Territoriality in Snow Geese or the protection of parenthood—Ryder's and Inglis's hypotheses re-assessed

PIERRE MINEAU and FRED COOKE

Recently, there has been an effort on the part of several authors to explain the phenomenon of territoriality in colonially nesting geese. Ryder (1975) proposed that territory size evolved in relation to a balance between the food requirements of the male and the number of neighbours against which he must protect his female from non-sexual harassment. Inglis (1976) reported that Ryder's views did not hold true for Icelandic Pink-footed Geese *Anser brachyrhynchus*. Harassment of nesting females did not take place and since territorial strife broke down shortly after the beginning of incubation, he hypothesized that territoriality was not important in supplying food for the breeding male but rather for the female prior to incubation.

We assess these hypotheses especially as they relate to the Lesser Snow Goose *Anser caerulescens caerulescens* and, based on an intensive observational study of this species, present an alternate hypothesis.

Study area and methods

The results presented below form part of a study which took place at the La Pérouse Bay (LPB) Lesser Snow Goose colony, 58·4°N, 94·4°W; 40 km east of Churchill, Manitoba. Observations were carried out during the 1977 nesting season from a hide 5 m high located in a section of the colony of high nest density (22 nests/ha of land). This density was a reflection of the abundance of suitable nest sites (dry elevated hummocks), all of which were used. The hide was constructed before arrival of the geese in 1976. The area under observation was closed to other biologists. The observers lived in the hide and most necessary movements to and from the hide took place after sundown. Positions of individually identifiable territorial males were mapped 10 consecutive times at 4–7 minute intervals usually three times per day (morning, afternoon and evening) during the entire nesting season. (See Mineau 1978 for more detailed information on methods.)

Mapping was interrupted when instances of rape (Mineau 1978) or intraspecific nest parasitism (Finney 1975) were observed since monitoring these occurences was the focal point of this study. 'Daily male home ranges' were calculated by joining all outermost positions for any given day and measuring the resulting land area. This was taken to be a crude indication of the male's attachment to nest and/or female. Only when the female was on the nest were positions of the male used. Sampling ended when the first egg began to pip.

Twelve territorial males out of a possible 45 under observation were retained for the analysis, the only criterion being proximity of the hide for better depth perception and good visibility. Daily home ranges were calculated only if 20 or more positions/day for any given male were available.

Results

The change in 'daily home range' over time was calculated. In order to compare area changes between different males, the 'daily home range' for any given male is here expressed as a percentage of the largest daily home range recorded for that individual. These percentages are then submitted to angular transformation and plotted against the stage of the nesting cycle (Figure 1). A highly significant regression is obtained ($F(1:136) = 848$, $P < 0{\cdot}001$) with positive slope. It is, therefore, apparent that the male ranges further away from his nest and mate as the season progresses. Movements of males related to rape attempts at other nests are not included in these data due to the mutual exclusiveness of the sampling methods (see above). However, these are infrequent enough (less than one attempt/day/male on average) that no significant change would result.

When all of an individual's daily home ranges for the laying and incubation periods are combined, the size of the 'overall ranges' thus obtained varies from 279 to 3,182 sq m of land or by a factor of 11·4. This is indicative of a very high inter-male variability in the land area utilized during the nesting period.

As the area utilized by any one male increases over time, one might expect an increased tolerance towards conspecifics, wherever two 'territories' were contiguous. Two 'pairs' of males were used for the calculation of 'daily home range' overlap, each member of a 'pair' being the other member's nearest neighbour. All four initiated nesting on the same date which allows for the use of a real time axis. The measure of overlap is calculated as the percentage of an individual's daily home range which overlaps with that of its nearest neighbour. Not surprisingly, overlap increases with time (Figure 2a). However, this increase is much more sudden than the increase in daily home range and this will now be considered.

In Lesser Snow Geese, it has been suggested that the legitimate parenthood of a male can be threatened in two ways. First, territorial males will attempt to inseminate (rape) females other than their own (Mineau 1978). Secondly, some females will lay their

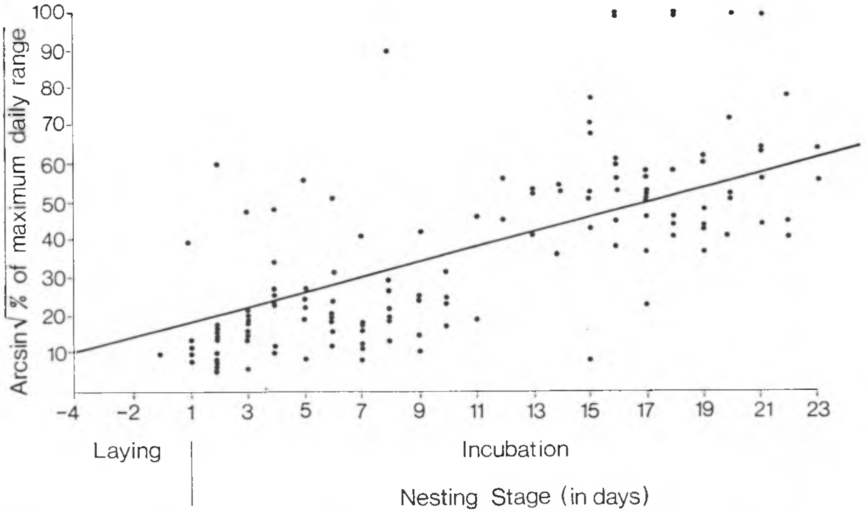

Figure 1. 'Daily home range' for 12 territorial males with respect to their nesting stage (see text). The 'daily home range' for any given male is expressed as the angular transformed proportion of the maximum 'daily home range' calculated for that male.

