MUNDY, N. I., C. S. WINCHELL, AND D. S. WOODRUFF. 1996a. Tandem repeats and heteroplasmy in the mitochondrial DNA control region of the Loggerhead Shrike (*Lanius ludovicianus*). Journal of Heredity 87:21-26.

MUNDY, N. I., C. S. WINCHELL, AND D. S. WOODRUFF. 1996b. Genetic differences between the endangered San Clemente Island Loggerhead Shrike (*Lanius ludovicianus mearnsi*) and two neighboring subspecies demonstrated by mtDNA control region and cytochrome *b* sequence variation. Molecular Ecology 6: in press.

MUNDY, N. I., AND D. S. WOODRUFF. 1996. Polymorphic microsatellite markers in the Loggerhead Shrike (*Lanius ludovicianus*) isolated from a library enriched for CA repeats. Molecular Ecology 6: in press.

SMITH, E. F. G., P. ARCTANDER, J. FJELDSÅ, AND O. G. AMIR. 1991. A new species of shrike (Laniidae: *Laniarius*) from Somalia, verified by DNA sequence data from the only known individual. Ibis 133:227-235.

SRIKWAN, S., AND D. S. WOODRUFF. 1996. DNA sequence variation and hornbill conservation. In press *in* Proceedings of the 2nd International Asian Hornbill Workshop, Bangkok, Thailand.

TABERLET, P., AND J. BOUVET. 1991. A single plucked feather as a source of DNA for bird genetic studies. Auk 108:959-960.

WOODRUFF, D. S. 1990. Genetics and demography in the conservation of biodiversity. Journal of the Science Society of Thailand 16: 117-132.

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Influence of Hatch Date versus Maternal and Genetic Effects on Growth of Black Brant Goslings

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Size of goslings at the end of their first summer is an important determinant of their fitness (Cooch et al. 1991a, Sedinger et al. 1995) because size influences first-year survival (Owen and Black 1989, Sedinger et al. 1995), size as adults (Cooch et al. 1991a, Larsson and Forslund 1991, Sedinger et al. 1995), and fecundity (Sedinger et al. 1995). Size of goslings is strongly associated with their hatch date, because late-hatching goslings grow more slowly than those hatching earlier (Cooch et al. 1991a, Sedinger and Flint 1991, Larsson and Forslund 1992, Lindholm et al. 1994).

Slower growth by late-hatching goslings has been attributed to poor foraging conditions experienced by these goslings, which is associated with the typical seasonal decline of nutrient levels in tundra plants eaten by geese (Sedinger and Raveling 1986) or reduced food abundance owing to grazing (Sedinger and Flint 1991, B. Person unpubl. data). Cooch et al. (1991a) controlled for genetic effects on growth by examining goslings from the same females nesting on different dates among years, or in later years during a long-term decline in growth (Cooch et al. 1991b). Other studies, however, have been unable to exclude the possibility that parental quality, or genetic or maternal effects, covaried with hatch date. If poorer-quality phenotypes or genotypes nest later, then late-hatching goslings may grow more slowly because they represent inferior genotypes, the eggs they hatched from were of poor quality, or they had poor-quality parents. We experimentally delayed hatching dates of Black Brant (*Branta bernicla nigricans*; hereafter "Brant") eggs to test influences of genetic and maternal effects on gosling growth.

Methods.—We removed the first egg from Brant nests and held them at ambient temperature for one to three days during the egg-laying period in 1991-1993. These eggs were then placed into nests containing one egg. To ensure that experimental eggs hatched synchronously with their foster siblings, it was necessary to delay only first eggs and to transfer these eggs into nests containing single eggs because Brant females begin incubation after laying their second egg (Flint et al. 1994). Switched eggs, therefore, hatched one to three days ($\bar{x} = 2$ days) later than they would have if not switched. We compared growth rates of goslings hatching from delayed eggs with growth rates of goslings hatching naturally on the

