

EFFECTS OF SPRING ENVIRONMENT ON NESTING PHENOLOGY AND CLUTCH SIZE OF BLACK BRANT¹

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Abstract. We studied the effects of timing of spring snowmelt on nesting phenology, nest site selection, and clutch size of Black Brant (*Branta bernicla nigricans*) breeding at the Tutakoke River colony, Yukon-Kuskokwim Delta, Alaska. In late springs, brant nested later; however, time between peak arrival at Tutakoke and nest initiation (6 to 12 days) was similar in early and late springs. Nest initiation was more synchronized in late springs than early springs. Height of nests relative to spring meltwater levels was lower in late springs than early springs, indicating that the interval between snowmelt and nest initiation was shorter. Reduced availability of nest sites and increased nesting synchrony in late years may result in greater competition for available nest sites and reduced site fidelity. Clutch size was greater in late springs than in early springs. This increase in clutch size may result from greater accumulation of endogenous reserves on spring staging areas in late springs, or from demographic changes in the breeding population.

Key words: Alaska, Black Brant, *Branta bernicla nigricans*, clutch size, nest initiation, nest site selection.

INTRODUCTION

Numerous studies have investigated the effects of spring environment on nesting phenology and reproductive performance of northern nesting geese (Raveling 1978, Ely and Raveling 1984). Response of geese to spring environmental conditions varies with breeding latitude and species. Several studies showed that delays in nesting result in reduced clutch size or, in extreme cases, greatly reduced breeding propensity (Barry 1962, MacInnes and Dunn 1988). However, other studies have found little or no effect of spring conditions on reproductive performance (Bruggink et al. 1994). Reproductive performance relative to environmental conditions is likely influenced by interspecific variation in reproductive strategies, or by intraspecific variation in reproductive strategies across latitudes or climatic conditions (Raveling 1978).

Raveling suggested that variation in response of geese nesting in Arctic and sub-Arctic regions to spring environment was the result of variation in timing of rapid follicle development. He pro-

posed that geese nesting in the high Arctic and species with long periods of incubation and gosling development commenced rapid follicle development during spring migration, and therefore could initiate nesting soon after arrival on the breeding grounds. Although this strategy ensures that geese are ready to nest soon after arrival, this strategy potentially results in greatly reduced reproductive performance in late springs if nest sites are unavailable until after completion of follicle development. Females that experience these conditions may reabsorb developing follicles (Raveling 1978), abandon nesting (Cooch 1961), or lay their eggs in nests of other geese (Syroechkovsky 1979). In contrast, Raveling (1978) suggested that geese nesting at lower latitudes or those requiring less time for incubation and gosling growth exhibit a more conservative reproductive strategy, initiating rapid follicle development following departure from spring staging areas or after arrival on the breeding grounds. This strategy provides a more flexible response to spring weather conditions. Recent studies generally have supported Raveling's premise; however, his hypothesis remains largely untested.

Our goal is to examine Raveling's (1978) hypothesis for Black Brant, *Branta bernicla nigricans* (hereafter brant), breeding on the Yukon-Kuskokwim Delta (YKD), Alaska. The YKD is a sub-Arctic breeding area (ca. 61°N). Brant are

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a small goose (ca. 1.5 kg) and require a shorter time for incubation and gosling development compared to other geese (Bellrose 1980). We therefore predicted that brant would exhibit a conservative reproductive strategy by initiating follicular development at departure from final spring staging areas or after arrival on the breeding grounds. We further predicted that brant would not experience follicular atresia in late springs. We could not directly assess the effect of spring environment on follicle development or atresia. We instead examined annual variation in time between arrival on the breeding grounds and nest initiation, and clutch size of brant. If brant exhibit a conservative reproductive strategy, we predicted that (1) time between arrival on the breeding grounds and nest initiation would approximate time required for rapid follicle development, and (2) clutch size would not be lower in late springs than in early springs. We further explored latitudinal variation in nesting phenology of brant by comparing our findings to previous studies of brant nesting in the Arctic (Southampton Island and Anderson River Delta, N.W.T.; Barry 1962, 1967). Spring habitat conditions also may affect distribution of nest initiation dates (Findlay and Cooke 1982) by altering nest sites available to brant. We examined these factors by comparing heights of nests relative to spring water levels and by measuring distribution and variance of initiation dates in early and late springs.

