REPRODUCTIVE IMPLICATIONS OF EGG-SIZE VARIATION IN THE BLACK BRANT

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ABSTRACT.—We analyzed variation in egg size of Black Brant (*Branta bernicla nigricans*) in relation to clutch size, laying date, female age, year, and position in the laying sequence. A total of 3,478 eggs was measured over three years. Egg size increased with clutch size and female age, and decreased with laying date, year, and position in the laying sequence. We did not detect a negative phenotypic correlation between clutch size and egg size. However, overlap in total clutch volumes for clutches of different sizes indicated trade offs occurred among individuals with comparable investments in their clutches. *Received 1 October 1991, accepted 30 March 1992.*

THE COMBINATION of clutch size and egg size determines the total energetic investment in clutch formation by a laying female. Egg size may affect female fitness through its effects on initial size, early growth and survivorship of hatchlings (Cole 1979, Ankney 1980, Thomas and Brown 1988, Sedinger and Flint 1991), whereas clutch size is related to fitness via its effect on the potential number of offspring produced (Lessells 1986).

Arctic-nesting geese rely heavily on stored lipid and protein reserves for egg production and incubation (Ankney and MacInnes 1978, Raveling 1979, Ankney 1984). Thus, nutrients available for a clutch are limited and at least partially predetermined when geese arrive on the breeding grounds. This limitation on reproductive investment, combined with the fitness advantages of both large clutches and large eggs, creates the potential for both ultimate and proximate trade offs between clutch size and egg size.

Lack (1947) first proposed that trade offs should occur between the number of offspring produced and the size of those offspring. Few examples of such trade offs between clutch size and egg size exist for waterfowl, and possible physiological mechanisms for such trade offs are unknown. The high repeatability of egg size, however, suggests that such trade offs likely occur among, rather than within, individuals (Lessells et at. 1989). That is, within the constraints imposed by limited nutrient reserves, individual females do not alter the size of eggs they lay in order to vary their clutch size. Thus, the size of eggs that females produce should influence their average clutch size for those spe-

cies with constraints on nutrients available for egg production (e.g. arctic-nesting geese). The trade off between clutch size (or number of offspring) and egg size (or size of offspring) is potentially an important component of the life-history characteristics of waterfowl (Rohwer 1988).

Intraspecific variation in egg size has been studied extensively in many species (for review, see Manning 1978). In waterfowl, egg size varies with female age (Cooper 1978, Newell 1988), clutch size (Cooper 1978, Batt and Prince 1979), laying date (Cooper 1978, Hill 1984), year (Cooper 1978, Newell 1988), and position in the laying sequence (Ankney and Bisset 1976, Cooper 1978, Cargill 1979). In general, younger females lay smaller eggs, and egg size declines with laying date and position in the laying sequence.

In this paper we examine relationships between egg size and female age, clutch size, laying date, year, and position in the laying sequence in Black Brant (*Branta bernicla nigricans*). We interpret these relationships in the context of trade offs between clutch size and egg size.

METHODS

Study area.—This study was conducted during the summers of 1987–1989 at the Black Brant colony located at the mouth of the Tutakoke River (61°15'N, 165°37'W), on the outer coastal fringe of the Yukon Delta National Wildlife Refuge, Alaska. The Tutakoke River colony has been the site of research on nesting ecology and demography of Black Brant since 1984 and, thus, a population of breeding adults marked with uniquely coded plastic tarsus bands existed at the initiation of our study. The Tutakoke River colony covers approximately 12 km². Nesting occurs in wet

sedge meadows dominated by *Carex ramenskii*, several hundred meters inland from coastal mudflats. Local nesting density is highly patchy, varying from 0.01 to 280 nests per hectare.

