

# THE TIMING OF EGG LAYING BY NORTHERN GEESE

DENNIS G. RAVELING

*Division of Wildlife and Fisheries Biology, University of California, Davis, California 95616 USA*

**ABSTRACT.**—The delay between the peak arrival and peak of nest initiation by Cackling Geese (*Branta canadensis minima*) in an unusually early spring season coincided with the time required for rapid yolk development. Even though nesting habitat was available, Cackling Geese could not nest earlier than they did because of their physiological state. A review of available data reveals that Canada Geese and Brant (*Branta bernicla*) regularly nest 10–13 days after their peak arrival at nesting areas, or after their departure from final spring staging areas. This is the interval required for rapid yolk development. Lesser Snow Geese (*Anser caerulescens caerulescens*) and Ross' Geese (*Anser rossii*) commonly nest within 3–5 days of their peak arrival at nesting areas. It is suggested that the stimuli causing rapid yolk formation are related to the events just prior to, or at the time of, migration from the usual final spring staging area to nesting areas for Brant and Canada Geese, and at the time of the migration to final staging areas by Lesser Snow and Ross' Geese. This plasticity in ovary preparation is related to weather patterns that affect spring thaw and the availability of nest sites. The probable ecological advantages of the varying patterns of ova formation in different species and populations of geese are related to the premium placed on earliest possible nesting versus maximizing reproductive opportunity by ova formation after arrival at the nesting area. Received 23 September 1976, accepted 20 September 1977.

GEESE breeding in northern latitudes commonly migrate to their nesting locations before snow and ice melt is completed. Egg laying is reported to be controlled by the availability of nest sites as functions of the disappearance of snow and ice, presence of open water around a nest site, recession of flooding caused by the melt, and the cessation of wind storms (Cooch 1958, 1961; Barry 1962, 1967; MacInnes 1962; Ryder 1967; Mickelson 1975). Annual arrival of geese on nesting grounds is often more predictable than the phenology of the spring thaw (Cooch 1961, Barry 1962). It is generally considered that geese are capable of egg laying almost immediately after their arrival on the nesting grounds, implying that the control of rapid ovarian follicular development is related to stimuli operative several days prior to the final migration to the nesting grounds. The purposes of this paper are: (a) to present data on the nesting chronology of Cackling Geese (*Branta canadensis minima*) that suggest a different timing of rapid yolk formation, at least for this subspecies; and (b) to review data on several species and populations that suggest variation in the timing of mechanisms influencing nesting chronology, and their probable adaptive significance to different populations.

## METHODS AND STUDY AREA

I studied the nesting ecology of Cackling Geese between 3 May and 1 July 1974 on the Yukon-Kuskokwim River Delta, Alaska (61°23'N, 165°27'W) in the vicinity of the U.S. Fish and Wildlife Service field station at Old Chevak, Clarence Rhode National Wildlife Range. Four study plots were established from 0.8 to 8.9 km (0.5 to 5.5 mi) north of the site described by Mickelson (1975). The study plots incorporated two basic elevations and habitat types containing ponds used by nesting geese (Mickelson 1975). Lowland flood plains were about 0.5 m above mean high tide and were characterized by sedges (*Carex rariflora* and *C. mackenziei*) and speargrass (*Poa eminens*). Upland tundra was about 1.2 m above mean high tide and was characterized by *Sphagnum* spp., tea (*Ledum* spp.), crowberry (*Empetrum nigrum*), dwarf birch (*Betula nana*), and oval leafed willow (*Salix ovalifolia*).