STUDY AREA

The Tutakoke River brant colony (61°15'N, 165°35'W) is located on the Bering Sea coast of the YKD, Alaska (Fig. 1). Most brant at Tutakoke nested in sedge meadows within 1 km of the coast. Spring breakup at Tutakoke River (mid-May to early June) was characterized by water from melting snow collecting in meltwater lakes, which were contained by higher elevation levees on the coast and along tidal sloughs. Water in these lakes drained when ice dams in coastal sloughs melted. Higher elevation coastal levees were typically the first areas free of snow and meltwater. Drainage of meltwater lakes generally proceeded from the northern to the southern portion of the colony. Because of intra-colony differences in timing of snowmelt, habitat features, and nest densities, we stratified the colony into 4 areas (strata A–D, Fig. 1). These strata

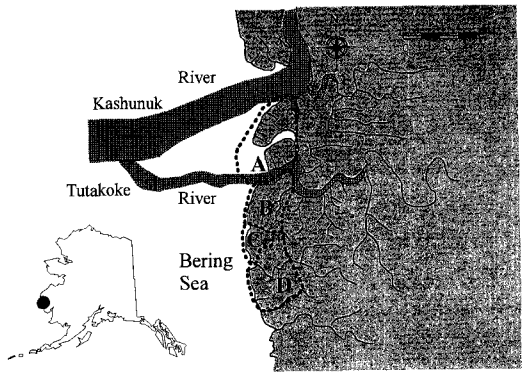


FIGURE 1. Location of the Tutakoke River Black Brant colony on the coast of the Yukon-Kuskokwim River Delta, Alaska. Strata boundaries are shown with dashed lines and each stratum is designated with a capital letter (A–D).

are described in more detail in Lindberg et al. (1995).

METHODS

SNOWMELT AND SPRING MIGRATION

We used the date the entire colony was 100% snow-free as an index of timing of spring. Because date of 100% snow melt was not available for Tutakoke River in 1986, we used snow melt data from a research camp (Old Chevak) located approximately 20 km to the northeast of Tutakoke for this year. Range of dates for 100% snow melt exhibited a clear dichotomy for both the Tutakoke and Old Chevak sites. We classified 1986, 1988, 1990, 1991, and 1993 as early springs, with the colony 100% snow free between 17–21 May at Tutakoke and between 6–13 May at Old Chevak. The remaining 3 years (1987, 1989, 1992) were classified as late, because 100% snow melt occurred between 28 May–2 June at Tutakoke and 18–22 May at Old Chevak.

We counted brant on the ground during spring to estimate peak arrival date at Tutakoke. Estimates of peak arrival were conducted from 5-m high towers twice each day. Because of differences in data collection protocol and incomplete tower counts, peak arrival was not estimated in 1987 or 1991.

NEST INITIATION AND CLUTCH SIZE

From 1987–1993 we located brant nests using two techniques. First, nests were found by searching 50-m radius plots ($n = 34$ to 49) lo-

cated in a stratified, random design throughout the breeding colony. We began searching for nests on plots as soon as the first eggs were laid in the spring (mid-May to early June), and we continued searches through the end of egg laying (early to late June). Each plot was searched every fourth day. While traveling between plots, we also searched for nests of brant previously marked with tarsal tags (Sedinger et al. 1995). During late incubation, we intensified our search for nests of marked brant by systematically searching the colony every day or every other day. For all nests, we recorded number of eggs and nesting stratum (see strata designations Fig. 1), and we labeled eggs for identification. We calculated initiation dates for nests discovered during laying by back-dating from the date the nest was found and assuming that 1 egg was laid each day. For nests not discovered during laying but with a known hatch date, we back-dated from the hatch date to calculate initiation date, assuming 24 days of incubation and that incubation began when the second egg was laid (Flint et al. 1994). Clutch size was defined as the maximum number of eggs observed in the nest. To minimize bias in estimates of clutch size created by partial predation before we found the nest, we only used nests discovered during laying to determine clutch size. We excluded nests with > 7 eggs ($n = 9$) because these clutches may have resulted from parasitic egg-laying.