Collection of nesting data and egg measurements.—We located nests by searching randomly located circular plots (radius 50 m) every fourth day from nest initiation through the completion of egg laying. Nests were assigned a unique nest number, and eggs present were assigned a sequence number and marked with permanent markers when they were located. If more than one new egg was present in the nest on a particular visit, laying sequence was established by the degree of shell staining on each egg; first eggs were the most heavily stained (pers. observ.; see also Cooper 1978). We estimated the date of nest initiation by back-dating from the date the nest was located, assuming that one egg was laid per day with a day skipped between eggs 4 and 5 (MacInnes 1962). Maximum lengths and breadths of eggs were measured to the nearest 0.1 mm with dial calipers for all nests located during initiation. We estimated volumes for all measured eggs from the relationship between egg volume and linear measurements (see below). Total volume of the clutch was determined by summing the individual volumes of all eggs in each clutch. Measurements of eggs for which we were uncertain of the laying sequence were used only in the analysis of total clutch volume. Nests for which an improbable number of eggs were laid between visits (e.g. four eggs in three days), or nests from which eggs marked on a previous visit had disappeared were excluded from all analyses.

We searched the entire colony during incubation to associate marked females with nests. Females were flushed from nests and their tarsus band codes, if present, were recorded. Eggs in nests of marked females were then measured (as described above). Most nests of marked birds were not on plots searched during egg laying. Therefore, initiation dates for these nests were unknown, egg-laying sequence could not be determined, and we were unable to detect either partial predation, and/or nest parasitism.

Repeatabilities.—We estimated repeatability of egg size, clutch size, and clutch volume as the proportion of the total variation in a characteristic (e.g. egg size) resulting from differences among individuals (Falconer 1981, Lessells and Boag 1987). This analysis used data on clutch size from marked individuals nesting in 1984–1986 (J. S. Sedinger unpubl. data) in addition to data collected during this study. Females younger than four years of age were excluded from the repeatability analysis owing to the possibility of age-related variation in egg size or clutch size (see below, Hamann and Cooke 1987, Finney and Cooke 1978, Rockwell et al. 1983).

Egg-volume estimation.—We collected a sample of 51 and 90 unhatched eggs in 1988 and 1989, respectively. The contents of these addled, infertile, or abandoned

eggs were removed, and the shells were dried. External volume was measured by sealing the holes in the shell with Parafilm, submerging the egg, and measuring the displacement of water to the nearest 0.5 cm³. Submersion was accomplished with a fine wire that had negligible displacement (<0.25 cm³). Internal volume was estimated by taring the sealed shell mass, filling the egg with distilled water, and re-weighing. A measured quantity of distilled water was weighed and water density was assumed to be constant (1 g/cm³). Parameters in the relationship between external measures of length and width and the measured volumes were estimated using Hoyt's (1979) equation. To estimate egg-shell thickness, eggs were cut in half longitudinally and shell thickness was measured to the nearest 0.01 mm with dial calipers. Shells were measured at both ends and at the midpoint of the long axis.

Statistical analysis.—Variation in mean egg volume among years and among clutches of three, four, and five eggs was examined using a two-way analysis of variance (ANOVA). The relationship between egg volume and position in the laying sequence was examined using nested ANOVA, with clutches as the nested factor. The relationship between egg size and nest initiation date was compared among years using a one-way analysis of covariance (ANCOVA), with year as a factor and nest initiation date as a covariate. We estimated repeatability of egg size, clutch size, and clutch volume using a one-way ANOVA to partition the variance into within- and among-individual components and then applied the equations of Lessells and Boag (1987). Standard errors of the repeatability estimates were calculated following Becker (1984).

Clutch size and egg size were compared for two-year-old and older females using a multivariate Hotellings T^2. Dates of nest initiation of two-year-old females were compared with those of older females with a *t*-test. A two-way ANCOVA on egg size grouped by year and clutch size, excluding females younger than age 3, with initiation date as a covariate, was used to assess the effects of age on the relationship of egg size and initiation date. All analyses were done using BMDP statistical software (Dixon 1985).