Dates of nest initiation (first egg of a clutch) were determined from finding nests before clutches were

TABLE 1. Chronology of events related to Cackling Goose nesting

Event	1969 <sup>a</sup>	1970 <sup>a</sup>	1971 <sup>a</sup>	1972 <sup>a</sup>	1974
Arrival of investigator	12 May	4 May	16 May	8 May	3 May
Meltwater flooding	13 May	18 May	28 May	26 May	3 May
Ice gone from ponds <sup>b</sup>	25 May	27 May	5 June	13 June	19 May
First Cackler seen	12 May	9 May	16 May	9 May	4 May
Peak arrival of Cacklers	?	?	23-25 May	23-26 May	12-13 May
First nest initiated	20 May	21 May	1 June	30 May	19 May
Peak of nest initiation	23-24 May	28-29 May	6-7 June	2-5 June	24-25 May
80% (+) of nests initiated by:	29 May	1 June	9 June	6 June	30 May
Interval between peak arrival and peak nest initiation	—	—	13 days	10 days	12 days
Average clutch size <sup>c</sup>	4.61	4.57	4.52	4.97	4.82

<sup>a</sup> From Mickelson (1973, 1975)

<sup>b</sup> See text

<sup>c</sup> From nests being incubated in Mickelson's study

complete and by back-dating from the day of hatching by allowing 26 days for incubation and a laying rate of 1 egg per day (Mickelson 1975). Geese were collected throughout the spring to obtain data on physical condition and gonad development. Unincubated eggs from nests at which females were collected were saved for studies on yolk development by C. R. Grau (cf. 1976) and T. Roudybush.

## RESULTS AND DISCUSSION

### SPRING THAW

Spring thaw in 1974 was exceptionally early. C. J. Lensink, former manager of Clarence Rhode, considered it the earliest ice breakup in the 13 years of his experience in the area (pers. comm.). Winter snow cover was unusually light and was 90-95% gone as judged from aerial photographs taken on 3 May. Nearest weather stations were on the Bering Sea coast 38.6 km (24 mi) from the study area, but these data may not precisely reflect snow and ice conditions of the inland study areas.

Evidence of the early spring was best indicated by the lowland flood plains, which were covered with meltwater when we arrived on 3 May. This flooding was 10-25 days earlier than during Mickelson's (1973, 1975) 4-year study (Table 1). Because of the shallow snow cover and negligible precipitation in May, meltwater was less than normal and drained rapidly off the lowlands. Ponds used for nesting by geese became ice-free between 13 and 19 May.

Larger, deeper ponds in the upland tundra with few or no islands were 90% ice-free by 23 May, although a few contained some ice until 28 May. These dates should not be compared directly to Mickelson's records because his study area was predominantly lowland containing shallower ponds which become ice-free sooner than larger, upland tundra ponds.

### MIGRATION AND NESTING CHRONOLOGY

Numbers of Cacklers seen daily varied from 4 on 4 May to 37 on 10 May. On the morning of 13 May, flocks of  $20 \pm$  were common and there were hundreds of Cacklers in the vicinity. This peak arrival was 12 days earlier than in the retarded springs of 1971 and 1972 (Mickelson 1973, 1975) (Table 1), but was probably little different than in the "average" or early years of 1969 and 1970 for which Mickelson only reported that numbers of geese peaked in mid-May.

As usual for arctic geese, nesting in 1974 was highly synchronized and 89% of all Cackler nests were initiated within 10 days (22 May-1 June). Greater synchrony

TABLE 2. Ovarian follicle development of adult female Cackling Geese collected before egg laying

Date	Largest ovarian follicle diameter (mm)	Projected date of possible nest initiation <sup>a</sup>
10 May	9	20 May
13 May	20 <sup>b</sup>	19 May
14 May	9	24 May
15 May	23	20 May
18 May	23	23 May
19 May	8	29 May
30 May	First egg in oviduct	30 May

<sup>a</sup> Based on estimated growth rate of 3 mm per day and an average diameter of 39 mm at ovulation—see text

<sup>b</sup> Ruptured by shot—size estimated

occurs in late seasons than in early ones (Mickelson 1973, 1975). An abundance of suitable ponds and nest sites free from snow, ice, or meltwater were available for 6–9 days before the peak of nest initiation by Cackling Geese. Of prime importance was the fact that the time interval between peak arrival of migrants and peak nest initiation was 10–13 days regardless if the season was exceptionally early, as in 1974, or late, as in 1971 and 1972 (Table 1).