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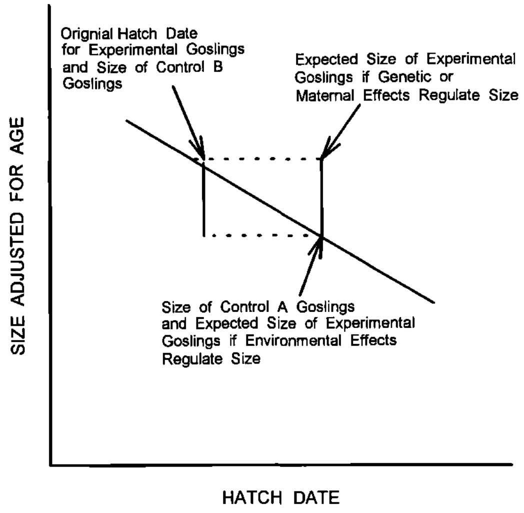

Fig. 1. Expected relationship between gosling size (adjusted for age) relative to hatch date. Under a hypothesis of seasonal variation in genetic or maternal effects on growth, delayed goslings are expected to be larger than unmanipulated goslings with whom they share a hatch date. If environmental factors regulate growth, delayed goslings are expected to be the same size as unmanipulated goslings with whom they share a hatch date. Under a hypothesis of environmental regulation of growth, delayed goslings are expected to be smaller than unmanipulated goslings sharing their expected pre-delay hatch date. Hypotheses shown here reflect either complete control by genetic-maternal effects or environmental effects. If both genetic-maternal and environmental effects influence growth, differences between delayed and control goslings would be intermediate to those shown. Effects of sex and year are not shown but would produce trajectories of size versus hatch date parallel to the one shown.

same date as switched eggs (Control A; Fig. 1) and with growth rates of goslings hatching naturally on the date switched eggs would have hatched if they had not been switched (Control B). If hatch date was the principal determinant of gosling growth rate, then delayed goslings would grow at a rate similar to unmanipulated goslings (Control A) hatching naturally on the same date. Under this hypothesis, delayed goslings would be the same size as Control A goslings when we controlled for sex, age, hatch date, and year. In contrast, if genetic or maternal effects were important determinants of growth rate, then experimentally delayed goslings would have grown faster than Control A goslings because of covariation between genetic and maternal factors, and nesting date. Under a hypothesis of covariation of genetic quality (or maternal effects) and nesting date, delayed goslings would have been larger when we controlled for sex, age, hatch date, and year. To assess our ability to detect treatment effects we performed an alternative analysis. We compared masses of delayed goslings with Control B goslings (hatching on the date on which delayed goslings would have hatched if they had not been delayed) while controlling for sex, age, year, and hatch date. In this analysis we predicted that delayed goslings would be smaller than Control B goslings sharing the same natural hatch date if environmental effects associated with hatch date were the principal influence on growth rate. We note that this experimental design does not control for effects of handling per se.

To estimate growth of experimental (delayed) and control goslings, we visited nests at hatching and placed web tags (Alliston 1975) on goslings. Broods were herded into corral traps during the adult flightless period when goslings were four to five weeks old. We weighed captured goslings (±10 g) using spring scales. We tested the null hypothesis that masses of goslings whose hatch dates were delayed did not differ from masses of Control A goslings using the General Linear Models procedure of SAS (SAS Institute 1985). In this analysis, year and sex were fixed factors and age, hatch date, and delay in hatch date were covariates. Although growth is a nonlinear process (e.g. Sedinger 1986, Sedinger and Flint 1991), growth is essentially linear over the range of ages (days) of goslings included in our analyses (Cooch et al. 1991a, Sedinger et al. 1995). Gosling size also declines approximately linearly with date (Cooch et al. 1991a, Sedinger and Flint 1991). We compared masses of delayed and Control B goslings using the same analysis, except that we used calculated pre-delay hatch dates (i.e. observed hatch date minus delay) for delayed goslings in the analysis. We restrict our analyses to mass, which is more sensitive to environmental conditions than linear measures such as tarsus length (Aubin et al. 1986, Cooch et al. 1991b, Sedinger and Flint 1991).