RESULTS

Estimation of egg volume.—The relationship between external volume and linear egg measurements was described by the equation:

$$V_{ex} = 8.22 + (0.4636LB^2)/1,000,$$

where V_{ex} is external volume in cm³, L is length in millimeters, and B is breadth in millimeters ($r^2 = 0.92$, $P = 0.0001$). Analysis of covariance indicated no annual difference in this relation-
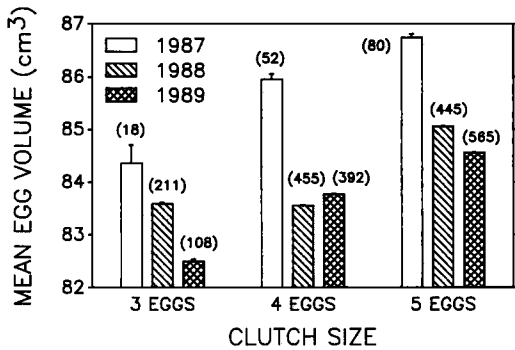
Fig. 1. Mean (whiskers indicate SE) egg volume for clutch sizes of three, four, and five eggs in 1987, 1988, and 1989. Egg volume varied significantly among clutch sizes and years ($P = 0.0032$ and 0.0007, respectively). Sample sizes in parentheses. Error bars less than 0.01 were not plotted.

ship for eggs collected in 1988 and 1989 ($F_{1,132} = 0.17, P = 0.68$). Analysis of covariance on the same form of equation fit to internal volumes, revealed significant differences in the slopes of the regression coefficients for eggs collected in 1988 versus 1989 ($F_{1,132} = 6.44, P = 0.012$). Mean shell thickness (grand mean of three points from each egg) did not differ between years ($t = 1.27$, df = 132, $P = 0.20$). However, when the three individual point measurements were considered separately, eggs from 1988 were significantly thicker at the large end of the long axis than eggs from 1989 ($t = 2.27$, df = 132, $P = 0.008$). No significant between-year differences occurred at the other two points of measurement ($P > 0.15$).

External volumes of eggs measured in the field were estimated from the fitted relationship between external volume and linear measurements. A total of 3,478 eggs was measured over three seasons. Mean egg volume was $84.0 \pm$ SE of 5.74 cm^3 (range 57.5–103.1 cm^3). We compared the estimated volumes of the collected eggs to the entire sample of measured eggs to determine if collected eggs were a representative sample of eggs from the entire population. Eggs collected for determination of volume in 1988 did not differ from the sample of eggs measured in that year ($t = 1.42$, df = 1203, $P = 0.15$); however, eggs collected in 1989 were significantly smaller than those measured in the field ($t = 3.50$, df = 2120, $P = 0.0005$).

Variation in egg size.—Egg volume varied significantly with clutch size ($F_{2,2317} = 5.77, P = 0.0032$) and year ($F_{2,2317} = 7.30, P = 0.0007$).

Smaller eggs were laid in 1988 and 1989 than in 1987, and larger eggs were laid in larger clutches (Fig. 1). As indicated in Figure 2, egg volume declined significantly with laying sequence for clutches of three, four, and five eggs, ($F_{1,109} = 28.23, P = 0.0001; F_{1,224} = 9.59, P = 0.002; F_{1,219} = 29.39, P = 0.0001$, respectively). Egg size declined significantly with date of nest initiation after controlling for clutch size and year effects ($F_{1,430} = 9.78, P = 0.0019$).

There was overlap in total estimated clutch volume among clutches of different sizes (Fig. 3). Clutch size explained 92% of the variation in total clutch volume ($r^2 = 0.918, P = 0.0001$). Absolutely and relatively more females laid clutches of fewer large eggs than vice versa in both zones of overlap. The range of average egg sizes was essentially the same for clutches of three, four, and five eggs (70.0–94.3 cm^3, 69.0–94.8 cm^3, 72.6–99.6 cm^3, respectively).

Repeatability and age-related variation.—Repeatabilities of egg size, clutch size and clutch volume of females older than three years were 0.78 ± 0.077 ($F_{24,27} = 8.444, P = 0.0001$), 0.14 ± 0.10 ($F_{74,92} = 1.359, P = 0.08$), and 0.14 ± 0.23 ($F_{17,19} = 1.347, P = 0.26$), respectively. Two-year-old females laid significantly smaller clutches of smaller eggs than did older females ($T^2_{2,289} = 15.97, P = 0.0004$). Additionally, two-year-old females initiated nesting significantly later than did older females ($t = 2.93$, df = 92, $P = 0.0042$). However, after restricting the analysis to females older than two years, egg size still declined with nest initiation date ($F_{1,61} = 6.41, P = 0.014$).