#### EGG DEVELOPMENT

Seven adult females were collected before they had laid eggs (Table 2). None had obvious atretic follicles. The average diameter of the yolk of 19 eggs measured by Roudybush (pers. comm.) was 39 mm. When rapid ovarian follicular development begins in domestic fowl it culminates only in ovulation or atresia and not in arrested development, and the rate of yolk growth is essentially linear after the first day or two (see review by Gilbert 1971). If this process is the same in geese, then the earliest possible date of potential egg laying of the collected birds can be estimated by comparing the size of the largest follicle to the average size at ovulation (Table 2). None of the females collected could have laid eggs before 19 May.

Grau (cf. 1976) determined that it took 12–13 days for the yolk of seven Cackling Goose eggs and three *B. c. moffitti* eggs to develop (pers. comm.). The delay between peak arrival and peak nest initiation (Table 1) corresponded almost exactly to the time necessary for rapid yolk development. Nesting by most of the population could not have been initiated earlier than recorded in 1974 even though habitat was available.

The pattern of spring migration by Cackling Geese between their time of departure from California in early- to mid-April and arrival on the nesting grounds is not well known. It appears that the stimulus for rapid ovarian follicular development occurred at the same time as the initiation of the final migration flight into nesting areas, or perhaps coincided with arrival itself.

#### OTHER CANADA GOOSE STUDIES

*Low Arctic Tundra*.—Dates of peak arrival and the mid-point of nest initiation (which closely approximates the peak of nest initiation) for small Canada Geese (*B. c. hutchinsii-parvipes* complex of MacInnes 1966) at the McConnell River Delta, Northwest Territories, Canada (60°50'N, 94°W) reported by MacInnes (1962) and MacInnes et al. (1974) are presented in Table 3. Disappearance of 50% of the snow cover was used as an index of weather and nest site availability, although the rate of snow melt may be highly variable in relation to pond availability.

TABLE 3. Chronology of events related to nesting of small Canada Geese at the McConnell River Delta, Northwest Territories (from MacInnes 1962 and MacInnes et al. 1974)

	Snow 50% gone	Peak arrival	Mid-point of nest initiation	Interval (days) between peak arrival and peak nest initiation
Early springs				
1960	28 May	29-30 May	8 June	9-10
1965	2 June	31 May	10 June	10
1966	1 June	30 May	8 June	9
1968	8 June	31 May	12 June	12
1971	22 May	28 May	6 June	9
Average	31 May	28 May	9 June	10
Late springs				
1959	11 June <sup>a</sup>	5 June	14 June	9
1964	5 June	4 June	12 June	8
1967	1 June	5 June	10 June	5
1969	12 June	7 June	17 June	10
1970	1 June	5 June	12 June	7
Average	6 June	5 June	13 June	8

<sup>a</sup> From MacInnes (1962); reported as both 4 and 9 June in MacInnes et al. (1974)

Major arrival of migrants was "early" in 5 years (28-31 May) and the delay to peak nest initiation was 9-12 days ( $\bar{x} = 9.9$ ). These results suggest that the delay might have been necessary for the maturation of ovarian follicles that were stimulated by the same factors (or at the same time) that stimulated the final migration to the nesting area. The timing of arrival to, and location of, the final spring staging areas after these geese leave the prairies of the Dakotas and southern Manitoba in early- to mid-May are not well documented.

Major arrival of migrants was late in 5 years (4-7 June) (Table 3), and the delay to peak nesting varied from 5-10 days ( $\bar{x} = 7.8$ ). Since there is probably little variation among races of Canada Geese in the time required for rapid ova formation, follicular development was proceeding in at least three of these years before the birds arrived on the nesting area, with the result that nest initiation was not delayed as much as arrival with respect to early seasons. This suggests that rapid follicular growth was stimulated at essentially the same time as in early seasons, but that the final migration was interrupted or prevented by unfavorable conditions. Presumably, weather conditions changed soon enough for the geese to arrive and begin egg laying with little delay compared to early seasons.