Results.—We captured 8 and 179 webtagged experimental (delayed) and control goslings, respectively, during banding in 1991–93. Experimental goslings averaged 28.4 ± SE of 1.5 days old (range 24 to 34 days) when captured, whereas control goslings averaged 30.6 ± 0.3 days old (range 23 to 38 days). Gosling mass at four to five weeks of age varied significantly among years and between sexes (Table 1). Mass declined significantly with increasing hatch date, but mass of delayed goslings did not differ significantly from that of Control A goslings hatching on the same date (Table 1). Masses of delayed goslings and Control B goslings that shared their original (i.e. pre-delay) hatch date were significantly different; delayed goslings were smaller than controls hatching on the original hatch dates of delayed goslings ($F = 4.33$, df = 1 and 180, $P = 0.04$; after controlling for year, sex, age, and hatch date). We estimated that experimental goslings were 39 ± 19 g smaller than Control B goslings (adjusted for age) for each day that

TABLE 1. Analysis of variance of effects of year, sex, hatch date, age, and experimental delay in hatch date on mass of Black Brant goslings (four to five weeks old) from the Tutakoke River colony.

Source	df	Type III SS	MS	*F*	*P*
Year	2	739,369	369,684	33.90	0.0001
Sex	1	47,970	47,970	4.40	0.0374
Hatch date	1	408,775	408,775	37.48	0.0001
Age	1	61,761	61,761	5.66	0.0184
Delay in hatch	1	874	874	0.08	0.7775
Error	180	1,963,121	10,906		

their hatch date was delayed. In contrast, experimental goslings were only 5.1 ± 18.2 g larger than Control A goslings (adjusted for age) for each day that their hatch date was delayed.

Discussion.—Our finding that male goslings were larger than female goslings is consistent with results of several other studies (Aubin et al. 1986; Cooch et al. 1991; Larsson and Forslund 1991, 1992; Sedinger and Flint 1991). Decline in gosling size, adjusted for age, with later hatch dates also is consistent with our earlier results (Sedinger and Flint 1991) and those of others (Cooch et al. 1991, Larsson and Forslund 1991, Lindholm et al. 1994). Lack of an effect on gosling mass of artificially delaying hatch date suggests that genetic variation or maternal effects account for little of the seasonal decline in growth rate.

Our statistical power to detect a treatment effect was diminished by the relatively small sample of experimental goslings we recaptured; the power to detect a significant effect of delaying hatch date of the magnitude we observed (5.1 g/day) was only 0.05 (Fig. 2). It is important to place this very low power in perspective. Artificial delay in hatch date, however, explained little variation (<0.1%) in gosling size. As an example of the minor effect of original (predelay) hatch date on size of experimental goslings, experimental goslings averaged 10.2 g (5.1 g/day × 2 days) larger than Control A goslings with whom they shared an actual hatch date. In contrast, the range of body masses for 33-day-old male goslings ($n = 10$) captured in 1993 was 445 g (395 to 840 g). The 33-day-old goslings in the 1993 sample all hatched within two days of each other, which could have explained as much as 38 g (based on hatch-date effects) of variation in these goslings. Accounting for hatch-date effects, experimental delay produced an effect that was only about 3% that of the variation in size owing to other sources. The relationship between power and treatment effect (Fig. 2) shows clearly that we had sufficient statistical power to detect treatment effects representing a significant proportion (20%) of variation in gosling size. Thus, we view our findings as indicating that genetic or maternal contributions to gosling quality accounted for little of the variation in gosling growth rate.

Cooch et al. (1991a) reported that gosling growth in Snow Geese (*Chen caerulescens*) was positively associated with brood size. Sedinger and Flint (1991) detected no brood effects on growth in Brant. Sample size for experimental goslings was too small to test for clutch (brood) size effects in this study. Experimental goslings hatched in nests with an average clutch size of five eggs, the largest common clutch size in Brant (Flint and Sedinger 1992). Therefore, the difference between experimental and Control B goslings cannot be attributed to a difference in brood size between the two groups.

This experiment strengthens the case for a primarily environmental explanation for the ubiquitous seasonal decline in growth rate among geese. We believe that seasonal decline in growth of goslings principally is driven by declining quantity and quality of food after hatch (Sedinger and Raveling 1986) because gosling growth is sensitive to availability of high-quality food (Larsson and Forslund 1991, Sedin-

