

REPRODUCTIVE SUCCESS AND SURVIVAL IN RELATION TO EXPERIENCE DURING THE FIRST TWO YEARS IN CANADA GEESE¹

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Abstract. We studied the relationship between family associations of immature Canada Geese (*Branta canadensis*) and their reproductive success as 2-year-olds and survival to three years. A higher proportion of immature Canada Geese associated with family members survived to breeding age and were more successful in reproducing in their first potential year of sexual maturity (age 2) than were geese that were not in family associations. These results illustrate the benefits of prolonged parental care outweighing costs to parents and the probable influence of family association on future successful breeding. Many reproductive failures of vertebrates with complex social organization may be related to experience during maturation.

Key words: *Branta canadensis maxima*, *Giant Canada Goose*, *life-history*, *parental care*, *reproduction*, *social structure*, *survival*.

Monogamy and parental care of young are dominant features of avian social organization (Lack 1968) which are especially striking in geese and swans. In geese, fewer than 10% of pairs in which both members are alive separate permanently (Black et al. 1996). In Canada Geese (*Branta canadensis*), young typically remain with their parents through the first winter of life and frequently rejoin them as yearlings (Raveling 1969b, 1979), sometimes up to their fourth year (Raveling, pers. observ.). Family groups are dominant to other geese (Boyd 1953, Raveling 1970, Black and Owen 1989), which provides access to better foraging conditions in winter flocks (Raveling 1970, Teunissen et al. 1985, Black et al. 1992).

Geese mature sexually at 2 years of age, but frequently fail to breed successfully until 3- or 4 years of age (Brakhage 1965, Raveling 1981, Kendall and Nichols 1995). A 2- to 4-year-old Canada Goose that is successful in rearing a brood is three times more likely to be successful the next year than is an unsuccessful bird of the same age (Raveling 1981). Thus, early attainment of successful experience in reproduc-

tion is associated with subsequent productivity by a pair (Raveling 1981).

The above features of natural history, social organization, and reproductive success raise important questions about the evolution of such behavior in terms of costs and benefits of family organization, parental investment, and parent-young conflict (Trivers 1972). The short-term benefits to the young in close family associations seem clear; they are attacked less, feed more, and are assured of access to food and space in relation to the dominance position of their parents (Boyd 1953, Raveling 1970). Parents incur some costs in that they spend more time alert and less time feeding than pairs without young (Scott 1980, Black et al. 1992). In both swans and geese, parents are involved in greater amounts of aggressive interactions than are non-parents (Raveling 1970, Scott 1980). Implicit in this scheme is that experience gained by young in families enhances their social status (Black and Owen 1987), survival, and reproductive success at a later time (Lack 1968). These benefits must more than counterbalance the costs to parents if family cohesiveness is to be favored by natural selection.

Substantial variation exists among individuals in reproductive success, wherein some individuals are highly successful in producing young each year (Raveling 1981, Lamprecht 1986, Choudhury et al. 1996), whereas other individuals rarely succeed. Nesting and brood rearing success are related to a high degree of aggressiveness (Raveling 1981, Black and Owen 1987) as is access to food in winter flocks (Black et al. 1992). Pairs that are most attentive to their nests are more successful than less attentive parents (Harvey 1971, Inglis 1977). Raveling (1981) offered two, not mutually exclusive, explanations for these observations: (1) if there is a strong genetic component to the variation in behaviors contributing to reproductive success, then such variability might be interpreted as an adaptive polymorphism in which different behavior types obtain different success rates under different environmental conditions, especially a fluctuating or patchy distribution of different types of predators, and (2) the behavior of passive individuals that did not strongly defend their nests or young, or chose poor nest sites might be related to variables in social organization encountered during maturation. Under the second hypothesis, in-

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dividuals with poor reproductive success may not have received the benefits, described above, of being a member of a large, close-knit, aggressive family.

Here we examine the social environment experienced by Giant Canada Geese (*B. c. maxima*) during their first two years of life in relation to their survival and future reproductive success. These data bear on the questions raised above on the long-term benefits of family association and prolonged parental care.