In the other two late seasons, the delay to peak nesting was 9 or 10 days, as in early seasons. If ovarian follicular development was proceeding as in other late seasons, nesting was prohibited by lack of suitable nest sites. These 2 years (1959 and 1969), as indexed by snow cover, were by far the two latest spring thaws, and follicular atresia and reduced clutch size should have resulted. Data presented for 1959 (MacInnes 1962) are inadequate to judge this, but, indeed, in 1969 the modal clutch changed from the usual 5, and occasional 4, to 3 eggs (MacInnes et al. 1974). There was also a shift to 3-egg clutches in 1967 (a late season of arrival, but short delay between arrival and egg laying, Table 3). Nutritional state affects the timing and number of eggs laid (cf. Jones and Ward 1976). Possibly geese were in poorer condition upon arrival based on food during migration, as suggested by MacInnes et al. (1974), but this could also be related to delay by interrupted migration once rapid oocyte formation was triggered and atresia resulting after development had proceeded for 12-13

TABLE 4. Chronology of events related to nesting of *B. c. interior* at Kinoje Lake, Ontario

Event	1967	1968	1969
Arrival of investigators	7 April	7 April	7 April
First geese seen	12 April	10 April	13 April
Majority of Bog-ponds ice-free	16 May	18 April	5-6 May
First major goose departure from Horicon, Wisconsin <sup>a</sup>	20-21 April	16-17 April	19-20 April
First major arrival of geese	28 April	16-17 April	24 April
First nest initiated	3 May	19 April	23 April
Peak of nest initiation (mid-point) <sup>b</sup>	14-15 May	27-28 April	1-2 May
Interval between peak arrival and peak nest initiation	16-17 days	11-12 days	7-8 days
Interval between first major departure from Wisconsin and peak nest initiation	24-25 days	11-12 days	11-13 days

<sup>a</sup> From R. A. Hunt (pers. comm.)

<sup>b</sup> Based on data from 81 and 112 dateable nests in 1968 and 1969, respectively; estimated for 1967 from 40 nests

days (thus resulting in poorer condition upon arrival, irrespective of their condition earlier in the spring).

*Sub-Arctic Muskeg*.—Observations of migration, nest site availability, and nest initiation for Canada Geese (*B. c. interior*) at Kinoje Lake, Ontario (51°35'N, 81°45'W) are provided in Table 4. Results are from a Mississippi Flyway Council and Ontario Ministry of Lands and Forests study by Raveling and H. G. Lumsden (unpublished data). Habitat descriptions may be found in Hanson and Smith (1950).

Availability of suitable nest sites was accurately indicated by the dates of ice disappearance from bog-ponds because flooding did not occur in the raised peat bogs. Spring thaw was unusually early in 1968 and nesting habitat was available when the geese arrived. Peak of nest initiation, however, did not occur until 11-12 days after the departure of the first major numbers of geese from the spring staging area and their apparent nonstop flight to the nesting areas. This suggests that rapid oocyte formation began just before or at the time of initiation of this migration and the temporal delay to nest initiation was necessary for ova maturation.

The migration flight of the first major departure of geese from Wisconsin in 1969 was apparently interrupted as major arrival did not occur until 4-5 days later (when weather at Kinoje changed and warming south winds occurred). In this case, as noted above for some years at the McConnell River (Table 3), the 7-8 day delay between peak arrival and peak nesting indicates that rapid yolk formation was proceeding when the geese arrived. The time interval between their departure from Wisconsin and peak nesting suggests again that rapid follicular growth was stimulated just before or at the same time as was the last migration flight.

The spring of 1967 was exceptionally retarded (latest in 17 years) as indicated by late migration, ice breakup, and nesting in Table 4. Follicular atresia should have resulted. Clutch size in 1967 (4.37) was significantly smaller than in 1968 (4.95) and in 1969 (4.64). There was not a significant difference between clutch sizes for 1968 and 1969. Raveling and Lumsden (unpublished) concluded that in addition to reduced production because of decreased size of clutches, large numbers of geese did not nest in 1967.