We tested for strata and year variation in nest initiation dates using ANOVA (PROC GLM, SAS Institute, Inc. 1990). We followed this ANOVA with a contrast (e.g., Neter et al. 1985) to examine a planned comparison of initiation dates in early and late springs. We described the relationship between spring environment and nest initiation in more detail by estimating the slope of the relationship between date of 100% snowmelt and date of nest initiation among strata with ANCOVA. In this ANCOVA model, date of 100% snowmelt was included as a continuous rather than as a class (year) variable. We tested the hypothesis that nesting was more synchronized in late springs than early springs by comparing the variance of initiation dates in late and early springs (Snedecor and Cochran 1980). We used tests of skewness (Snedecor and Cochran 1980) to compare distributions of nest initiation dates in early and late springs.

We tested for variation in clutch size among years and strata with ANCOVA. We included

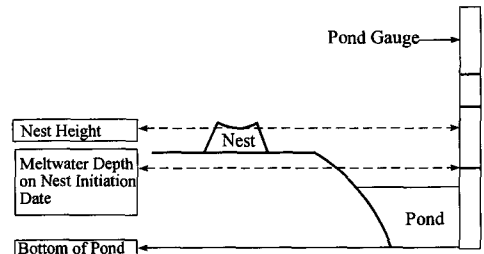


FIGURE 2. Diagram of technique used to determine height of nests (NH) relative to meltwater (MW) depth on the day the nest was initiated. NH and MW were recorded from either the bottom of the pond or the pond water level on the day the measurements were taken and were measured with line levels or transits.

initiation date as a covariate in the ANCOVA model because clutch size declines with initiation date (Flint and Sedinger 1992). The covariate, initiation date, was expressed as deviation in days from the modal initiation date for each year. We used a contrast to compare clutch size in late and early springs. As described in our analysis of initiation dates, we estimated slope of the relationship between spring environment and clutch size by including the continuous variable, date of 100% snowmelt, rather than the class variable (year) in the ANCOVA model. We tested the hypothesis that distribution of clutch sizes was independent of spring phenology (i.e., early vs. late) with χ^2 test of independence.

NEST HEIGHT

From 1986–1988 and in 1992, we determined height of nests relative to spring meltwater by marking and dating water levels on gauges located in two ponds (plots 22 and 41) in stratum C (Fig. 1 and 2). Water levels were marked approximately every 3 days (range 2–5 days) before and during nest initiation. We used linear interpolation to estimate meltwater levels between dates when water level was measured. After completion of incubation, we used line-levels and transits to determine height of nests relative to the pond bottom (H_p) and relative to meltwater depth on the date the nest was initiated (H_w) (Fig. 2). A negative value for H_w indicated that the nest was flooded when the first egg was laid, and a positive value indicated the nest was above meltwater depth on the initiation date. H_p and H_w were recorded for a random sample of nests within approximately a 100 m radius of the pond gauge.

We used ANCOVA to examine the relationship between H_p and initiation date among years and plots. Initiation date was expressed as deviation in days from the modal initiation date for each year. Because H_p was measured relative to the pond bottom and height of pond bottoms varied across years and plots, these heights were not comparable across years or plots. Therefore, we only tested for differences in the slope of the relationship between H_p and initiation date between plots, among years, and among years within plots.

We used ANCOVA to examine year and plot variation in H_w ; initiation date was included as a covariate. Unlike H_p , H_w was comparable across years and plots. We used contrasts to compare H_w in late and early springs.

RESULTS

SPRING ENVIRONMENT

The difference in average date of 100% snow melt for late and early springs was 10 days (Fig. 3). Time between peak arrival and peak nest initiation ranged from 6 to 12 days, averaging 11 days in late years (1989 and 1993) and 9 days in early years (1988, 1990, 1993). We observed a positive correlation ($r = 0.84$) between arrival dates and date of 100% snowmelt, but this correlation was not significant ($P = 0.07$).

