their wintering area. It is obvious from this study that the seasonal decline in clutch size in this Barancle Goose colony is not consistent with the NRH as schematically shown in Fig. 4a. Females do not produce small clutches late in the season due to longer prelaying periods. Fig. 4b summarizes the results from the present study where geese arrive at the breeding area at different times, and where late arrivers use relatively less of their reserves in the production of eggs, more on incubation and have better body condition at hatching.

There are at least two mutually non-exclusive explanations why geese allocate their resources differently in relation to the time of breeding season. Firstly, the breeding season in the high Arctic is short, and those which arrive late may shorten their season by producing smaller clutches and use more reserves on incubation to shorten the incubation period. Using more reserves on incubation also gives females an opportunity to increase nest attentiveness. This may reduce the incubation period and decrease the chances that the eggs are taken by predators (Aldrich and Raveling 1983). Prop and de Vries (1993) found that the probability of hatching eggs increased progressively for Svalbard Barnacle Geese who started egg laying later in the season. Such an investment may also synchronize hatching with those nesting earlier. To synchronize hatching will be adaptive because a large number of goslings may satiate local predators (Findlay and Cooke 1982).

Secondly, if the chances that offspring fledge decrease with date of egg laying (Cooke et al. 1984, Sedinger and Raveling 1986, Prop and de Vries 1993, Lindholm et al. 1994), females may vary the relative allocation of resources to production of young and their own survival in relation to the time of the season. Those which arrive early spend relatively more reserves on eggs at the expense of body condition at hatching but they presumably produce more fledglings (Prop and de Vries 1993). This suggests a tradeoff between investment in young and survival (e.g., Williams 1966, Charnov and Krebs 1974). A number of bird studies (Lindén and Møller 1989) indicate that there exists a negative relationship between body mass at the end of the breeding season and the chance to survive and produce in the future. This also has been re-

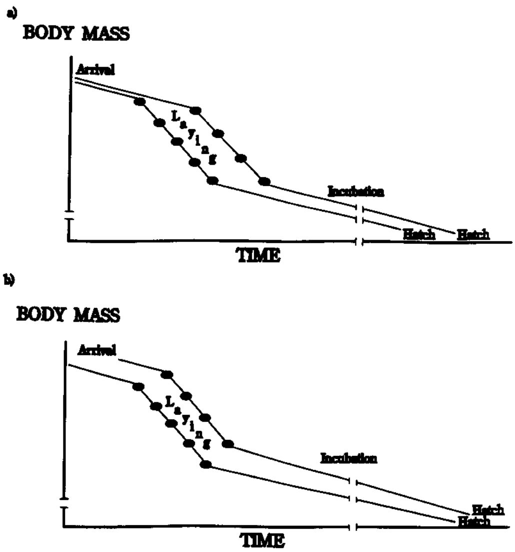

FIGURE 4. a) A graphical model of the nutrient reallocation hypothesis for seasonal decline in clutch size (redrawn from Rohwer 1992). A female that delayed nesting might lay only 4 eggs because stored nutrients have been used for maintenance. In the simplest form of this model, all individuals arrive together and have the same level of nutrient reserves at arrival, at the end of laying and at hatching. b) A graphical model based on the results from this study. Geese with the longest delay lay the largest clutches, are in poorer body condition after laying and hatching, and have longer incubation periods. Geese with short prelaying periods allocate fewer reserves for eggs, start incubation with more reserves and also have better body condition at hatching compared to early nesters. They therefore allocate more reserves for incubation, survival and future fecundity.

corded in long-lived species (Jacobsen et al. 1995). The benefit of producing small clutches may be an adaptation to shorten the breeding season and/or to synchronize hatching. However, it may also suggest a possible trade-off between investment in eggs and own survival, related to the time of breeding and the chances that the young survive and recruit to the population (Toft et al. 1986, Hamann and Cooke 1989).

Differences in costs and benefits to rear young during the breeding season may as well be used to explain yearly variation in clutch size. In years of late snow melt and egg laying, the chances that young would survive may decrease. In such years females may profit from spending less reserves on eggs and more on self-maintenance and survival. Such an allocation of reserves results in a negative relationship between yearly variation in egg-laying date and clutch size, a pattern found in several arctic nesting geese (Rohwer 1992).

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