#### OTHER SPECIES

*Brant*.—The best data on the relationship of gonadal development to nesting chronology were provided by Barry (1962) for Atlantic Brant (*Branta bernicla hrota*)

nesting on Southampton Island, Northwest Territories. Brant arrived on 7 or 8 June regardless of the progress of the spring thaw. In 1953, nesting habitat was available at the time of Brant arrival, but the peak of egg laying was 10 days later. This pattern of regular arrival and at least a 10-day delay to peak nest initiation, regardless of season phenology, was also evident in Pacific Brant (*B. b. nigricans*) (Barry 1967). This, again, suggests that rapid ovarian follicular growth was stimulated just prior to or at the same time as final migration to, or arrival at, nesting areas. Egg laying probably could not have occurred earlier because of the time needed for ova maturation. When nesting was delayed longer than 10–13 days, clutch sizes decreased because of follicular atresia (Barry 1962).

*Lesser Snow Goose*.—Cooch (1958:52) reported that egg laying by Lesser Snow Geese (*Anser caerulescens caerulescens*) usually began within 3 days of their arrival at Southampton Island in Hudson's Bay. Barry (1967) collected adult female Lesser Snow Geese with mature ovarian follicles on 31 May and 3 June, in a year (1960) when peak arrival was 1 June at the Anderson River Delta, Northwest Territories (69°44'N, 128°44'W). At this location, the final flight to nesting sites was about 322 km (200 mi) from their final staging area on the MacKenzie River in the interior where spring thaw was much earlier than at coastal nesting areas. Geese arrived at this staging area in mid-May, but exact dates of peak arrival were not reported or known. It appears that the time at which rapid ova maturation begins in Lesser Snow Geese coincides with their migration to, or arrival at, the final staging area before flight to the nesting areas. When nesting is delayed longer than 3 days, clutch sizes decrease (Cooch 1961).

*Ross' Goose*.—It is clear from Ryder's (1967, 1972) data on Ross' Geese (*Anser rossii*) in the Perry River region of the Northwest Territories (67°22'N, 102°10'W) that they are similar to Lesser Snow Geese in being capable of nesting soon after arrival at nesting areas. The chronology and pattern of Ross' Goose migration between the prairies of east-central Alberta and their nesting areas are not well known. Arrival dates were more variable than intervals between arrival and nesting. Thus, factors which stimulated migration to the nesting areas were closely related to weather conditions resulting in thaw at the nesting areas and availability of nest sites. Correlated with this predictability of available nest sites was stimulation of rapid ovarian follicle growth sufficiently in advance of the birds' arrival so that egg laying proceeded within at least 3 days, for the bulk of the population. Massive failures of Ross' Goose reproduction during Ryder's studies did not occur as they have in Lesser Snow Geese (Cooch 1961), but neither were the delays from peak arrival to peak of nesting as long as in some years for Lesser Snow Geese.

#### NATURE OF STIMULUS FOR OVA MATURATION

Photoperiod stimulation is responsible for testicular recrudescence in most temperate and high latitude zone birds (see reviews by Lofts and Murton 1968, 1973; Farner and Lewis 1971; Lofts 1975). Females also respond to photostimulation, but in the few species studied to date a block to ovarian growth occurs at the onset of rapid yolk development if appropriate proximate factors are lacking (usually mate and appropriate nest site). Whether or not the oocytes develop under photostimulation alone, ovulation can be inhibited by the lack of appropriate nesting conditions, and this has been demonstrated in both captive and wild geese (Wood 1964, Barry 1962).

It is conceivable that rapid yolk synthesis is irreversibly controlled by photoperiod

at a precise time in geese and that different timing response mechanisms (see Murton and Kear 1973) in different species account for the variation in time of development reviewed here. It is most likely, however, that geese require additional proximate stimuli to cause rapid oocyte development as for other wild species studied to date (Lofts and Murton 1973). Geese in captivity at temperate latitudes, including species that normally spend the winter near the latitudes at which they were captive, commonly nest up to a month earlier than in the wild without having to experience a transition to arctic daylength (Davies, et al. 1969, Murton and Kear 1973). If photoperiod caused full follicular development this early in the wild, then atretic follicles should be apparent upon the arrival of geese at nesting areas. Only the follicles corresponding to a normal clutch (4-7) develop rapidly in sequence (Wood 1964). In four adult female Cackling Geese collected at the onset of incubation in the 1974 season, the number of atretic follicles plus clutch size equaled the normal full clutch potential, as also reported for Brant and Lesser Snow Geese by Barry (1962, 1967).