METHODS

During 1968, 1969, and 1970, individually identifiable plastic neck-collars were placed on 1,406 Giant Canada Geese at the Marshy Point Goose Sanctuary on the edge of Lake Manitoba, Canada (50°30'N, 98°W). All geese were banded during July, August, or September before the opening of the local hunting season.

Results reported herein address reproductive success of geese during their first potential breeding season as 2-year-olds and the social environment experienced during their first and second years of life. We refer to geese <2 years old as immatures, although infrequent nesting by 1-year-old Giant Canada Geese occurs in a more southern population (Drobney et al. 1999). Success in reproduction was defined by the presence on the breeding area of a brood (at least one young) that had fledged. Individuals classified as successful breeders were observed at least twice with fledged young. Association of a marked goose with family members was identified when possible whenever a marked bird was observed at any time of the year and was based on behavioral criteria, which were: unity in local movements, preflight and flight behavior, and in agonistic encounters; acceptance or tolerance by other geese, especially adult males; performance of the "triumph ceremony," a conspicuous display exhibited by family-related birds (Fischer 1965, Raveling 1969a, 1969b, 1970).

Social experience of immatures was determined from August to March–April 1968–1971. Geese were observed on the breeding grounds an average of two times per week before they migrated in autumn. The primary winter location for this population was Rochester, Minnesota which Raveling visited for 1-week periods each October, November, and March to record presence and behavior of marked geese (Raveling 1978, 1979). Additional visits to Rochester were made in February 1969, December 1969 and 1970, and January 1970. Overall, social status of immature geese was determined an average of 20 times (range 2–44) during the first two years. Breeding success of known-age 2-year-olds was determined during August–September 1970 and only during an intensive 1-week observation period in mid-September 1971 and 1972 before the hunting season opened.

We used resighting of neck-collared individuals as an index of survival. Because a substantial number of birds lost their identifying collar (up to 25% per year, Raveling 1978), the results are more strictly those geese surviving, which retained their neck-collar, and were observed. Therefore, our results underestimate true local survival (Lebreton et al. 1992). Unless neck-collar retention was related in some unknown manner to social status, the results should be an unbiased com-

parison of survival of geese experiencing different family associations.

Many geese were not identified as to their social category because of few observations or the lack of behaviors allowing us to classify their social status. Single geese, that is, those without parents or siblings, were difficult to identify because they seldom exhibited agonistic or triumph ceremony behaviors that were the most reliable indicators of social relationships. We believe that many of the geese in the "unknown" status category were singles and they have been combined in the single category in survival analyses. Thus, in analyses of the relationship between social status during the first 2 years of life and survival, we contrast individuals known to be in a family unit during winter with those that were not.

DATA ANALYSES

We used logistic regression to directly relate reproductive success as a 2-year-old to family status during the first or second year of life. We did four separate analyses of this type. In each case, presence of goslings before fall migration following the third summer (reproductive success as a 2-year-old) was the response variable. Independent variables in these analyses were proportion of observations an individual was with other family members or the mean number of family members an individual was observed with during both the first and second years of life. Thus, we performed four analyses with either proportion of observations with other family members or mean number of family members individuals were observed with during their first or second years of life as the independent variable. Analyses using observations from the first and second years of life were not independent, as the same individuals, with one exception, were used in both analyses. We used likelihood-ratio tests comparing full regression models, intercept plus independent variable, against models containing only the intercept to test hypotheses about the effects of the independent variable on reproductive success.

RESULTS

SOCIAL EXPERIENCE AND FUTURE REPRODUCTIVE SUCCESS

We recorded reproductive success for 43, 2-year-old females for whom we also recorded family status in their first year and 40 females for whom we recorded family status in their second year. Six of the 43 females for which we observed family status in their first year had young in their third fall, and 6 of 40 females observed in their second year had young in their third fall. Likelihood-ratio tests showed that probability of successfully producing young was significantly related to mean family size in the first ($\chi^2_1 = 72.3, P < 0.001$) and second years ($\chi^2_1 = 58.3, P < 0.001$). Probability of successfully producing young was significantly related to the proportion of time immature Canada Geese spent with other family members in both their first ($\chi^2_1 = 61.0, P < 0.001$) and second years ($\chi^2_1 = 107.5, P < 0.001$).