NEST INITIATION

We obtained nest initiation dates for 3,556 nests from 1987–1993. Initiation date varied among years ($F_{6, 3528} = 680.8$, $P < 0.001$) and strata ($F_{3, 3528} = 5.0$, $P = 0.002$), and pattern of initiation dates varied among strata over years (year \times strata interaction, $F_{18, 3528} = 3.3$, $P < 0.001$; Fig. 3). Mean (\pm SE) initiation date in late springs (2 June \pm 0.1 days, $n = 1,424$) was 7 days later ($F_{1, 3528} = 534.0$, $P < 0.001$) than mean initiation date (26 May \pm 0.1 days, $n = 2,132$) in early springs, and peak (modal) initiation dates differed by 6 days (late spring = 1 June, early spring = 26 May). We observed a significant positive relationship ($F_{1, 3548} = 4,507.8$, $P < 0.001$, $\beta = 0.672$) between date of 100% snowmelt and initiation date, however, the slope was less than 1.0 ($P < 0.001$). Additionally, the relationship between date of 100% snowmelt and initiation date varied among strata ($F_{3, 3548} = 6.9$, $P < 0.001$). Variance of initiation date in early years (11.4 days) was greater than variance in late years (9.9 days; $F_{2132, 1424} = 1.2$, $P < 0.001$),

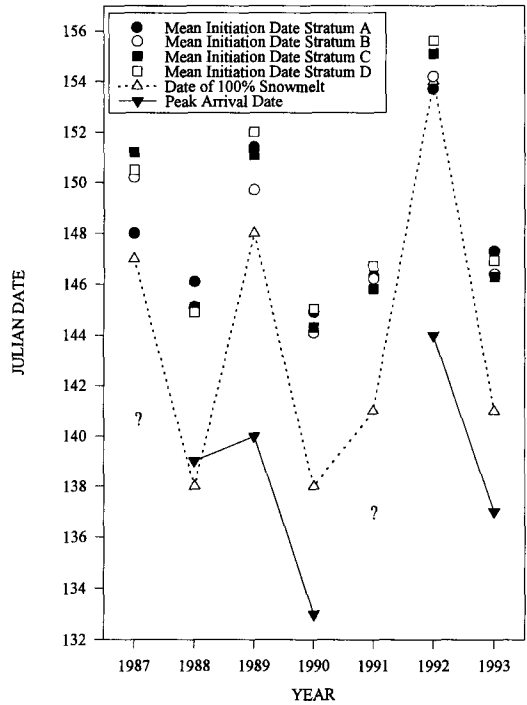


FIGURE 3. Mean initiation dates by strata for Black Brant nesting at the Tutakoke River colony, Alaska, 1987–1993. Date the colony was 100% snow free is shown by a dashed line and peak arrival date is shown by a solid line. Date of peak arrival was not available in 1987 or 1991. Day 132 is 12 May.

indicating that nesting was more synchronized in late years (Fig. 4). Distribution of nest initiation dates was positively skewed ($P < 0.01$) in both early and late years (Fig. 4).

CLUTCH SIZE

From 1987–1993, we measured clutch size for 1,751 nests (Table 1). We found no significant variation in clutch size among strata ($F_{3, 1624} = 0.8$, $P = 0.52$), and data were therefore pooled across strata. Clutch size varied among years ($F_{6, 1737} = 5.1$, $P < 0.001$). We observed a negative relationship between clutch size and initiation date ($F_{1, 1737} = 181.6$, $P < 0.001$, $\beta = -0.047$); however, this relationship was not constant across years ($F_{6, 1737} = 2.8$, $P < 0.05$; Fig. 5). Mean (\pm SE) clutch size (least square estimates) in late springs (4.40 ± 0.03 , $n = 804$) was greater than mean clutch size in early springs (4.23 ± 0.03 , $n = 947$; $F_{1, 1737} = 25.6$, $P < 0.001$). Similarly, clutch size was positively related to date of 100% snowmelt ($F_{1, 1748} =$

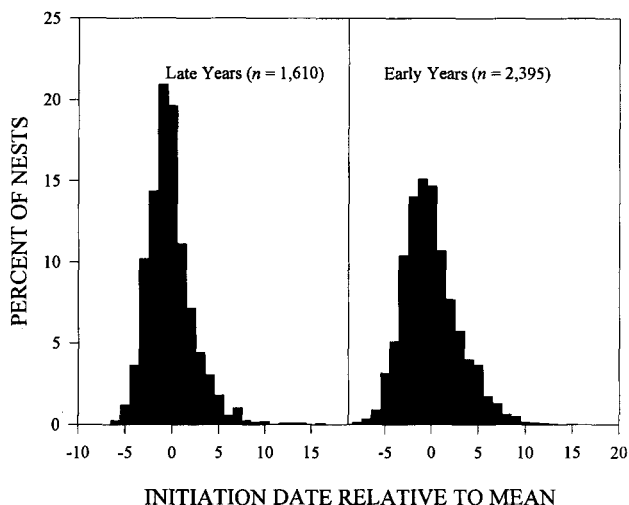


FIGURE 4. Distribution of nest initiation dates in early (1987, 1989, 1992) and late springs (1988, 1990, 1991, 1993) for Black Brant at the Tutakoke River colony, Alaska.

