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EGG MASS, POSITION IN THE LAYING SEQUENCE, AND BROOD SIZE IN RELATION TO CANADA GOOSE REPRODUCTIVE SUCCESS

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ABSTRACT.—To better understand the effects of egg mass and position in the laying sequence on reproductive success of Canada Geese (*Branta canadensis*), I determined the fate of eggs, marked embryos near hatching, and recaptured goslings near fledging. Hatching success did not correlate with egg mass and position in the laying sequence. The probability of recapturing marked goslings near fledging was not associated with relative egg mass or position in the laying sequence. These results suggest that egg mass and position in the laying sequence have no short-term implications for the fitness of the chick produced. A reduced survival rate of goslings in larger broods in one year suggests that brood size could be a factor limiting clutch size in Canada Geese. *Received 17 Mar. 1986, accepted 16 Mar. 1987.*

Hatching and fledging success in Anserinae can be reduced by extrinsic (environmental) factors such as predation (Vermeer 1970, Cooper 1978), climate (Cooper 1978), and intraspecific competition (Ewaschuk and Boag 1972). Intrinsic factors such as egg size, egg quality, and position in the laying sequence have been shown to correlate with hatching and fledging success in some nidicolous species (Parsons 1970, Murton et al. 1974, Howe 1976, O'Connor 1979, Rofstad and Sandvik 1985) but in contrast, little is known regarding these factors for nidifugous species. Brood size also influences fledging success in some nidifugous species (Safriel 1975, Andersson and Eriksson 1982), but not in others (Heusmann 1972, Glasgow 1977, Clawson et al. 1979, Rohwer 1985).

Here, I examine the effects of egg size and position in the laying sequence on hatching and fledging success of Canada Geese (*Branta canadensis*). I address the following questions: (1) Are hatching and fledging success related to egg mass at laying and position in the laying sequence? (2) Does brood size at hatching correlate with brood size near fledging?

STUDY AREA AND METHODS

The study was carried out in 1983 and 1984 near Brooks, Alberta (50°35′N, 111°54′W). From late March to early May each year, I searched for nests daily at Gleddie Lake. In six other reservoirs nearby, I searched for nests every 2 to 4 days. Nearly all nests had 1 or 2 eggs when found, although some had 3. When more than 1 egg was found in a nest, the degree of staining of eggs was used to assess the order of laying (Cooper 1978). Subsequent

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visits to the nest allowed me to determine the position in the laying sequence of additional eggs. Upon discovery, each egg was weighed with a spring scale and its maximum length and breadth were measured with vernier calipers to the nearest 0.1 mm. I considered a clutch successful if at least 1 egg hatched. In each successful clutch, the fate of each egg was classified as successful, disappeared or preyed upon, broken, incubated but not hatched, deserted, or flooded. I considered an egg successful if a gosling emerged from the shell.

At Gleddie Lake, I marked individual members of most broods at the time the eggs were pipped, by tagging each embryo in the egg with a numbered web-tag (after Alliston 1975). I marked 171 goslings from 32 broods in 1983 and 151 from 29 in 1984. Banding drives were conducted 8 and 6 weeks after the peak of hatching in 1983 and 1984 respectively, to capture flightless adults and goslings. All goslings were examined for the presence of a web-tag.

In 1984 at other reservoirs, 44 clutches of 6 eggs with the completed laying sequence known were removed from their nests during the last week of incubation and placed in an incubator at the Brooks Wildlife Center.

I defined hatching success as the proportion of eggs surviving to the time of hatching that produced a chick (Cooper 1978, Koenig 1982). Brood size was defined as the number of goslings leaving the nest. Because most of the mortality of goslings occurs during the first 2 weeks of life (e.g., MacInnes et al. 1974, Zicus 1981), I considered the number of goslings reaching fledging age as the number recaptured.

The effect of position in the laying sequence and egg mass on hatching and fledging success were analyzed with 3-way contigency tables (Sokal and Rohlf 1981). The position in the laying sequence of each egg was classified as being either first, middle, or last laid. I also assigned each egg to two categories of sizes: small, if the fresh mass was below the mean value for both years of study (i.e., 163 g), or large, if equal or above this value. The significance of an interaction was tested by a test of partial association (Dixon et al. 1983). To control for sources of between year variation in the analysis of the relationship between the percentage of goslings recaptured per brood and mean egg mass, I standardized means of egg masses per clutch by subtracting from each mean egg mass the grand mean for the year it was taken.

