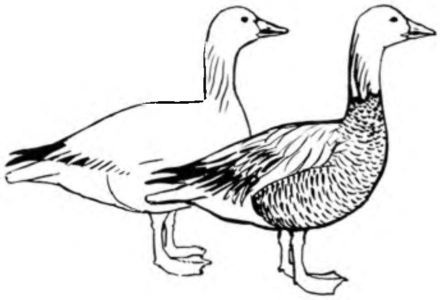
Reaction of Lesser Snow Geese *Anser caerulescens* to early nest failure



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Arctic-breeding geese are adapted to short breeding seasons. After loss of a first clutch they do not renest, probably due to time limitation. Thus, all reproductive effort goes into one clutch per year. Furthermore, arctic geese are determinate layers (Cooch 1958), i.e. maximum clutch size is determined by a limited number of developing follicles, and they cannot react to partial clutch loss during laying by producing extra eggs.

Several events that are detrimental to a clutch can occur at any time between nest initiation and hatch, such as egg loss, i.e. predation of single eggs without the parents abandoning the nest, abandonment by the parents of a nest containing one or more intact eggs, and abandonment of the nest after egg predation. Only the last two cases involving nest abandonment represent **nest failure** and will be dealt with in the following.

Nest failures can occur during incubation or during laying. Whereas failures during incubation always result in a nil reproductive success for the current year - as arctic geese do not lay replacement clutches - failure during laying may not mean total reproductive failure.

Nest failure during laying due to abandonment or predation is common. In Lesser Snow Geese *Anser caerulescens caerulescens* it ranges from 15 to 35% of all initiated nests with an average of 21%; total nest failures during incubation are comparatively infrequent and range from 1 to 20% with an average of 7% (Cooke *et al.* 1982 and unpublished data). Most pre-incubation nest failures occur at the one-egg stage (Hamann 1983 and unpublished data). Constraints on egg-laying leave geese with three possible reactions to nest failure during laying (early nest failure, ENF): clutch continuation, parasitic laying, or non-breeding. We expect birds to react to ENF with the strategy that maximizes their fitness after partial clutch loss.

Possible costs and benefits of these three options are the following: 1. **Clutch continuation**, where the female lays remaining eggs in a new nest and incubates them, so salvaging eggs that are left after partial clutch loss; here, birds must acquire a new nest site and invest energy of egg-laying, incubation and brood-rearing just as for a complete clutch. By laying eggs and taking care of them, geese probably ensure the highest possible hatching success for remaining eggs, but expend energy similar to that necessary for a full clutch. 2. **Parasitism**, i.e. laying eggs in other females' nests, may reduce hatching success of remaining eggs (due to poor timing), but saves investment of incubation and brood-rearing that may not be profitable when the clutch is reduced. Thus, parasitism could be an alternative salvage strategy after ENF. 3. **Non-breeding** means that reproductive success for the current year is zero. Arctic-nesting geese can resorb developing follicles, thereby reducing their potential clutches; this has been interpreted as reallocation of resources from reproductive tissue to body maintenance to keep a female's body reserves above a critical level (Barry 1962, Ryder 1970, Hamann 1986, Thomas 1988). We do not know to what extent follicular atresia is physiologically possible, i.e. if females can resorb all remaining follicles after first eggs have been laid (and lost). However, we consider this a third option for geese after ENF. The energy drain that laying of a full clutch and raising a brood imposes on a female may jeopardize her survival to the nest breeding season and future reproduction. Raising a reduced brood may not be worth the increased risk of not surviving to the nest season; in long-lived species such as geese, reallocation of reproductive resources to body maintenance in a year with partial clutch failure may, therefore, increase lifetime reproductive success.

Which of the three strategies is chosen may depend on nest site availability, female condition, or timing of partial clutch loss. Virtually no data on reactions to ENF in arctic geese exist, although Barry (1962) observed "some" Atlantic Brant *Branta bernicla* building new nests and continuing clutches. No observations on *Anser* species have been published, and there are no systematic studies of clutch completion in arctic-nesting geese.

Some studies of Lesser Snow Geese, which addressed different questions, give indirect hints to patterns of strategies after ENF. Lank *et al.* (1989) considered the possible identity of parasitic females/pairs, and found that overall rates of nest parasitism were not increased in years when overall rates of pre-incubation failure were high. Thus, parasitism may not result primarily from nest failure. Hamann (1983) found that geese laying late in the season had more post-ovulatory follicles than there were eggs in their nests; possible explanations for this are parasitic laying of first eggs and subsequent establishment of a nest or, alternatively, continuation nesting after ENF.

Here, we present results of an experiment to test reaction of Lesser Snow Geese to ENF. Although the dimensions of this experiment are small, we consider it important because it is the first to examine responses to ENF. We report direct observations of behaviour of marked birds after ENF, and examine data from a long-term study of a Lesser Snow Goose colony for further indications of prevailing strategies after ENF.

Methods

Nest failure experiment

The experiment was done in a Lesser Snow Goose colony at La Pérouse Bay (LPB) near Churchill, Manitoba, in the summers of 1991 and 1992. Many birds in this colony are individually marked with coloured leg-bands.