18.2, $P < 0.001$) and increased by 0.015 ± 0.004 eggs day⁻¹. Distribution of clutch sizes was not independent of spring phenology ($\chi^2_5 = 36.3$, $P < 0.001$), which was largely explained by an increase in the proportion of 5-egg clutches in late springs (Fig. 6). Five-egg clutches accounted for 45% ($n = 804$) of clutch sizes in late springs and only 34% ($n = 947$) in early springs.

NEST HEIGHT

We found no annual variation in the relationship between H_p and initiation date between plots ($F_{3, 193} = 2.5$, $P = 0.06$) or within plots ($F_{3, 193} = 2.34$, $P = 0.07$). Brant nesting later used lower elevation nest sites ($F_{1, 199} = 10.3$, $P = 0.002$; $\beta = -1.06$, plot 22; $\beta = -0.03$, plot 41).

H_w varied among years ($F_{3, 193} = 5.3$, $P = 0.002$), between early and late springs ($F_{1, 193} = 8.5$, $P = 0.004$), and between plots ($F_{1, 193} =$

41.9, $P < 0.001$). In late springs, mean (least squares estimate) H_w (\pm SE) was negative (i.e., below meltwater level) when nests were initiated (1987: $H_w = -1.31 \pm 0.67$, $n = 48$; 1992: $H_w = -2.00 \pm 1.08$, $n = 17$), whereas in early years mean H_w was positive (1986: $H_w = 0.25 \pm 0.51$, $n = 86$; 1988: $H_w = 0.70 \pm 0.63$, $n = 55$). Therefore, when nests were initiated, nest sites were lower relative to meltwater levels in late years than in early years. H_w increased ($F_{1, 193} = 36.4$, $P < 0.001$) with later nest initiation, in-

TABLE 1. Least-squares estimates of mean clutch size for Black Brant nesting at the Tutakoke River colony, Alaska, 1987–1993.

Year	Mean	SE	<i>n</i>
1987	4.37	0.05	285
1988	4.24	0.05	276
1989	4.43	0.05	285
1990	4.20	0.06	219
1991	4.25	0.06	223
1992	4.41	0.06	234
1993	4.13	0.06	229

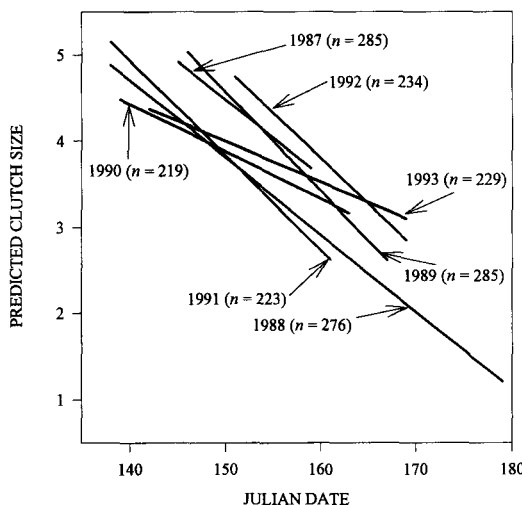


FIGURE 5. Relationship between clutch size and initiation date for Black Brant nesting at the Tutakoke River, Alaska, 1987–1993. Day 140 is 20 May.

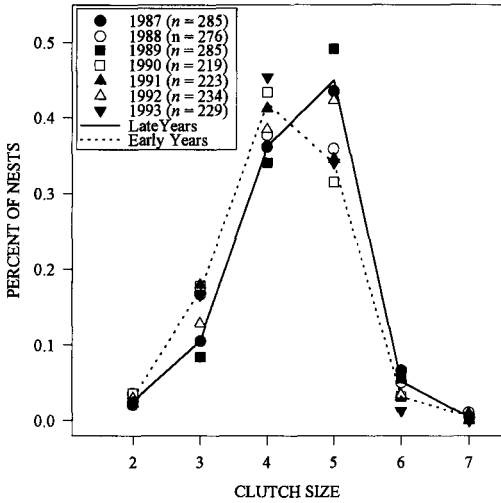


FIGURE 6. Distribution of clutch sizes for Black Brant nesting at the Tutakoke River, Alaska, 1987–1993. Mean percent of clutch sizes is shown with a solid line for late springs (1987, 1989, 1992; closed symbols) and a dashed line for early springs (1988, 1990, 1991, 1993; open symbols).

dicating that meltwater levels receded faster than declines in elevation of nests used by brant.