For Canada Geese and Brant, stimulation of ova formation was associated with the events immediately preceding, or at the same time of, final migration to nesting areas. In early seasons, ova maturation in Canada Geese occurred mostly after arrival on nesting grounds. Arrival of Canada Geese on nesting areas was more variable than in Brant and, at least in some seasons, much ova development occurred before arrival at nesting sites. The Kinoje Lake data suggest that the stimulation for rapid ova development was, however, still associated with their migration departure from the usual final spring staging area. Since Lesser Snow and Ross' Geese regularly nest within 3-5 days of their major arrival, data on arrival at their final staging areas from which they proceed to nesting grounds are needed. Barry's (1967) observations suggest that rapid oocyte formation is stimulated at the time of arrival to the migration staging area closest to the nesting grounds.

Variability in the exact timing of ova maturation coupled with weather patterns that result in thaw and the availability of nest sites would be the most precise adaptation for successful reproduction in geese (for females). Spring migrations are variable in most species in the exact time of occurrence in association with weather, especially changes in frontal systems which result in warming southerly winds (cf. Blokpoel and Gauthier 1975). Following winds presumably reduce the energetic costs of migrating, but the same weather patterns will usually hasten spring thaw. Thus, arrival on or in proximity to nesting areas in synchrony with slight yearly variations in seasonal phenology is assisted. Synchronization of ovary preparation for laying with these same weather patterns would allow the best chance for maximum reproductive success. I suggest that the gonadotropin release responsible for final ova maturation (see Follett and Davies 1975) is stimulated at the same time as, or just before, this final migration. Perhaps the cues by which the migration is presumably stimulated also trigger this hormonal release.

Increased metabolic activity associated with hormonal release and the onset of this final migration may be related to accelerated ovary development once the animal is photoresponsive. Rutledge (1974) demonstrated that spermatogenesis in the starling (*Sturnus vulgaris*) was characterized by elevated body temperature. Elevated thyroid hormone secretion is also implicated by the increased metabolism and is related to avian migration and *Zugunruhe*, and to normal gonad development in domestic mallards (*Anas platyrhynchos*) (see Assenmacher 1973 for review). Although large doses of thyroxin can have deleterious effects on egg production in domestic fowl, moderate rates of administration, or naturally high rates of secretion of thyroxin,

increase egg production (see Falconer 1971 for review). The fact that activation of the thyroid could be part of the mechanism bringing about testicular regression (Assenmacher 1973) in males at the same time as stimulating rapid yolk formation in females is not contradictory. Barry (1962) demonstrated that Brant testes were regressing in weight while ovary development was proceeding. Thus, it is plausible that stimuli that affect the timing of the final migration flight of geese to or near their nesting grounds also stimulate a complex hypophyseal hormone release affecting thyroid secretion that metabolically affects, or interacts with, gonadotropins or gonadal steroids to cause ova development at the most propitious time for reproduction to occur.

Appropriate pair behavior is also usually necessary for follicle maturation (see review by Lofts and Murton 1973). Copulations by geese occur before arrival on nesting areas and are rarely observed early in spring migration (Cooch 1958, 1961; Barry 1962, 1967; MacInnes 1962; Ryder 1967; Mickelson 1975; personal observations). This aspect of sexual behavior probably peaks at geographic areas from which geese make their final migration to nesting grounds and thus it coincides with the time at which rapid ova formation is initiated. As eggs of geese must usually be fertilized by stored sperm, copulation might normally be necessary to stimulate the hormone release resulting in yolk development.

The importance of pair relations in preparation for reproduction by geese is further indicated by weight changes of individually marked Giant Canada Geese (*B. c. maxima*) of known social status weighed at least twice during the period of spring fat accumulation (R. M. McLandress and Raveling, unpublished data). Weights of seven adults that were paired increased 27 to 38%. Weight declined 7% and gained less than 1% in two unpaired adults.

