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Does Sex Ratio Vary with Egg Sequence in Lesser Snow Geese?

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In a recent paper Ankney (1982) documents from a sample of 29 4-egg clutches of Lesser Snow Geese (*Chen caerulescens*) that the first 2 eggs generally produce male goslings and the last 2 generally produce females. This unusual finding led him to postulate three possible mechanisms to explain the data. These are (1) nonrandom segregation of the sex chromosomes in the heterogametic sex (female) at the time of oogenesis, (2) earlier and/or faster growth of those ovarian follicles that subsequently produce males, and (3) temperature-influenced sexual differentiation in the egg.

In an attempt to investigate this phenomenon further and to discriminate among the possible explanations, we analyzed the data collected between 1975 and 1981 at the La Pérouse Bay nesting colony of Lesser Snow Geese in northern Manitoba.

The data are presented in essentially the same format as those collected by Ankney. The eggs in this study were not incubator hatched, however, and goslings were sexed only at approximately 5 weeks of age. In order to know the egg sequence and sex of resulting goslings, we had to check nests daily that had been found at the one-egg stage, number the eggs as they appeared in the nest, visit these nests at least once during the hatch period, and mark individual goslings with a small metal web tag. The egg from which the gosling hatched was recorded, but this was possible only when the gosling had not completely detached itself from the shell (approximately 50% of all goslings can be so recorded). We rounded up and banded the goslings at 4-5 weeks of age. Web-tagged goslings were sexed by cloacal examination at this time. Of the web tagged families, 25-50% were recaptured. Some of the goslings in those families had disappeared, mainly due to predation. Because Lesser Snow Geese females occasionally lay eggs in the nests of other individuals (Cooke and Mirsky 1972), it is clear that some of the

eggs recorded in this study were not laid by the female who was the owner of the nest. During the 7 years of this study, however, the frequency of this nest parasitism has not exceeded 9% (Cooke et al. unpublished) and is unlikely to have influenced the results. Obvious cases of dump eggs were removed from the sample.

We examined only those families from nests with original clutch sizes of 3 through 6. A total of 280 families with one or more goslings the egg sequence of which was known was available for analysis (Table 1). For none of the clutch sizes is there a correlation between sex ratio and egg sequence. Because the data were collected in the field and because the goslings were not sexed until 5 weeks of age, the number of incomplete families is considerable, and there is the possibility that differential mortality at the egg or gosling stage obscured the effect described by Ankney. Sex and sequence information was available on only 54% of the 1,218 eggs laid in the families reported in Table 1, whereas 82% of the 116 eggs in Ankney's study were both sexed and sequenced. To see if this introduced a potential bias, we used only the 46 families from which total information on sex and sequence was available (Table 2). Again there is no evidence for a within-clutch nonrandom sex distribution; in fact the data from 5- and 6-egg clutches are extremely close to expectation. Even in those clutches for which all eggs are accounted, there is no evidence of anything other than random segregation of sex. This is consistent also with the findings of Harmsen and Cooke (1983), who analyzed the distribution of sexes among broods of the Lesser Snow Goose of various family sizes and found that apart from one minor exception they conformed to binomial distributions.

As pointed out by Fiala (1980), it is conceivable that the clutches in which there was no mortality were themselves a nonrandom sample of the total

TABLE 1. Sex of Lesser Snow Goose goslings from sequential eggs in 3- through 6-egg clutches.

Clutch size	Sex	Egg sequence						Total	Number of families	G ²	df	Probability
		1	2	3	4	5	6					
3	♂	19	14	16	—	—	—	49	55	0.43	2	0.81
	♀	17	17	18	—	—	—	52				
4	♂	25	34	29	31	—	—	119	104	0.66	3	0.88
	♀	33	36	31	31	—	—	131				
5	♂	24	22	19	27	17	—	109	89	1.59	4	0.81
	♀	27	22	22	22	23	—	116				
6	♂	2	5	7	8	7	7	36	32	1.92	5	0.86
	♀	4	9	11	9	9	5	47				

TABLE 2. Sex of Lesser Snow Goose goslings from sequential eggs in 3- through 6-egg clutches—complete families only.

Clutch size	Sex	Egg sequence						Number of families	G ²	df	Probability
		1	2	3	4	5	6				
3	♂	6	7	5	—	—	—	14	0.59	2	0.75
	♀	8	7	9	—	—	—				
4	♂	6	9	9	10	—	—	19	1.916	3	0.59
	♀	13	10	10	9	—	—				
5	♂	6	6	5	6	6	—	11	0.29	4	0.99
	♀	5	5	6	5	5	—				
6	♂	1	1	1	1	1	2	2	—	—	—
	♀	1	1	1	1	1	0				

clutches examined, but this would lead to the rather far-fetched hypothesis that a nonrandom production of offspring in terms of sex and sequence was corrected by pre fledging mortality. In other words, in those families in which there was an excess of males in early eggs and females in late eggs, there would have to be a selective elimination of males that resulted from early eggs and females that resulted from late eggs. We consider such an explanation highly unlikely.