DISCUSSION

NESTING PHENOLOGY

The interval between peak arrival and peak nest initiation ranged from 6 to 12 days for brant nesting at Tutakoke. Based on Barry's (1962, 1967) studies of Atlantic (*B. b. hrota*) and Black Brant in the Arctic, Raveling (1978) hypothesized that brant initiate rapid follicle development upon departure from the last spring staging area or upon arrival on the nesting area. Our results are consistent with this prediction as time for rapid follicle development is about 12 days in geese (Alisauskas and Ankney 1992). In addition, the interval between arrival and nest initiation was similar in early and late springs, even though nest sites were available several days prior to onset of nesting in early springs. Therefore, brant were unable to take full advantage of early springs, which may reflect a cost associated with their strategy of follicle development.

Unlike brant breeding in the Arctic (Barry 1962), brant nesting at Tutakoke did not experience delays > 12 days between peak arrival and nest initiation, or total reproductive failure in late years (Raveling 1978, this study). Intra-

specific variation in the response of brant to spring environment may be related to proximity of spring staging areas to breeding areas and, therefore, the ability of brant to predict snow-melt conditions on breeding grounds (Petersen 1992). Izembek Lagoon, Alaska is the principal staging area for brant during spring migration (Ward and Stehn 1989). Barry (1967) suggested that brant required from 3 to 6 days for migration from Izembek to the breeding grounds at Anderson River, N.W.T. In contrast, brant breeding at Tutakoke likely use Chagvan and Nanvak bays, Alaska as staging areas following departure from Izembek (D. H. Ward, unpubl. data), a distance of 350 km from Tutakoke River. Furthermore, brant breeding at Tutakoke maintained a stable arrival-to-initiation interval by nesting earlier relative to spring phenology in late springs than in early springs. Capacity of brant to nest earlier relative to spring conditions is limited, however, as indicated by the fact that even at Tutakoke River some females laid eggs in water in late springs. We expect that reduced ability to predict spring conditions, as for Arctic breeding brant, may force more females to skip breeding in late springs.

CLUTCH SIZE

Clutch size of brant nesting at Tutakoke increased in late springs. In contrast, previous studies of northern nesting geese have observed reduced clutches in late springs (Barry 1962, Dau and Mickelson 1979, Ely and Raveling 1984) or no relationship between time of spring thaw and clutch size (Petersen 1992, Bruggink et al. 1994). Declines in clutch size in late springs were correlated with increased delays between arrival and nest initiation, which presumably resulted in use of reproductive reserves for maintenance and atresia of developing follicles (Raveling 1978, MacInnes and Dunn 1988).

Brant could conserve or augment reproductive reserves in late years by feeding after arrival on breeding areas (Budeau et al. 1991, Gauthier and Tardif 1991), or by increasing reproductive reserves before arrival. Although brant feed at Tutakoke prior to nest initiation (Lindberg, unpubl. data), we do not believe that food intake was greater in late springs than early springs. Brant were not present on the breeding areas during prenesting for longer periods in late springs than early springs. In addition, brant

nested earlier relative to spring thaw in late springs, and food resources were therefore probably less available during prenesting in late springs compared to early springs (Prop and de Vries 1993). However, if date of arrival on staging areas is consistent among years, brant may increase foraging time on spring staging areas in late springs. Female brant staging at Izembek Lagoon during the fall increase body weight by approximately 7.8 g day^{-1} (Dau 1992). Ebbs and Spaans (1995) suggest that reproductive performance of Brent Geese (*B. b. bernicla*) is positively correlated with reserves accumulated on spring staging areas. Therefore, in late springs, females may arrive on breeding grounds with more reserves than in early springs because of increased foraging time on spring staging areas.