#### ECOLOGICAL ADAPTATIONS

The general adaptive nature of early nesting by northern geese is well known. Later nesting than that observed would result in insufficient time for molt and preparation for migration in autumn (Cooch 1961, Barry 1962). Synchrony of hatching with the temporal availability of high-protein new growth of sedges and grasses is required for growth of the young (Murton and Kear 1973). Earlier nesting than that usually observed would expose eggs to freezing, access to mammalian predators because of connection of islands to the mainland by ice, and flooding at the time of spring runoff.

Within the above constraints, different species of geese have different migration patterns in relation to ova maturation and ability to lay eggs upon arrival at nesting areas. Brant nesting habitat is usually the latest available and they arrive later than other geese. This is ecologically, and evolutionarily, related to their sea coast habitat and marine food supply. Their small size, short growth period, and marine habitat, which freezes later in autumn than inland ponds and lakes, allows later nesting than the other species. Ova preparation after arrival rather than before seems to be the best strategy for maximum reproductive opportunity for Brant.

The pattern exhibited by Lesser Snow and Ross' Geese would be best when the earliest possible nesting in all years is at a high premium. Ross' Geese nest on larger lakes to the interior of delta habitat favored by Lesser Snow Geese. These lakes thaw slightly later than pond and delta habitat and Ross' Geese nest later than Lesser Snow Geese. Presumably, their small size and shorter period of growth is permissive



to use of this habitat. The premium for earliest possible nesting by Lesser Snows in terms of the time required for hatching, molt, and growth related to the summer season was provided by Cooch (1958, 1961).

It is difficult to reconcile why small Canadas exhibit a different pattern of ova preparation in relation to arrival than Lesser Snow Geese. Perhaps it is a function of the proximity of habitat and food supplies important in the timing of peak spring weight accumulation during migration. It is also possible that Canada Goose reproduction is not as severely constrained by late spring seasons as it is for Lesser Snow Geese. Canada Geese nesting at the same latitudes as Lesser Snow Geese are slightly smaller in body size (except at the two most recent and southern Lesser Snow Goose colonies), and presumably they could reach flight stage in later seasons that would select more strongly against Lesser Snow Geese. Thus, a more variable ova maturation in relation to events permitting arrival and nesting by Canada Geese would be a more effective average response than the more all-or-none strategy exhibited by Lesser Snow Geese.

Almost complete failures of reproduction by Brant and Cackling Geese on the Yukon-Kuskokwim Delta, Alaska, because of late spring weather, have never been recorded (C. J. Lensink, pers. comm.) as they have for Lesser Snow Geese and Brant at higher latitudes in the interior arctic (Cooch 1961, Barry 1962). The maritime influence on the west coast results in earlier thaws and later freezes than on the Arctic Ocean and Hudson's Bay coasts. Ova formation by Cackling Geese (and, again, for Brant) after arrival on nesting areas provides the most flexible response to obtain maximal production in relation to annual variations in availability of nesting habitat because seasons are never, or rarely, so retarded as to make nesting ill-adaptive.

#### ACKNOWLEDGMENTS

This study was funded by a faculty research grant from the College of Agriculture, University of California, Davis and by the U.S. Fish and Wildlife Service, which provided logistic support, supplies, and equipment. I am grateful to C. J. Lensink, Manager of Clarence Rhode National Wildlife Refuge, for advice and support in the field and review of the manuscript, and to M. R. Petersen for field assistance. J. Hout and J. Paniyak also provided essential assistance. I benefited from discussions with, and review of the manuscript by, R. G. Schwab and C. R. Grau, University of California, Davis.