The analysis of the data reported above does not indicate the presence of any nonrandom process operating on sex distributions, either within or among clutches, during the period from oogenesis to 5-week-old gosling.

It is very difficult to explain the discrepancy between our results and those of Ankney. One possibility is that the phenomenon varies from season to season and that by combining data from several seasons we have masked the effect. To check this we examined the data from four-egg clutches for four separate years when adequate samples were available (Table 3). Though the sample sizes are small, they provide no evidence for aberrant sex ratios in

any of the seasons. Furthermore, there is no indication that the relationship between sex and egg sequence varies significantly among seasons (three-way contingency, $G^2 = 6.02$, $df = 9$, $P < 0.74$).

Another possible explanation for the discrepancy between our results and those of Ankney could be that the phenomenon occurs only early or late in the season and that our results, having been collected over the entire season, would average out opposing early-season and late-season phenomena. We disaggregated our results using two different methods: (1) eggs laid in clutches that were initiated early in the season and late in the season in relation to mean initiation date, and (2) eggs laid before and after the mean egg-laying date. In both cases, sex ratios and sequence of sexes were not significantly different for different segments of the season. This contrasts our results also with the findings of Howe (1977) for Common Grackles (*Quiscalus quiscula*).

It seems much more likely that with Ankney's data the G-test, though significant at the 1% level, was nevertheless a result of a rare random deviation from the null hypothesis of equality of sex ratio regardless of egg sequence. His analysis may have suffered from a typical Type I statistical error. With relatively small sample sizes, even three or four birds can make the difference between a highly significant and a non-significant result. Mayr (1938) reported a significant deviation from a 0.5 sex ratio for American Kestrels (*Falco sparverius*) based on a small sample; Newton and Marquiss (1979) found no such deviation in a much larger sample of the same species and interpreted Mayr's data as a statistical artifact.

We would have preferred to have been able to confirm Ankney's interesting finding but have failed to do so despite a considerably larger sample size. We feel that, before we accept the view that sex is determined by other than random chromosomal mechanisms in Snow Geese, we need much more convincing evidence than that provided by Ankney (1982). It is clearly going to be important to continue to investigate the question of sex ratio and sequence

TABLE 3. Egg sequence and sex ratio of four-egg clutches of Lesser Snow Geese—four separate seasons.

Season	Sex	Egg sequence				Number of families
		1	2	3	4	
1975	♂	3	7	6	7	18
	♀	6	6	7	6	
1977	♂	6	6	3	6	22
	♀	8	3	7	4	
1980	♂	6	10	9	6	26
	♀	11	12	6	8	
1981	♂	9	10	8	9	26
	♀	5	8	7	10	

in this and other species of birds, especially in the light of recent suggestive evidence of sex-ratio distortions in relation to laying sequence in Ring-billed Gulls (*Larus delawarensis*) (Ryder 1979) and in Red-winged Blackbirds (*Agelaius phoeniceus*) (Fiala 1981). It is, however, going to be absolutely necessary to work with large sample sizes and to use sampling techniques that exclude possible biases.

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Effects of Intraspecific Piracy on Breeding Ring-billed Gulls

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Interspecific food stealing among members of the family Laridae has received considerable attention in recent years (e.g. Hatch 1970, Hopkins and Wiley 1972, Dunn 1973). Piracy also may occur intraspecifically, as was first reported by Hays (1970) for Common Terns (*Sterna hirundo*) attempting to feed their young. Recently, we published a preliminary description of intraspecific piracy in breeding Ring-billed Gulls (*Larus delawarensis*; Elston et al. 1977). In such instances, adult or young Ring-billed Gulls steal from conspecifics during attempts by adults to feed their young.

During the 1978 and 1979 breeding seasons, we monitored feeding attempts at a Ring-billed Gull colony, situated near Rogers City (Presque Isle County), Michigan, to determine how intraspecific piracy affected adult gulls supplying food to their young (see Southern and Southern 1981 for a colony description). The incidence of food stealing was low for about 10 days following the onset of hatching. Before the onset of piracy, adults efficiently fed their young and showed little hesitation before regurgitating food.

After piracy started, however, feeding behavior changed noticeably. Adults paced near their begging chicks and alternated between regurgitating food and reswallowing it. Frequently, adults interrupted feeding attempts to chase or threaten neighboring adults or chicks that showed an interest in the feeding attempt (Southern and Southern in press). These behavioral changes resulted in prolonged feeding attempts, which often were not completed. In this paper, we examine these behavioral changes and their effects on the efficiency of parental care.

This study was conducted between 21 May and 20 July in both 1978 and 1979. Mean nest density at this colony was 1.85 m²/nest in 1978 and 1.32 m²/nest in 1979 (Southern and Southern 1981). Observations were made for 2-h periods at each of three study plots from the first through the eighth week post-hatching. In 1978, 534 feeding attempts were monitored during 136 h of observation, and, in 1979, 1,000 feeding attempts were observed during 147 h. Observations were made between 0800 and 1600 h each day, weather permitting. A feeding was considered to start when one or more chicks initiated begging, i.e. assumed a hunched posture and pecked at the adult's bill. Once a feeding started, it was monitored

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