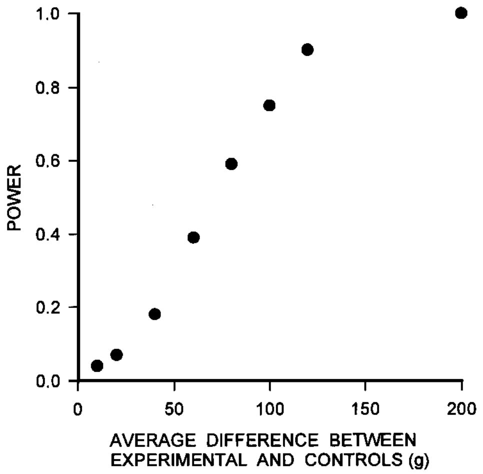

Fig. 2. Statistical power (Neter et al. 1990) to detect treatment effects for comparison of experimental goslings with both Control A and Control B goslings. Standard error of estimated treatment effects varied slightly between the two comparisons (18.22 and 18.95 for comparison with Control A and Control B, respectively). Treatment effects shown are the expected mass difference (difference in mass per day of delay × 2 days delay) between treatment and controls.

ger 1992, Cooch et al. 1993). We could not, however, exclude the role of parental quality in the seasonal decline in gosling growth (e.g. Mulder et al. 1995). If higher-quality adults (e.g. socially dominant) breed earlier than lower-quality adults (Daan et al. 1990), such adults might facilitate growth of their goslings by defending patches of higher-quality food. In our experiment, variation in parental quality associated with hatch date potentially was confounded with seasonally declining quality of foraging conditions for goslings. In Lindholm et al.'s (1994) study, goslings were reared in a common environment, separate from their parents. Therefore, a seasonal decline in growth rate in their study cannot be attributed to parental phenotype. We plan to assess the influence of parental behavior on gosling growth rate by switching entire clutches between early- and late-nesting pairs. If parental quality is an important determinant of gosling growth, then goslings from eggs provided to earlier-nesting adults should grow faster than those from later-nesting pairs.

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LITERATURE CITED

ALLISTON, W. G. 1975. Web-tagging ducklings in pipped eggs. Journal of Wildlife Management 39: 625–628.

AUBIN, A. E., E. H. DUNN, AND C. D. MACINNES. 1986. Growth of Lesser Snow Geese on arctic breeding grounds. Condor 88:365–370.

COOCH, E. G., R. L. JEFFRIES, R. F. ROCKWELL, AND F. COOKE. 1993. Environmental change and the cost of philopatry: An example in the Lesser Snow Goose. Oecologia 93:128–138.

COOCH, E. G., D. B. LANK, A. DZUBIN, R. F. ROCKWELL, AND F. COOKE. 1991a. Body size variation in Lesser Snow Geese: Environmental plasticity in gosling growth rate. Ecology 72:503–512.

COOCH, E. G., D. B. LANK, R. F. ROCKWELL, AND F. COOKE. 1991b. Long-term decline in body size in a Snow Goose population: Evidence of environmental degradation? Journal of Animal Ecology 60:483–496.

DAAN, S., C. DIJKSTRA, AND J. M. TINBERGEN. 1990. Family planning in the Kestrel (*Falco tinnunculus*): The ultimate control of covariation of laying date and clutch size. Behaviour 114:83–116.

FLINT, P. L., AND J. S. SEDINGER. 1992. Reproductive implications of egg-size variation in the Black Brant. Auk 109:896–903.

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.

LARSSON, K., AND P. FORSLUND. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619–636.

LARSSON, K., AND P. FORSLUND. 1992. Genetic and social inheritance of body and egg size in the Barnacle Goose (*Branta leucopsis*). Evolution 46: 235–244.

LINDHOLM, A., G. GAUTHIER, AND A. DESROCHERS. 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting Greater Snow Geese. Condor 96:898–908.

MULDER, R. S., T. D. WILLIAMS, AND F. COOKE. 1995. Dominance, brood size and foraging behavior during brood-rearing in the Lesser Snow Goose: An experimental study. Condor 97:99–106.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied linear statistical models, 3rd ed. Irwin, Homewood, Illinois.

OWEN, M., AND J. M. BLACK. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. Journal of Animal Ecology 58:603–617.

SAS INSTITUTE. 1985. SAS user's guide: Statistics, version 5. SAS Institute, Cary, North Carolina.

SEDINGER, J. S. 1986. Growth and development of Canada Goose goslings. Condor 88:169–180.

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. Journal of Animal Ecology 55:1083–1102.

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