Alternatively, increased clutches in late springs may reflect reduced breeding propensity by younger brant. Clutches of 2-year-old brant are significantly smaller than clutches of brant > 2 years old (Flint and Sedinger 1992). If proportionally fewer 2-year-old brant nest in late springs, then the increase in clutch size we observed may reflect a change in the age structure of brant nesting at Tutakoke.

We attempted to reduce sources of bias in clutch size estimates by limiting our sample to nests discovered during laying. Cooke et al. (1995) noted two additional sources of bias in clutch size estimates; nest parasitism and preincubation nest failure. Parasitic egg-laying has been observed in brant, and an increase in nest parasitism during late springs could explain the increased clutch size we observed. In late springs, however, the increase in clutch size was largely the result of a proportional increase in 5-egg clutches, which are commonly observed in brant (Flint and Sedinger 1992), rather than an increase in clutches > 5 (Fig. 6). Preincubation nest failure may negatively bias clutch size estimates as females lay smaller clutches in subsequent nest attempts (i.e., continuation clutches, Cooke et al. 1995). Although we have observed continuation clutches in brant (Lindberg et al., unpubl. data), we have no data suggesting a higher rate of continuation nesting in early springs. Detected nest abandonment during laying was 0.8% ($n = 3,530$) in early springs and 0.9% ($n = 2,314$) in late springs.

NESTING SYNCHRONY AND SITE SELECTION

Our finding of more synchronized nesting in late springs than in early springs is consistent with

previous studies of northern nesting geese. Distributions of initiation dates for brant at Tutakoke were positively skewed in both early and late springs. Findlay and Cooke (1982) observed a positive skew in the distribution of initiation dates for Lesser Snow Geese (*A. c. caerulescens*) in early springs and a negative skew in late springs. They suggested that changes in these distributions were the result of differences in the availability of nest sites. Fewer nest sites were available to early nesting pairs in late springs. In early springs, nest site availability was not a limiting factor, and the positive skew reflects selection for early nesting (Cooke et al. 1995).

Brant used highest elevation nest sites first in both early and late years. Because of meltwater flooding, availability of higher elevation nest sites was more limited in late years than early years. Although female brant generally return to previously used nest sites (Lindberg et al. 1995), we suggest that early nesting females are forced to disperse to available nest sites in late springs to maintain earliest possible nesting (Lindberg 1996).

Selective pressures for early nesting may be more prevalent in late years. Brant with earlier hatch dates had higher growth, survival, and fecundity than brant with late hatch dates (Sedinger and Flint 1991, Sedinger et al. 1995) as availability of high quality foods declines during the season (Sedinger and Raveling 1986). Cooch et al. (1991) suggested that declines in growth rates of goslings may be steeper in late springs than early springs. The inability of brant to immediately exploit available nest sites in early springs and the conservative strategy of timing of follicle development exhibited by these geese suggests that higher costs are associated with nesting later in late springs than early springs.

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LITERATURE CITED

ALISAUSKAS, R. T., AND C. D. ANKNEY. 1992. The cost of egg laying and its relationship to nutrient re-