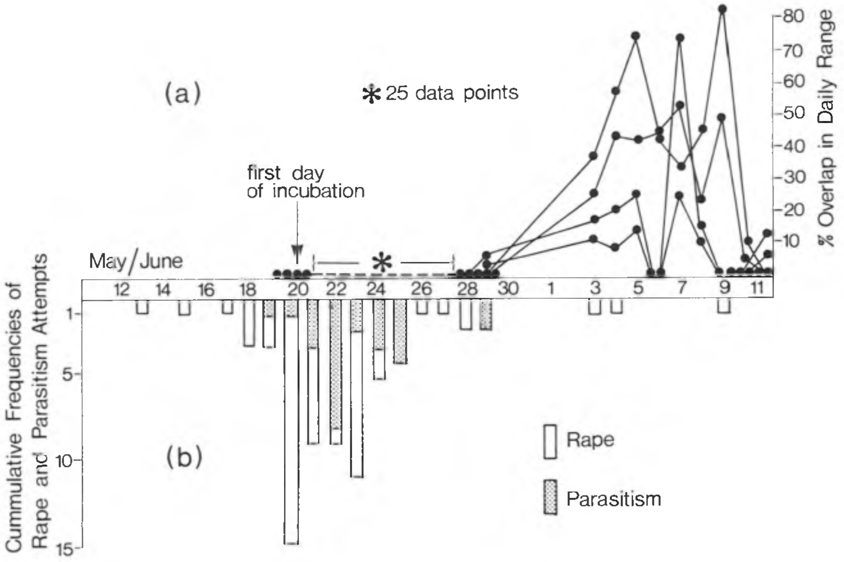

Figure 2. 'Daily home range overlap' for four territorial males with respect to date and incidence of rape and parasitism attempts on the study area (see text).

eggs in another female's nest (intra-specific nest parasitism) to the possible detriment of the host's progeny (Finney 1975). The frequency of rape and parasitism attempts (on the area under observation) peaks during early incubation as shown by Figure 2b.

When Figure 2 as a whole is considered, the inverse relationship between home range overlap and the combined frequency of rape and parasitism attempts is striking. If this is more than a coincidence, it suggests an explanation which can be phrased in proximate or ultimate terms. Either: (1) Lesser Snow Goose males monitor conspecific activity in the general vicinity of their nest and regulate their movements accordingly; or (2) the sudden increase in range overlap has evolved in response to the highly predictable drop in rape and parasitism attempts.

Discussion

A factor too often overlooked in the consideration of goose territoriality is that there is indeed very little evidence to suggest that aggressiveness in the male serves to defend anything but the actual nest site and the female. Inherent in the widely accepted definition of territoriality are two separable factors: defence and area. As first noted by Emlen (1957) the idea that the area carries special significance to the bird as something to be defended stems *a priori* from the definition and is entirely hypothetical. Indeed, 'territory size' in geese appears to be highly variable and may not be the meaningful entity it is often assumed to be.

For example, the 'defended area' is not fixed but moves with the female (reviewed by Cooper (1978) for Canada Geese *Branta canadensis*, Jenkins (1944) and this study in Snow Geese) although the nest itself continues to be defended. The size of the 'defended area' is further subject to extreme individual variation; it may vary with cover (Ewaschuk & Boag 1972) or with temperature and general activity state of the pair (Jenkins 1944; Mineau 1978). At the physiological level, territoriality is probably under hormonal influence since injections of testosterone propionate have been shown to increase aggressiveness in Ring Doves *Streptopelia risoria* (Bennett 1940).

According to Ryder (1975) the territory is a fixed entity the size of which is a balance between the nutritional requirements of the gander and the number of neighbours against which the female must be protected. Ryder bases this hypothesis on his observations of weight loss in nesting male Ross's Geese *Anser rossii* and observations of non-sexual harassment of the female in the absence of her mate in Canada geese (Ewaschuk & Boag 1972).

Inglis (1976), however, argued that territorial strife could not function to secure a food source for the male since most of the feeding takes place late in incubation, by which time conspecific animosity is at it's lowest. The same holds true of Lesser Snow Geese (Mineau 1978). Ankney (1978) similarly found that nutrient reserves in the Lesser Snow Goose are crucial to the male early in the nesting season when the amount of feeding is minimal.