Only 2-year-old females associated with other family members >75% of the time in their first or second years successfully produced young (Fig. 1). Individuals associated with ≥ 4 other family members in their

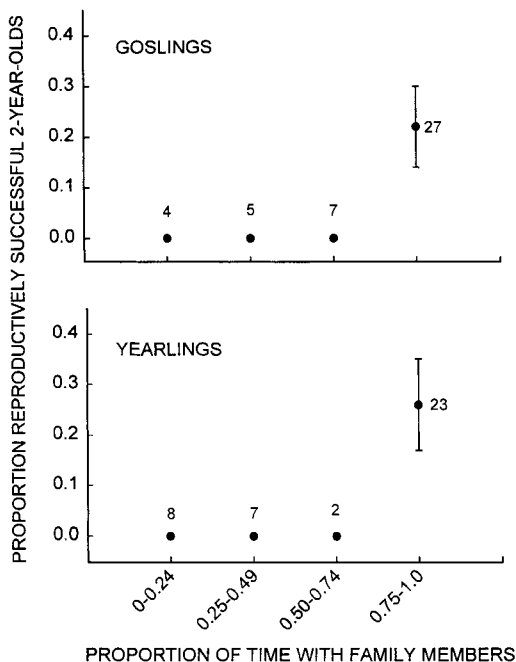


FIGURE 1. Relationship between proportion of observations of female Giant Canada Geese with other family members during their first (gosling) or second (yearling) summer-winter and the probability these females were observed with goslings as 2-year-olds. Sample sizes are adjacent to data points. Error bars are standard errors. Data have been pooled into categories for graphical presentation in Figures 1 and 2, but logistic regression was performed on individual data points.

first year were substantially more likely than other females to successfully breed as 2-year-olds (Fig. 2).

SOCIAL EXPERIENCE AND SURVIVAL

Single immature Canada Geese, or those that were unidentified as to social status, were 1.44 times more likely to die or disappear than immatures raised in a family (Table 1). As Canada Geese are a prized game species, a major portion of this mortality in the first year of life is related to hunting. Forty of the 548 (7.3%) banded immatures identified as being in families were shot and the band numbers were reported to the U.S. Fish and Wildlife Service compared to 81 recoveries of the 489 (16.6%) single or unidentified-status immatures. Therefore, singles and unidentified-status young geese were 2.28 times more likely to be shot by hunters than young in families. Young geese and single geese typically make up a disproportionately large component of the birds shot by hunters (Hanson and Smith 1950).

The large effect of social status on survival during the first year of life was not apparent thereafter (Table 1). The rate of disappearance between the first and second year of life of young that had been raised in families (39.8%) was nearly identical to the disap-

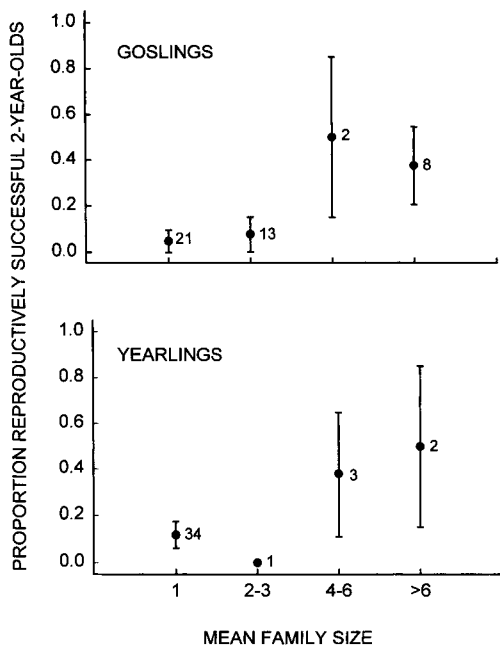


FIGURE 2. Relationship between the mean size of the family units within which female Giant Canada Geese were observed during their first (gosling) or second (yearling) summer-winter and the probability these females were observed with goslings as 2-year-olds. Sample sizes are adjacent to data points.

pearance of nonfamily yearlings (36.7%) ($\chi^2_1 = 0.5, P > 0.4$). Similarly, the disappearance rates of geese between 2 years of age (when they are first capable of reproduction) and 4 years of age (when they began to be most successful in reproduction; Raveling 1981) were nearly identical ($\chi^2_1 = 0.2, P > 0.6$) for geese that had been raised in families (54.3%) and for nonfamily raised geese (56.6%). The greater mortality incurred by nonfamily geese during their first year of life resulted in a significantly smaller proportion of them in the population in future years compared to geese raised in families (Table 1).