RESULTS

Hatching success.—A total of 118 nests (67 in 1983; 51 in 1984) were discovered and followed through the hatching period at Gleddie Lake. Broken eggs in 7 nests that were not attributable to predation or strife between adjacent territorial pairs were not different in mass from the intact eggs of their clutch (Wilcoxon signed-ranks test; $T = 0.507$, $P > 0.30$). Thirty-three and 30 clutches were successful in 1983 and 1984, respectively. Because there were no differences between naturally and artificially incubated clutches in the proportion of unsuccessful eggs (G-test; $G = 0.961$, df $= 2$, $P > 0.50$), I combined these data to increase sample sizes. Hatching success was independent of the position in the laying sequence and the relative size of the egg (Table 1). Moreover, of successful clutches in which at least one fully incubated egg did not hatch (N = 33), the mean mass of these unhatched eggs was not different from the mean mass of successful eggs within the same clutch ($T = 0.90$, $P > 0.35$, N = 33).

TABLE 1
HATCHING OF EGGS IN RELATION TO THEIR POSITION IN THE LAYING SEQUENCE AND THEIR RELATIVE SIZE, 1983–1984

		Number		Partial association[a]			
Position	Size	Hatched	Unhatched	Effect	df	G	P
First	Below mean[b]	59	3	HSP[c]	2	4.81	0.071
First	Above mean	30	4	HS	1	0.63	0.320
Middle	Below mean	173	12	HP	2	1.86	0.355
Middle	Above mean	178	9	SP	2	13.00	0.002
Last	Below mean	60	3				
Last	Above mean	27	6				

[a] Interaction among variables.
[b] $\bar{x} = 163$ g.
[c] Test of partial association of a 3-way contingency analysis, factors: H, hatching success; S, size of the egg; P, position in the laying sequence.

Fledging success.—There was no relationship between the size of a brood and its probability of disappearing in 1983 (Table 2). In 1983 mean egg mass of clutches in which at least one gosling was recaptured was smaller than that from clutches in which no goslings were recaptured (t-test; $t = 2.40$, df $= 30$, $P = 0.02$), but there was no difference in 1984 ($t = 1.27$, df $= 27$, $P = 0.22$). Among the 40% (13/32: 1983) and 34% (10/29: 1984) of broods in which no goslings were recaptured, a high percentage had probably moved overland to other areas or simply fledged and left the study area by the date of the banding drive (see Giroux 1980).

To reduce the bias created by departures of broods from the study area, the following analyses were performed on the set of data that includes only broods in which at least one gosling was recaptured. There was no significant correlation between age of the brood and percentage of goslings recaptured in both years of study (Spearman rank correlation, 1983, $r_s = -0.04$, $P = 0.86$, N = 19; 1984, $r_s = -0.16$, $P = 0.52$, N = 19). The probability of a gosling being recaptured was independent of its position in the laying sequence and the relative size of the egg from which it hatched (Table 3). Within each clutch, there was no difference between the mass of eggs from which recaptured and not recaptured goslings hatched both in 1983 ($t = 0.283$, $P > 0.75$, N = 19) and 1984 ($t = 0.440$, $P > 0.66$, N = 19). In addition, the percentage of goslings recaptured in a clutch was not related to standardized mean egg mass of the clutch (Fig. 1).

The effect of brood size on survival rates was investigated by comparing brood size at hatching with the number of goslings recaptured per brood. The number of goslings recaptured per brood was not statistically different among brood sizes in either year, nor in the 2 years combined (Table 4).

TABLE 2

NUMBER OF BROODS RECAPTURED AS A FUNCTION OF BROOD SIZE IN THE STUDY AREA, 1983–1984

Year		Brood size 1	3	4	5	6	7	8	G^a	df	P
1983	Recaptured	1		4	7	5	1	1	1.68	2	>0.25
	Not recaptured	1		5	2	4	1	0			
1984	Recaptured		2	6	4	5	2	0	1.16	2	>0.50
	Not recaptured		2	1	4	2	1	0			
1983–1984 combined	Recaptured	1	2	10	11	10	3	1	0.03	2	>0.97
	Not recaptured	0	2	6	6	6	2	0			

[a] Sizes of brood were grouped in 3 classes: ≤4 goslings; 5 goslings; ≥6 goslings.

To see whether larger broods lost proportionately more goslings than did smaller broods, I tested whether the slope of a regression line drawn through the logarithms of the number recaptured and the initial brood size differed from one (after Ricklefs et al. 1978). I found that larger broods lost proportionately more goslings than did smaller broods ($t = 2.69$, df = 17, $P = 0.02$) in 1984, but not in 1983 ($t = 1.77$, df = 17, $P = 0.09$).