#### LITERATURE CITED

- ASSENMACHER, I. 1973. The peripheral endocrine organs. Pp. 183-206 in *Avian Biology*. Vol. 3. (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- BARRY, T. W. 1962. Effect of late seasons on Atlantic Brant reproduction. *J. Wildl. Mgmt.* 26: 19-26.
- . 1967. The geese of the Anderson River Delta, Northwest Territories. Unpublished Ph.D. Thesis, Edmonton, Univ. Alberta, Canada.
- BLOKPOEL, H., & M. C. GAUTHIER. 1975. Migration of Lesser Snow and Blue Geese. *Can. Wildl. Serv. Rept. Ser. No. 32*. 28 pp.
- COOCH, F. G. 1958. The breeding biology and management of the Blue Goose (*Chen caerulescens*). Unpublished Ph.D. dissertation, Ithaca, N. Y., Cornell Univ.
- . 1961. Ecological aspects of the Blue-Snow Goose complex. *Auk* 78: 72-89.
- DAVIES, C., H. FISCHER, & E. GWINNER. 1969. Die brutzeiten einiger gansearten und ihrer bastarde in identischen bedingungen. *Oecologie* 3: 266-276.
- FALCONER, I. R. 1971. The thyroid glands. Pp. 459-472 in *Physiology and biochemistry of the domestic fowl*. Vol. 1. (D. J. Bell and B. M. Freeman, Eds.). New York, Academic Press.
- FARNER, D. S., & R. A. LEWIS. 1971. Photoperiodism and reproductive cycles in birds. Pp. 325-370 in *Photophysiology*. Vol. 6. (A. C. Giese, Ed.), New York, Academic Press.
- FOLLETT, B. K., & D. T. DAVIES. 1975. Photoperiodicity and the neuroendocrine control of reproduction in birds. Pp. 199-224 in *Avian physiology*. (M. Peaker, Ed.). New York, Academic Press.

- GILBERT, A. B. 1971. The ovary. Pp. 1163-1208 in *Physiology and biochemistry of the domestic fowl*. Vol. 3. (D. J. Bell and B. M. Freeman, Eds.), New York, Academic Press.
- GRAU, C. R. 1976. Ring structure of avian egg yolk. *Poultry Sci.* 55: 1418-1422.
- HANSON, H. C., & R. H. SMITH. 1950. Canada Geese of the Mississippi Flyway: With special reference to an Illinois flock. *Illinois Nat. Hist. Surv. Bull.* 25: 67-210.
- JONES, P. J., & P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea *Quelea quelea*. *Ibis* 118: 547-574.
- LOFTS, B. 1975. Environmental control of reproduction. Pp. 176-197 in *Avian physiology*. (M. Peaker, Ed.). New York, Academic Press.
- , & R. K. MURTON. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J. Zool.* 155: 327-394.
- , & ———. 1973. Reproduction in Birds. Pp. 1-107 in *Avian biology*. Vol. 3. (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- MACINNES, C. D. 1962. Nesting of small Canada Geese near Eskimo Point, Northwest Territories. *J. Wildl. Mgmt.* 26: 247-256.
- . 1966. Population behavior in eastern arctic Canada Geese. *J. Wildl. Mgmt.* 30: 536-553.
- , R. A. DAVIS, R. N. JONES, B. C. LIEFF, & A. J. PAKULAK. 1974. Reproductive efficiency of McConnell River small Canada Geese. *J. Wildl. Mgmt.* 38: 686-707.
- MICKELSON, P. G. 1973. Breeding biology of Cackling Geese (*Branta canadensis minima*, Ridgway) and associated species on the Yukon-Kuskokwim Delta, Alaska. Unpublished Ph.D. dissertation. Ann Arbor, Univ. Michigan.
- . 1975. Breeding biology of Cackling Geese and associated species on the Yukon-Kuskokwim Delta, Alaska. *Wildl. Monogr.* No. 45. 35 pp.
- MURTON, R. K., & J. KEAR. 1973. The nature and evolution of the photoperiodic control of reproduction in certain wildfowl (Anatidae). *J. Reprod. Fert. Suppl.* 19: 67-84.
- RUTLEDGE, J. T. 1974. Circannual rhythm of reproduction in male European Starlings (*Sturnus vulgaris*). Pp. 297-345 in *Circannual clocks*. (E. T. Pengelley, Ed.). New York, Academic Press.
- RYDER, J. P. 1967. The breeding biology of Ross' Goose in the Perry River region, Northwest Territories. *Can. Wildl. Serv. Rept. Ser.* No. 3. 56 pp.
- . 1972. Biology of nesting Ross' Geese. *Ardea* 60: 185-215.
- WOOD, J. S. 1964. Normal development and causes of reproductive failure in Canada Geese. *J. Wildl. Mgmt.* 28: 197-208.