- serves in waterfowl, p. 30–61. In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], Ecology and management of breeding waterfowl. Univ. Minn. Press, Minneapolis, MN.
- BARRY, T. W. 1962. Effects of late seasons on Atlantic Brant reproduction. *J. Wildl. Manage.* 26:19–26.
- BARRY, T. W. 1967. The geese of the Anderson River Delta, Northwest Territories. Ph.D. diss., Edmonton Univ., Alberta, Canada.
- BELLROSE, F. C. 1980. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, PA.
- BRUGGINK, J. G., T. C. TACHA, J. C. DAVIES, AND K. F. ABRAHAM. 1994. Nesting and brood-rearing ecology of Mississippi Valley Population Canada Geese. *Wildl. Monogr.* 126.
- BUDEAU, D. A., J. T. RATTI, AND C. R. ELY. 1991. Energy dynamics, foraging ecology, and behavior of prenesting Greater White-fronted Geese. *J. Wildl. Manage.* 55:556–563.
- COOCH, F. G. 1961. Ecological aspects of the Blue-Snow Goose complex. *Auk* 78:72–89.
- COOCH, E. G., D. B. LANK, A. DZUBIN, R. F. ROCKWELL, AND F. COOKE. 1991. Body size variation in Lesser Snow Geese: environmental plasticity in gosling growth rate. *Ecology* 72:503–512.
- COOKE, F., R. F. ROCKWELL, AND D. B. LANK. 1995. The Snow Geese of La Pérouse Bay: natural selection in the wild. Oxford Univ. Press, Oxford.
- DAU, C. P. 1992. The fall migration of Pacific Flyway Brent *Branta bernicla* in relation to climatic conditions. *Wildfowl* 43:80–95.
- DAU, C. P., AND P. G. MICKELSON. 1979. Relation of weather to spring migration and nesting of Cackling Geese on the Yukon-Kuskokwim Delta, Alaska, p. 94–104. In R. L. Jarvis and J. C. Bartonek [eds.], Management and biology of Pacific Flyway geese. Oregon State Univ. Book Stores, Corvallis, OR.
- EBBINGE, B. S., AND B. SPAANS. 1995. The importance of body reserves accumulated in spring staging areas in the Temperate Zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* 26:105–113.
- ELY, C. R., AND D. G. RAVELING. 1984. Breeding biology of Pacific White-fronted Geese. *J. Wildl. Manage.* 48:823–837.
- FINDLAY, C. S., AND F. COOKE. 1982. Synchrony in the Lesser Snow Goose (*Anser caerulescens caerulescens*) II. The adaptive value of reproductive synchrony. *Evolution* 37:724–734.
- FLINT, P. L., M. S. LINDBERG, M. C. MACCLUSKIE, AND J. S. SEDINGER. 1994. The adaptive significance of hatching synchrony of waterfowl eggs. *Wildfowl* 45:248–254.
- FLINT, P. L., AND J. S. SEDINGER. 1992. Reproductive implications of egg-size variation in the Black Brant. *Auk* 109:896–903.
- GAUTHIER, G., AND J. TARDIF. 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. *Condor* 93:701–711.
- LINDBERG, M. S. 1996. Demographic components of philopatry and nest-site fidelity of Pacific Black Brant. Ph.D. diss., Univ. Alaska, Fairbanks, AK.
- LINDBERG, M. S., J. S. SEDINGER, AND E. A. REXSTAD. 1995. Estimating nest site fidelity of adult female Black Brant with multistate modeling and geographic information systems. *J. Appl. Stat.* 22: 725–735.
- MACINNES, C. D., AND E. H. DUNN. 1988. Components of clutch size variation in Arctic-nesting Canada Geese. *Condor* 90:83–89.
- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1985. Applied linear statistical models. Irwin, Homewood, IL.
- PETERSEN, M. R. 1992. Reproductive ecology of Emperor Geese: annual and individual variation in nesting. *Condor* 94:383–397.
- PROP, J., AND J. DE VRIES. 1993. Impact of snow and food conditions on reproductive performance of Barnacle Geese *Branta leucopsis*. *Ornis Scand.* 24:110–121.
- RAVELING, D. G. 1978. The timing of egg laying by northern geese. *Auk* 95:294–303.
- RAVELING, D. G., AND H. G. LUMSDEN. 1977. Nesting ecology of Canada Geese in Hudson Bay Lowlands of Ontario: evolution and population regulation. Ontario Ministry Nat. Resources. Fish and Wildl. Res. Rep. 98.
- SAS INSTITUTE. 1990. SAS/STAT user's guide, Version 6, 4th ed., Vol. 2. SAS Institute, Inc., Cary, NC.
- SEDINGER, J. S., AND P. L. FLINT. 1991. Growth is negatively correlated with hatch date in Black Brant. *Ecology* 72:496–502.
- SEDINGER, J. S., P. L. FLINT, AND M. S. LINDBERG. 1995. Environmental influence on life-history traits: growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology* 76:2404–2414.
- SEDINGER, J. S., AND D. G. RAVELING. 1986. Timing of nesting by Cackling Canada Geese in relation to the quality and availability of their food plants. *J. Anim. Ecol.* 55:1083–1102.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods. Iowa State Univ. Press, Ames, IA.
- SYROECHKOVSKY, E. V. 1979. The laying of eggs by white geese into strange nests. *Zoologicheskii Zhurnal* 58:1033–1041. [In Russian]
- WARD, D. H., AND R. A. STEHN. 1989. Response of Brant and other geese to aircraft disturbances at Izembek Lagoon, Alaska. Final Report, U.S. Fish Wildl. Serv., Alaska Fish Wildl. Res. Center, Anchorage, AK.