DISCUSSION

Predictive equations.—In 1989, the sample of unhatched eggs for which we determined volumes was significantly smaller than the entire sample of measured eggs. This suggests that smaller eggs had lower viability, or that females producing small eggs were less likely to hatch their clutches in that year. Similar observations of lower hatching success among small eggs have been reported in other birds (Martin and Arnold 1991). The range in volume of eggs for which we measured volume directly included all but 7 cm^3 of the range of predicted volumes of eggs we measured in nests. Thus, estimated egg volumes (based on linear measurements) were extrapolated only 7.3% above and 10.5% below the size range of eggs from which we
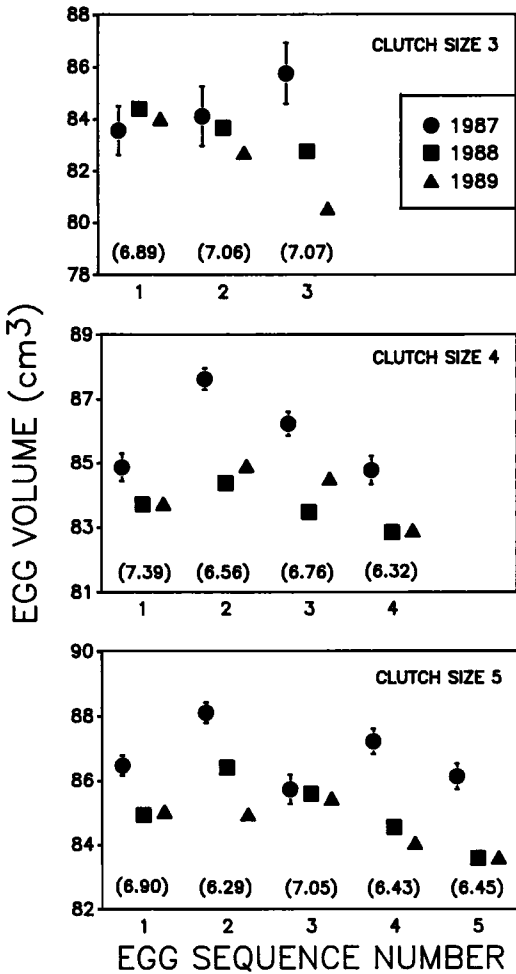
Fig. 2. Mean (±SE) egg volume versus laying se-
quence for clutches of three, four, and five eggs. There
was a significant difference in egg volume with laying
sequence within all clutch sizes (P = 0.0001, 0.002,
0.0001, respectively). Error bars less than 0.1 were not
plotted. Average coefficient of variation for each egg
number presented in parentheses. Minimum sample
size for each egg number in clutches of three, four,
and five eggs in 1987 were 6, 10, and 12, respectively.
Similarly, minimum sample sizes for 1988 and 1989
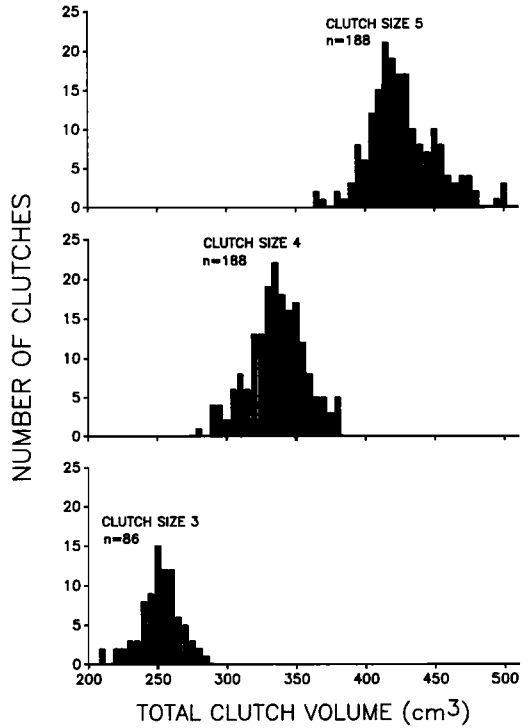were 67, 110, 85, and 32, 87, 103, respectively.