DISCUSSION

Effect of egg mass on hatching and fledging success.—Egg mass does not correlate with hatching success for Canada Geese (this study), Lesser Snow Geese (*Chen caerulescens caerulescens*; Cargill 1979), Red Grouse (*Lagopus lagopus scoticus*; Moss et al. 1981), and Ring-billed Gulls (*Larus delawarensis*; Ryder 1975). Wang (1982) reported that unhatched eggs were 3.2 g lighter on average than hatched ones for Giant Canada Geese (*B. c. maxima*). He suggested that small females that were in poorer condition laid smaller eggs and left their nest more often exposing eggs to cold stress. In Mallards (*Anas platyrhynchos*), large incubated eggs were more resistant (higher % of them hatching) to prolonged exposure at 0°C than were small eggs (Batt and Cornwell 1972). Natural differences in mass of eggs of Canada Geese may be not large enough to affect hatching success significantly in years of normal weather.

Larger eggs produced larger chicks in Canada Geese (Leblanc 1986), Snow Geese (Ankney 1980), and Mallards (Rhymer 1982). Larger precocial chicks survived longer than smaller chicks in controlled experiments (Ankney 1980, Moss et al. 1981, Rhymer 1982). In a natural environment, Cole (1979) showed that in one year larger Snow Goose goslings survived better than did smaller ones. The following year, how-

TABLE 3
NUMBER OF GOSLINGS THAT WERE RECAPTURED AT PREFLEDGING IN RELATION TO THEIR POSITION IN THE LAYING SEQUENCE AND THEIR RELATIVE SIZE (DETERMINED BY EGG MASS AT LAYING), 1983–1984

		Persistence		Partial association[a]			
Position	Size	Recaptured	Not recaptured	Effect	df	*G*	*P*
First	Below mean[b]	8	12	PeSP[c]	2	3.59	0.166
First	Above mean	9	4	PeS	1	0.39	0.534
Middle	Below mean	25	18	PeP	2	2.99	0.225
Middle	Above mean	41	37	SP	2	10.42	0.006
Last	Below mean	6	14				
Last	Above mean	6	7				

[a] Interaction among variables.
[b] $\bar{x}$ = 163 g.
[c] Test of partial association of a 3-way contingency analysis, factors: Pe, persistence; S, size of the egg; P, position in the laying sequence.

ever, the pattern was reversed, with smaller chicks surviving better than larger ones. Other researchers have found no relationship between survival of the chick and egg size (Herring Gulls [*Larus argentatus*], Davies 1975; Kittiwakes [*Rissa tridactyla*], Barrett and Runde 1980; Great Skuas [*Catharacta skua*], Williams 1980; and Canada Geese, this study). Egg mass may influence survival in Canada Geese, but because the effect may be small, detecting it can be difficult (Rotenberry and Wiens 1985). As for hatching success, the effect of egg mass on fledging success may depend on the occurrence of infrequent, but severe, environmental conditions, and its importance may only be revealed during "bottle-neck" years.

Effect of position in the laying sequence on hatching and fledging success.—The first egg of a clutch had poorer hatching success than all other eggs in Giant Canada Geese (Cooper 1978, Wang 1982). Seven failed eggs were either the last laid or second last laid egg in the Hooded Crow (*Corvus corone*) (Rofstad and Sandvik 1985). The second and the third egg were more successful in producing young than the first or the fourth egg in the Shag (*Phalacrocorax aristotelis*) (Snow 1960). In these studies, however, the presence of a relationship between egg mass and position in the laying sequence precluded determining which one of these 2 factors was the most important. If egg quality is associated with position in the laying sequence, some eggs from particular positions may be more likely to fail. Parental protection may also differ among eggs of different positions because females are progressively more attentive to their nest during laying (Cooper 1978). These factors, however, did not seem to play an important role in