DISCUSSION

IDENTIFICATION OF SOCIAL CLASSES

Although we believe most geese in the unidentified social category were singles, a proportion of these

TABLE 1. Survival of Canada Geese in relation to their social organization experienced as immatures.

Status as immature	n	% surviving to ^a		
		age 1	age 2	age 3
Family	548	63.0	38.0	17.3
Single or unidentified	489	46.8	29.7	12.9
<i>P</i> ^b		<0.001	<0.01	<0.05

^a Through breeding season at that age.
^b χ^2 test.

geese were probably members of families. Raveling depended most upon observing marked individuals in unified activities, especially in agonistic encounters, or a family in the triumph ceremony to identify social relationships. The proportion of the day occupied by such activities was relatively small. Therefore, to the extent the unidentified class contained some individuals that should have been in the family class, our comparison of survival between single individuals and those in families was conservative. That is, if family young in the unidentified class behaved and survived in a manner equal to those identified in the family category, then the chances of survival for the true singles and very weak family associated young must be even poorer than indicated in the tables.

SOCIAL EXPERIENCE AND FUTURE FITNESS

Ganders with large families are the most dominant individuals in a flock, and young geese assume the dominance status of their gander, but only when the family is close together (Fischer 1965, Raveling 1970). Large families have priority in access to food and loafing sites (Raveling 1970). Single geese, especially immatures, are the most submissive individuals in a flock and they are repeatedly rebuffed by other geese (Raveling 1970).

In Barnacle Geese (*B. leucopsis*), goslings with more aggressive parents were themselves more aggressive (Black and Owen 1987). Young geese that experienced long-term stability in family associations, especially the benefits of being a member of a large family, were most successful at rearing a brood as 2-year-olds, possibly because they maintained higher body masses during their first two winters than other immature geese (Black and Owen 1989). Thus, prolonged close family association was related to increased chances for offspring to reproduce at an earlier age, and probably for them to be repeatedly successful in the future. Even among the oldest geese, some individuals were more frequently successful than others (Raveling 1981). As a result, about 17% of the breeding-age geese raised 50% of the young and formed the productive core of the population (Raveling 1981).

Young that were obviously associated with families enjoyed a much greater probability of surviving to maturity than those not so associated. Even though much of this mortality was caused by hunting, it is reasonable to assume that nonfamily young also were more vulnerable to "natural" predators as well as other sources of mortality. Young in families no doubt benefit from the vigilance of adult males.

EXPERIENCE VS. GENETIC CONTROL OF VARIABILITY

Variation in successful breeding by individuals at their first opportunity, which is associated with subsequent success in rearing young (Raveling 1981), is strongly related to family associations during maturation. Goslings from large Barnacle Goose broods grew faster and survived fall migration better than goslings from small broods, which resulted primarily from effects of brood size itself, rather than covariance between brood size and other variables (Loonen et al. 1999). In unmanipulated broods, clutch size, and consequently brood size, is strongly influenced by environmentally-

determined individual quality (Sedinger et al. 1995). Because high-quality individuals repeatedly nest early in the season (Findlay and Cooke 1982) and lay large clutches (Findlay and Cooke 1987, Larsson and Forslund 1992), the potential exists for some females to repeatedly produce large clutches. Although existing data do not allow a quantitative estimate of the contribution of additive genetic variance to these traits, it is difficult to explain maintenance of genotypes that continually fail to recruit offspring into the breeding population. Therefore, we favor the hypothesis that family size and association are important environmental determinants of fitness for young geese. Simply put, some geese may not be capable mates, or capable nest or brood defenders due to their experiences while young.

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