Fig. 3. Overlap in total clutch volume for clutches
of three, four, and five eggs. Zones of overlap define
ranges of reproductive investment where females with
different egg size phenotypes engage in trade offs
involving clutch size and egg size.

obtained our predictive equation. Further, the
lack of annual variation in the equations used
to estimate external volume from linear mea-
sures suggests that, while egg volume may have
varied, egg shape did not. Therefore, we believe
that the calculated external egg volumes in our
analysis provide accurate estimates of true egg
volumes.

Variation in shell thickness.—Annual variation
in the relationship between egg measurements
and internal shell volume must have been
caused by variation in patterns of egg-shell
thickness, because the relationship between ex-
ternal volume and egg measurements did not
exhibit such annual variation. Shells differed in
thickness between years at only one measured
point, which changed the internal volume rel-
ative to external measurements. The cause of
shell thinning in 1989 at one location on the
shell is unknown. Eggs were larger with re-
sulting larger shell surfaces in 1988 than in 1989,
which potentially magnified the between-year
difference in the amount of calcium deposited
in each egg. Annual variation in calcium avail-
able to females might have caused the variation
in shell thickness among years.

Within-clutch variation in egg volume.—The same
general relationship between egg size and po-
sition in the laying sequence that we observed
in Black Brant has been reported for Canada
Geese (*Branta canadensis maxima*, Cooper 1978;

B. c. moffitti, Leblanc 1987) and American Coots (*Fulica americana,* Arnold 1991). Also, Cargill (1979) reported that the last egg was the smallest in clutches of Lesser Snow Geese (*Anser caerulescens caerulescens*). The increase in size of the second egg relative to the first in clutches larger than three eggs may be related to physiological or morphological constraints on the size of the first egg. Parsons (1976) showed that egg size increased between the first and second egg in initial clutches of Herring Gulls (*Larus argentatus*), but not in clutches from renesting attempts, suggesting that the first-laid egg of the season is small, but not necessarily the first-laid egg in all clutches. However, the lack of an increase in egg size in three-egg clutches does not support this hypothesis, unless some fraction of three-egg clutches represent continuation clutches for which the first egg was laid elsewhere. This hypothesis can perhaps best be examined in captive waterfowl that can be induced to renest.

Consistent with Arnold (1991), we do not believe that the decline in egg size with laying sequence is a response to limited nutrient reserves (Alisauskas and Ankney 1985). Leblanc (1987) observed a similar pattern of declining intraclutch egg size among captive Canada Geese fed *ad libitum*. Further, variation among wild females in the total reserves available for laying should allow some females to lay a clutch with little or no reduction in egg size, while others could show a substantial decline in egg size. If declining nutrient reserves during egg laying explain the decline in egg size, then variation in the size of reserves available to individual females should increase the variation in egg size with increasing egg number, especially for the last-laid egg (Slagsvold et al. 1984). This is because some females should have more reserves remaining than required for one egg but insufficient reserves for two additional eggs. These females should lay large last eggs under the hypothesis that remaining reserves influence egg size. In contrast, females with fewer reserves than required for an average egg should lay a smaller egg. The net effect of these two influences would be increased variation in the size of the last egg. We did not observe increased variation in egg size with egg number (Fig. 2). Therefore, the nutrient limitation hypothesis is not consistent with the observed pattern of intraclutch variation in egg size.

Parsons (1972) hypothesized that the in-

traclutch decline in egg size in gulls may be an adaptation to synchronize hatch. We propose that this hypothesis may also apply to the intraclutch egg-size variation in Black Brant. First-laid eggs in Black Brant receive substantial incubation during the laying of subsequent eggs (P. L. Flint and M. S. Lindberg unpubl. data). Smaller eggs require less incubation (Worth 1940, Parsons 1972, Martin and Arnold 1991); thus, a reduction in egg size for later eggs in a clutch could help synchronize hatching within clutches.