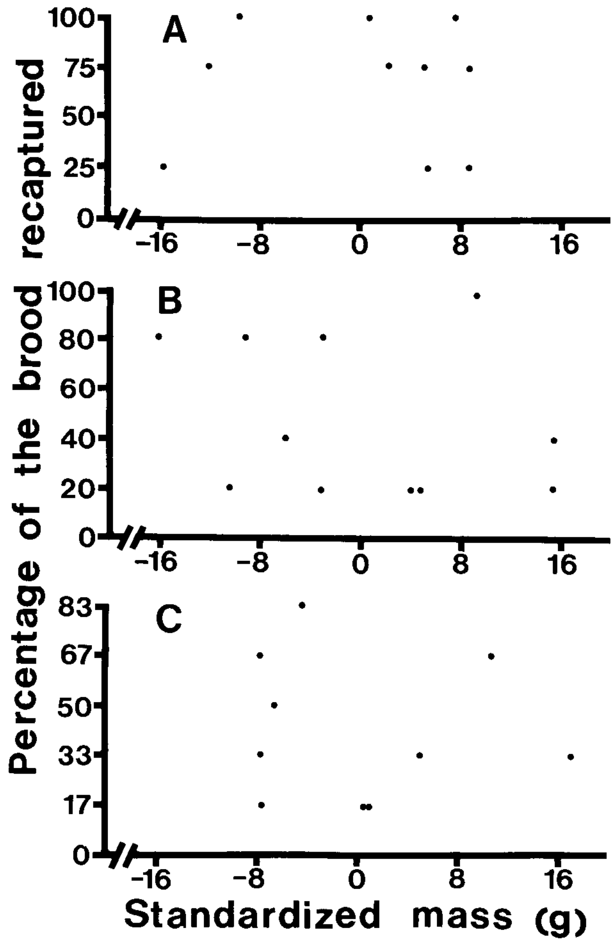

FIG. 1. Relationship between standardized mean egg mass (see text for method of standardization) and percentage of the brood recaptured in broods of 4 (A), 5 (B), and 6 (C) Canada Goose goslings. Spearman rank correlation, A, $r_s = 0.07$; B, $r_s = 0.07$; C, $r_s = 0.06$.

my study, as hatching success was not associated with position in the laying sequence.

In precocial species, hatching usually occurs synchronously (within 12 h), allowing the entire brood to leave the nest simultaneously. Thus, differences in hatching times are small relative to those found in many altricial species. Slight differences in hatching time, however, could be reflected in different levels of awareness in the gosling and also in different

TABLE 4

AVERAGE NUMBER OF GOSLINGS RECAPTURED IN DIFFERENT SIZES OF BROOD, 1983–1984

Brood size[a]	1983			1984			Years combined		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
1	1.00		1				1.00		1
3				3.00	0.00	2	3.00	0.00	2
4	2.50	1.00	4	2.83	1.47	6	2.70	1.25	10
5	2.57	1.72	7	2.00	1.41	4	2.36	1.57	11
6	2.40	1.14	5	2.60	1.82	5	2.50	1.43	10
7	3.00		1	2.00	1.41	2	2.33	1.15	3
8	3.00		1				3.00		1
P[b]		0.87			0.86			0.90	

[a] Number of goslings leaving the nest.

[b] Determined by a Kruskal-Wallis one-way ANOVA, comparing numbers of goslings recaptured per brood.

degrees of imprinting. Because last laid eggs hatch last (Cargill and Cooke 1981, Syroechkovsky 1975; but see Cooper and Hickin 1972), goslings from these eggs are probably the most likely to suffer mortality. Syroechkovsky (1975) found that late-hatched goslings of Snow Geese experienced higher mortality rates than did other goslings in the brood. In his study, however, the last laid eggs were also the smallest eggs. Position in the laying sequence may not reflect the potential for reaching fledging age in precocial species because there is a strong selection for synchronous hatching. This tends to reduce the advantages given by early positions in the laying sequence. Therefore, it remains to be demonstrated that position *per se* also affects fledging success in precocial species.

Effect of brood size on fledging success.—Although in 1983 larger broods did not produce proportionately the same number of goslings as did smaller broods on the study area, the underlying causes of this phenomenon are not understood. Such lower survival rates for larger broods have also been documented in Common Goldeneye ([*Bucephala clangula*], Andersson and Eriksson 1982) and in experimental larger broods of Semipalmated Sandpipers ([*Calidris pusilla*], Safriel 1975). Rohwer (1985) found no effect of brood size on survival rates of Blue-winged Teal ducklings (*Anas discors*). Other researchers that compared abnormal brood sizes to normal brood sizes did not detect any differences in survival rates between these two groups (Heusmann 1972, Clawson et al. 1979).

Crèching behavior occurred in my study area. Larger broods may not have joined other broods as early as did smaller broods. Consequently, they may not have taken advantage of the dilution effect against predation (Munro and Bédard 1977). Larger broods also may have been easier for predators to detect (Safriel 1975) and attack. Although these explanations may be valid, I have no data that indicate that predation was an important factor of mortality.

The clutch size of Anserinae appears to be primarily limited by the amount of reserves females can carry to the breeding grounds at high latitudes (Ryder 1970, Ankney and MacInnes 1978, Raveling 1979). However, my results on reduced survival rates with increased brood size imply selective pressure against larger clutches of Canada Geese. The survival rate of broods, along with the amount of body reserves available prior to laying, may have contributed to the evolution of clutch size in Canada Geese in similar environments. Other studies are needed to investigate this factor.

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