We observed Lesser Snow Goose pairs from an observation hide and identified individually marked birds with the first egg in their nest. Then we forced birds to abandon their nest by destroying the egg and leaving remains next to the nest. Subsequently, the area around experimental nests was observed intensively in an attempt to observe reaction of experimental pairs to ENF. After onset of incubation, these observations were discontinued, but we made efforts to observe the experimental birds elsewhere.

Relationship between pre-incubation failures and clutch sizes

If we assume that all birds that suffer ENF react similarly, we can predict the relation between proportion of nests in a colony that suffer ENF and mean clutch size of the colony. This relation will depend on which strategy birds choose after ENF.

If all birds that fail early relocate and lay a continuation clutch, we predict an inverse correlation between mean annual clutch size of those nests that reach incubation and annual proportion of ENF. Alternatively, if birds that fail early lay parasitically, we predict a positive correlation between clutch size in nests that are incubated and proportion of ENFs across years because some nests contain extra eggs from failed females. If all birds turn to non-breeding after ENF we expect no effect of proportion of ENF on mean clutch size.

We examined this relationship using nest history data collected at LPB between 1973 and 1991 (for details of data collection methods see Finney & Cooke 1978). In particular, we used yearly means of total clutch size including parasitic eggs (mTCL), yearly means of laying date (mLDT), and yearly proportion of nests failed (predated and/or abandoned) before incubation (pENF, proportions arcsine-transformed for analyses).

Total clutch size in Lesser Snow Geese is correlated negatively with laying date (Cooch 1958, Hamann *et al.* 1986) and has undergone a long-term decline at LPB (Cooch *et al.* 1989). We used multiple regression to examine whether pENF can explain remaining variation in mTCL after effects of mLDT and year (the long-term decline) have been removed.

Results

Nest failure experiment

We destroyed eggs at two nests in 1991 and one nest in 1992. These low sample sizes were due to difficulty in identifying individual birds at their nests early enough; at the one-egg stage, birds are not closely attached to nests, and it was difficult to assign birds to nests by behavioural observations. Systematic searches for one-egg nests, which may have increased the number of potential experimental nests, were not done so as to minimize disturbance of observed birds. An extended study area would have provided more nests to be manipulated, but this would have been at the expense of intensive observations of the surrounding area immediately after manipulation.

All three pairs abandoned their nests immediately after we destroyed the eggs. In 1991, one pair moved 32 m from its old nest, built a new nest and laid the remaining clutch; the eggs hatched successfully. The second pair in 1991 was not seen again during nesting, but was observed during brood-rearing with three goslings, so they relocated and continued their clutch elsewhere, but distance of relocation was unknown. The pair whose nest we destroyed in 1992 was not seen again.

Relationship between pre-incubation failures and clutch sizes

We performed a multiple linear regression using mTCL as the dependent variable and year, mLDT and pENF as independent variables. After year and mLDT were entered into the model, pENF provided no additional information to predict mTCL, i.e. there was no correlation between pENF and clutch size after effects of laying date and the long-term decline in clutch size were removed.

There are several possible explanations for this result: a) not all geese employ the same strategy after ENF and subsequent effects on mTCL are cancelled; b) most geese opt for non-breeding; c) even if most geese that suffer ENF opt for clutch continuation or parasitism, overall effects on clutch size may be too small to detect.

Discussion

Evidence that continuation laying occurs in arctic-nesting geese after abandonment of a first nest is provided by this study and complements the anecdotal observations of Barry (1962).

Neither of the other two possible reactions to ENF has been observed. The experimental pair in 1992 may have employed either strategy; due to an unusually late spring and slow snow melt, nest sites were highly limited in 1992, and this pair may have been unable to acquire another territory for clutch continuation.

Non-breeding, *per se*, is the most difficult of the three strategies to observe. Birds who opt out of breeding often leave the area entirely and undergo a northward moult migration (Abraham 1980). Thus, direct evidence for switching to non-breeding after ENF is difficult to obtain.

Although the result of the analysis of long-term data is ambiguous, we conclude that not all geese employ the same strategy after ENF. If they did, we would expect a significant contribution of pENF to mTCL. (The possibility that all geese turn into non-breeders after ENF is contradicted by our observations of continuation laying and therefore can be rejected as an explanation for lack of a relation between these two variables.)

Beyond our finding that some Snow Geese continue clutches in new nests after ENF, more information is desirable about extent of clutch continuation, parasitic laying or non-breeding in arctic geese after ENF. Large-scale trapping and radio-tagging of females in early laying, which would require a considerably larger effort (and budget), would facilitate following geese after ENF even if they became parasites or non-breeders.

Our evidence that clutch continuation at new nest sites can occur after ENF is important for other studies of arctic-nesting geese. For instance, studies involving clutch size should consider that observed clutch size is not necessarily true clutch size for a female, even if her nest has been monitored from first egg onwards. Similarly, researchers concerned with intra-clutch variation in variables such as egg size, hatching success, etc. should be aware that the first egg in an observed clutch is not necessarily the female's first of the year. Whereas the possible inflation of observed clutch sizes by parasitic eggs has been considered by researchers, the possible reduction due to continuation laying after pre-incubation nest failure has been neglected.

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