Temporal and clutch-size-related variation in egg size.—Annual variation in egg size has been observed in Lesser Snow Geese (Newell 1988), Canada Geese (Cooper 1978), and Black Brant (Rohwer and Eisenhauer 1989). Cooper (1978) suggested that annual variation in the age structure of the population might explain variation in mean egg volumes among years. This could also explain the pattern we observed in Black Brant. Eggs hatched in only 2% and 7% of the nests on the Tutakoke River colony in 1984 and 1985, respectively (J. S. Sedinger unpubl. data). Nesting success increased substantially following removal of Arctic foxes (*Alopex lagopus*) beginning in 1986 (Anthony et al. 1991). Female Black Brant tend to return to their natal colony to breed (J. S. Sedinger and P. L. Flint unpubl. data); thus, the proportion of two- and three-year-old females in the breeding population should have increased during each year of this study. Because two-year-old females laid smaller eggs than older females, the reduction in egg size among years was associated with, and could have resulted from, a higher proportion of two- and three-year-old females in the breeding population in 1989. Rohwer and Eisenhauer (1989), however, observed annual variation in egg mass in a population of Black Brant that was relatively stable in size and, thus, could have had a stable age distribution.

The positive relationship between mean egg volume and clutch size found by us and by Rohwer and Eisenhauer (1989) could have resulted from variation in female age. Two-year-old females laid smaller clutches of smaller eggs compared to older females. The positive correlation between egg volume and clutch size may have resulted from the positive relationships between age and clutch size, and age and egg size (i.e. small clutches were disproportionately produced by two-year-old females who also laid smaller eggs).

The cause of the seasonal decline in egg size after accounting for age is unknown. Hill (1984) observed a comparable seasonal decline in egg size of Tufted Ducks (*Aythya fuligula*), which he attributed to younger females laying later. Age did not completely explain the seasonal decline in egg size in Black Brant, however, because egg size also declined with initiation date after two-year-olds were eliminated from the analysis. Thus, the observed decline was not strictly related to two-year-old females nesting later. However, age-specific variation in egg size of Black Brant has not been documented, and egg size may continue to increase beyond age 2. Additionally, previous breeding experience may influence egg size, and we could not control for experience. Thus, the effect of age and/or breeding experience on the seasonal decline in egg size deserves further consideration. An alternative hypothesis, that the reduction in egg size with laying date was caused by reduced nutrient reserves among late or delayed-nesting females, seems unlikely because the high repeatability of egg size (see below) suggests that females do not alter egg size in relation to their nutritional status.

Clutch size did not completely explain the variation in total clutch volume (Fig. 3). Clutches of different sizes overlapped in the volume of reserves invested. The relative size of the zones of overlap we observed in Black Brant are considerably smaller than those reported for Lesser Snow Geese (Ankney and Bisset 1976), despite the slightly smaller sample sizes for Lesser Snow Geese. The size of the zones of overlap is ultimately determined by variation in egg size in the population. The coefficient of variation in egg size we observed in Black Brant (0.063) is smaller than that reported for egg mass in Lesser Snow Geese (0.075; Newell 1988). Therefore, the smaller zones of overlap that we observed may be due to greater normalizing selection on egg size in Black Brant.

Repeatabilities.—The high repeatability of egg volume in Black Brant is consistent with that reported in other species of waterfowl (Batt and Prince 1979, Duncan 1987, Lessells et al. 1989). However, the high repeatability of a trait that may be related to fitness (P. L. Flint and J. S. Sedinger unpubl. data; Cole 1979, Newell 1988) is difficult to reconcile with theory (Mousseau and Roff 1987). The lower repeatability of clutch size is also consistent with the literature (Lessells et al. 1989) and the low repeatability of

clutch volume is probably a result of the low repeatability of clutch size. The repeatability for clutch volume could only exceed that for clutch size if females were flexible in their phenotypic egg size.