Our observations further discount the possibility that the territory is established early and maintained for later use as a food source. Not only does the overlap between Lesser Snow Goose neighbours increase over time, but late in incubation, non-neighbouring individuals are also allowed in close proximity to the nest to feed. Given these observations and the wide discrepancy between the area used by different Lesser Snow males during the course of the nesting season, it seems unlikely that territory size is related to the nutritional requirements of the male. Our observations suggest that food is often (not always) obtained in the vicinity of the nest but that by late incubation, those areas are neutral ones.

As for the type of non-sexual harassment observed by Ewaschuk & Boag (1972) and more recently by Cooper (1978) in Canada Geese, it does not seem to occur in any other goose species observed to date except in the context of competition for nest sites.

Inglis (1976) also considers the territory to be a fixed entity. His suggestion that the function of territoriality is to defend a food source for the female up to and during the laying period cannot be discounted by our observations although areas off the territory are often preferred by the female at this stage. However, it has been reported elsewhere (Ankney & MacInnes 1978) that the quantity of food available to the laying female is negligible and that again, nutrient reserves accumulated before arrival on the colony are crucial. The importance of an early food source for the female, therefore, would seem to be geographically variable.

We suggest that the two intraspecific factors mentioned above, namely rape and intra-specific nest parasitism are crucial to the understanding of goose 'territoriality'. Protection of parenthood is key to the reproductive success of a monogamously mated male. From the evidence presented above, it would seem that the male Snow goose is sensitive to the possibility of loss of parenthood. In short, we hypothesise that 'territoriality' in geese serves in part to provide a 'buffer zone' between nest and potential nest parasites and more important between female and potential rapists. Recognizing the importance of nest site competition as yet another function of male aggressiveness, we conclude that there is no conclusive evidence to show that 'territoriality' in geese serves to defend anything but the female and the nest itself.

Acknowledgements

We would like to thank K. F. Abraham, M. A. Bousfield, R. F. Healey, C. Murray and B. Rattray who were directly involved with this work at one stage or another. Earlier drafts were reviewed by D. V. Weseloh as well as by the Queen's Snow Goose crew. Financial assistance was in the form of a Canadian Wildlife Service contract (# 7576–048) to Pierre Mineau. The study during which these data were collected was part of an ongoing research program on snow goose biology funded by the National Research Council, the Manitoba Department of Mines, Resources and Environmental Management, the Canadian Wildlife Service and the Department of Supply and Services.

Summary

Ryder's and Inglis' hypotheses on the function of territoriality in colonially nesting geese are examined in the light of new information available for the Lesser Snow Goose *Anser caerulescens caerulescens*. We suggest that male aggressiveness serves in part to provide a buffer zone between the nest and potential nest parasites as well as between the female and potential rapists. We further conclude that there is no evidence to show that 'territoriality' in geese serves to defend anything but the female and the nest itself.

References

Ankney, C. D. 1978. The use of nutrient reserves by breeding male Lesser Snow goose *Chen caerulescens caerulescens*. *Can. J. Zool.* 55: 1984–7.

Ankney, D. A. & MacInnes, C. D. 1978. Nutrient reserves and reproductive performance of female Lesser Snow geese. *Auk* 95: 459–71.

Bennett, M. A. 1940. The social hierarchy in Ring Doves. II. The effect of treatment with testosterone propionate. *Ecology* 21: 148–65.

Cooper, J. A. 1978. The history and breeding biology of the Canada geese of Marshy Point, Manitoba. *Wildl. Mono.* 61.

Emlen, J. T. Jr. 1957. Defended area? A critique of the territory concept and of conventional thinking. *Ibis* 99: 352.

Ewaschuck, E. & Boag, D. A. 1972. Factors affecting hatching success of densely nesting Canada geese. *J. Wildl. Mgmt.* 36: 1097–106.

Finney, G. H. 1975. Reproductive strategies of the Lesser Snow goose, *Anser caerulescens*. Unpubl. Ph.D. Thesis, Queen's Univ., Kingston, Ontario, 152 pp.

Inglis, I. R. 1976. Agonistic behaviour of breeding Pink-footed geese with reference to Ryder's hypothesis. *Wildfowl* 27: 95–99.

Jenkins, D. W. 1944. Territory as a result of despotism and social organization in geese. *Auk* 61: 30–47.

Mineau, P. 1978. The breeding strategy of a male Snow goose (*Anser caerulescens*). Unpubl. M.Sc. Thesis, Queen's Univ., Kingston, Ontario, 152 pp.

Ryder, J. P. 1975. The significance of territory size in colonial nesting geese—an hypothesis. *Wildfowl* 26: 114–6.

Pierre Mineau, Canadian Wildlife Service, Canada Centre for Inland Waters, P.O. Box 5050, Burlington, Ontario L7R 4A6, Canada.

Fred Cooke, Biology Department, Queen's University, Kingston, Ontario, Canada.