If stored nutrients limit clutch size, then the low repeatability of clutch size and clutch volume suggests that individuals are highly variable in their condition on arrival. Thus, while reserves are correlated with body size (Ankney and MacInnes 1978), condition of individual females at the start of laying must vary sufficiently among years to alter clutch size.

Our inability to detect egg dumping in clutches used in the repeatability analysis must have increased the within-female variation in our repeatability estimates of both egg size and clutch size. Thus, we may have underestimated the true repeatability of clutch size and egg size. Undetected partial predation had little effect on the estimated repeatabilities for egg size; however, it would have caused us to underestimate repeatability of clutch size.

Relationship between clutch size and egg size.— Consistent with our results, Rohwer (1988) and Rohwer and Eisenhauer (1989) failed to find negative phenotypic relationships between clutch size and egg size within several populations of waterfowl. Further, Lessells et al. (1989) did not find negative phenotypic or genotypic covariances between clutch size and egg size in Lesser Snow Geese. They argued that their results failed to support the hypothesis of a trade off between clutch size and egg size and, thus, the nutrient-limitation hypothesis for control of clutch size in waterfowl.

While we also failed to detect a trade off between clutch size and egg size, we find several points interesting. First, females laying different clutch sizes produce approximately the same range of egg sizes (Fig. 3). We expected that large-egg-size phenotypes would be less likely to lay large clutches, unless larger females lay larger eggs and have larger nutrient reserves. We have not, however, detected a relationship between body size and egg size in Black Brant (J. S. Sedinger unpubl. data).

Second, where clutch volumes overlap for clutches of different size (e.g. four and five eggs) females laying different clutch sizes are making the same investment in their clutches. In these zones of overlap, where investment in the clutch is held constant, there is a trade off between clutch size and egg size. Thus, trade offs have

not been found among individuals with different investments in their clutch (i.e. differences in mean egg size across clutch sizes) (Rohwer 1988, Rohwer and Eisenhauer 1989), yet they do occur among individuals with the same investment in their clutch (i.e. zones of clutch volume overlap). However, only the extreme egg-size phenotypes, a small proportion of the total population, are engaged in this second form of trade off.

Finally, the use of stored reserves, the high repeatability of egg size, and the low repeatability of clutch size are all conditions that should allow the detection of a trade off between clutch size and egg size among females with different investments in their clutch (Rohwer and Eisenhauer 1989). Thus, our inability to detect trade offs between egg size and clutch size among females with different investments in their clutches, argues against the nutrient-limitation hypothesis as the sole mechanism regulating clutch size in the Black Brant.

LITERATURE CITED

ALISAUSKAS, R. T., AND C. D. ANKNEY. 1985. Nutrient reserves and energetics of reproduction in American Coots. Auk 102:133–144.

ANKNEY, C. D. 1980. Egg weight, survival, and growth of Lesser Snow Goose goslings. J. Wildl. Manage. 44:174–182.

ANKNEY, C. D. 1984. Nutrient reserves of breeding and molting Brant. Auk 95:459–471.

ANKNEY, C. D., AND A. R. BISSET. 1976. An explanation of egg-weight variation in the Lesser Snow Goose. J. Wildl. Manage. 40:729–734.

ANKNEY, C. D., AND C. D. MacINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.

ANTHONY, R. M., P. L. FLINT, AND J. S. SEDINGER. 1991. Arctic fox removal improves nest success of Black Brant. Wildl. Soc. Bull. 19:176–184.

ARNOLD, T. W. 1991. Intraclutch variation in egg size of American Coots. Condor 93:19–27.

BATT, B. D. J., AND H. H. PRINCE. 1979. Laying dates, clutch size, and egg weights of captive Mallards. Condor 81:35–41.

BECKER, W. A. 1984. Manual of quantitative genetics. Academic Enterprises, Pullman, Washington.

CARGILL, S. M. 1979. Parental investment and hatching success in clutches of the Lesser Snow Goose (Anser caerulescens caerulescens). B.Sc. thesis, Univ. Western Ontario, London.

COLE, R. W. 1979. The relationship between weight at hatch and survival and growth of wild Lesser Snow Geese. M.Sc. thesis, Univ. Western Ontario, London.

COOPER, J. A. 1978. The history and breeding biology of the Canada Goose of Marshy Point, Manitoba. Wildl. Monogr. No. 61.

DIXON, W. J. 1985. BMDP statistical software manual. Univ. California Press, Berkeley.

DUNCAN, D. C. 1987. Variation and heritability in egg size of the Northern Pintail. Can. J. Zool. 65:992–996.

FALCONER, D. S. 1981. Introduction to quantitative genetics. Longman, London.

FINNEY, G., AND F. COOKE. 1978. Reproductive habits in the Snow Goose: The influence of female age. Condor 80:147–158.

HAMANN, J., AND F. COOKE. 1987. Age effects on clutch size and laying dates of individual female Lesser Snow Geese Anser caerulescens. Ibis 129:527–532.

HILL, D. A. 1984. Laying date, clutch size and egg size of the Mallard (Anas platyrhynchos) and Tufted Duck (Aythya fuligula). Ibis 126:484–495.

HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73–77.

LACK, D. 1947. The significance of clutch size in birds. Ibis 89:302–352.

LEBLANC, Y. 1987. Intraclutch variation in egg size of Canada Geese. Can. J. Zool. 65:3044–3047.

LESSELLS, C. M. 1986. Brood size in Canada Geese: A manipulation experiment. J. Anim. Ecol. 55:669–689.

LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. Auk 104:116–121.

LESSELLS, C. M., F. COOKE, AND R. F. ROCKWELL. 1989. Is there a trade off between egg weight and clutch size in wild Lesser Snow Geese (Anser c. caerulescens)? J. Evol. Biol. 2:457–472.

MacINNES, C. D. 1962. Nesting of small Canada Geese near Eskimo Point, Northwest Territories. J. Wildl. Manage. 26:247–256.

MANNING, T. H. 1978. Measurements and weights

of eggs of the Canada Goose, *Branta canadensis*, analyzed and compared with those of other species. Can. J. Zool. 56:676–687.

MARTIN, P. A., AND T. W. ARNOLD. 1991. Relationships among fresh mass, incubation time, and water loss in Japanese Quail eggs. Condor 93:28–37.

MOUSSEAU, T. A., AND D. A. ROFF. 1987. Natural selection and the heritability of fitness components. Heredity 59:181–197.

NEWELL, L. 1988.. Causes and consequences of egg weight variation in the Lesser Snow Goose (*Anser caerulescens caerulescens*). M.Sc. thesis, Queen's Univ., Kingston, Ontario.

PARSONS, J. 1972. Egg size, laying date, and incubation period in the Herring Gull. Ibis 114:536–541.

PARSONS, J. 1976. Factors determining the number and size of eggs laid by the Herring Gull. Condor 78:481–492.

RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96:234–252.

ROCKWELL, R. F., C. S. FINDLAY, AND F. COOKE. 1983.

Life history studies of the Lesser Snow Goose (*Anser caerulescens caerulescens*). I. The influence of age and time on fecundity. Oecologia 56:318–322.

ROHWER, F. C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. Auk 105:161–176.

ROHWER, F. C., AND D. I. EISENHAUER. 1989. Egg mass and clutch size relationships in geese, eiders, and swans. Ornis Scand. 20:43–48.

SEDINGER, J. S., AND P. L. FLINT. 1991. Growth rate is negatively correlated with hatch date in Black Brant. Ecology 72:496–502.

SLAGSVOLD, T., J. SANDVIK, G. ROFSTAD, O. LORENTSEN, AND M. HUSBY. 1984. On the adaptive value of intra-clutch egg size variation in birds. Auk 101:685–697.

THOMAS, V. G., AND H. C. P. BROWN. 1988. Relationships among egg size, energy reserves, growth rate and fasting resistance of Canada Goose goslings from southern Ontario. Can. J. Zool. 66:957–964.

WORTH, B. C. 1940. Egg volumes and incubation periods. Auk 57:44–60.