

# SEX RATIO VARIES WITH EGG SEQUENCE IN LESSER SNOW GEESE

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**ABSTRACT.**—I found that in 4-egg clutches of Lesser Snow Geese (*Chen caerulescens caerulescens*) the first 2 eggs laid produced mostly males (64%) and the last 2 produced mostly females (72%). To interpret the functional significance of this phenomenon adequately, it is necessary to determine the mechanism whereby it occurs. I propose and discuss three possible mechanisms: nonrandom segregation of sex chromosomes, earlier or faster growth of ovarian follicles that subsequently produce males, and temperature-influenced sexual differentiation. Received 10 August 1981, accepted 17 February 1982.

HOWE (1977) reported seasonal changes in the primary sex ratio of Common Grackles (*Quiscalus quiscula*) and hypothesized that nonrandom segregation of the sex chromosomes was the mechanism whereby these changes occurred. Ryder (1979) noted that there was an apparent association between egg sequence and sex ratio in Ring-billed Gulls (*Larus delawarensis*), but he did not propose a mechanism to explain the phenomenon. To my knowledge, Ryder's report is unique, as no one else has reported on sex-ratio variation within the entire laying sequence for any other bird species. [Fiala (1981) found that in four-egg clutches of Red-winged Blackbirds (*Agelaius phoeniceus*) last eggs produced more females than males, but synchronous hatching prevented associating other hatchlings with the eggs from which they hatched.]

Here, I report that in 4-egg clutches of Lesser Snow Geese (*Chen caerulescens caerulescens*, which includes both blue and white phases and are here referred to as snow geese), the first 2 eggs usually produce male goslings and the last 2 eggs usually produce females. Nonrandom segregation of sex chromosomes could explain this, but at least two other mechanisms are possible: faster and earlier growth of ova that subsequently produce males or environmental sex determination.

## METHODS

The data were obtained at the McConnell River (60°50'N, 94°25'W), Northwest Territories, Canada in 1975. To obtain pipping eggs for later growth and survival experiments (Ankney 1980), I established a nest transect on 28 May, shortly after the geese began

arriving at the colony. Each nest was marked with a numbered stake, and the eggs in each were sequentially numbered with waterproof ink. Nearly all nests had one egg when found, though some had two. When a nest contained two eggs, the cleanest (whitest) egg was considered the last laid and given the number 2; that may not have always been correct but would not have biased the results presented here. Nests were revisited daily and new eggs numbered until the clutch was complete. Clutches were removed from nests when at least one egg was pipping, and the eggs were hatched in an incubator made from a wooden box heated by four 100-watt bulbs. Because I intended to compare the growth and survival of goslings from eggs of different weights, the clutches were selected to reflect the range of egg weights found on the transect (88–161 g, 933 nests). I determined the mean fresh egg weight of all eggs in marked nests ( $\bar{x} = 121$  g,  $SD = 7$  g,  $n = 3,880$  eggs) and chose clutches so that I had approximately equal numbers of eggs in these categories: *Light* eggs =  $\bar{x}$  minus  $> 1 SD = < 114$  g; *Average* eggs =  $\bar{x} \pm 1 SD = 114$ –128 g; and *Heavy* eggs =  $\bar{x}$  plus  $> 1 SD = > 128$  g. Clutches of four eggs were used, as they were the most common on the transect (511/933 nests).

When a gosling hatched, it was immediately tagged in the web of each foot with individually numbered metal tags, and its egg number was recorded. Goslings were sexed when they were removed from the incubator, about 24 h after they hatched. Sex was determined by the presence or absence of a "penis." All surviving goslings were checked again when they were 20 days old, and all initial determinations were found to be correct.

Data were obtained from 29 clutches, but the number of goslings for which I obtained sequence and sex data did not equal 116 (29 × 4), because 4 eggs disappeared between clutch completion and the time the clutches were removed from nests, 7 eggs did not hatch, and 10 goslings died while hatching or immediately thereafter. The latter birds could have been

sexed, but unfortunately they were not. Data were analysed with G-tests (Sokal and Rohlf 1969: 589).

RESULTS AND DISCUSSION

The sex of goslings was not independent ( $P < 0.01$ ) of egg sequence (Table 1); the first 2 eggs in a clutch tended to produce males (64%), and the last 2 tended to produce females (72%). The overall sex ratio, however, did not differ ( $P > 0.9$ ) from unity. For 24 of the clutches, I determined the sex of goslings from both the first and second eggs, and the ratio was 30 males : 18 females; for 17 of the clutches, I determined the sex of goslings from both the third and fourth eggs, and the ratio was 12 males : 22 females. Those ratios are very different ( $G = 5.78$ ;  $P < 0.025$ ). Thus, it is highly unlikely that these results were produced by sex-biased mortality of the goslings that did not hatch or died very early.

These data raise two questions: (1) is it adaptive for the female goose to produce offspring in such a manner [female birds are the heterogametic sex (e.g. Rothwell 1976) and thus produce "male" or "female" eggs], and (2) by what mechanism(s) does this phenomenon arise?

The data appear to be further support for the Trivers-Willard (1973) hypothesis that females in good condition should show a male bias in their offspring and those in poor condition a female bias (but see Meyers 1978). In 4-egg clutches of snow geese, the first 2 eggs weigh more, on average, than do the last 2 eggs (125 g vs. 117 g, Ankney unpubl. data), and goslings from heavy eggs grow faster initially than those from light eggs (Ankney 1980). If it were adaptive for a female snow goose to produce large sons (see Ankney 1977), then producing males from first eggs in a clutch might be an adaptation to accomplish that. Apparently, females are investing slightly more in their male offspring than in their female offspring. This supports the Trivers-Willard hypothesis, because female snow geese rely heavily on stored nutrient reserves for egg production (Ankney and MacInnes 1978) and are thus in better condition when they lay their first 2 eggs than when they lay their last 2 eggs. This may be the first case of within-female variation, as opposed to among-female variation (e.g. Howe 1977, McClure 1981), that supports the Trivers-Willard hypothesis. To be truly supportive, however, the phenomenon must be produced, directly or indirectly, by some mechanism under

TABLE 1. Sex of Lesser Snow Goose goslings from sequential eggs in four-egg clutches ( $n = 29$  clutches).<sup>a</sup>

Sex	Egg number				Total
	1	2	3	4	
Male	17	16	7	5	45
Female	10	9	17	14	50
TOTAL	27	25	24	19	95

$G = 12.294, P < 0.01$

<sup>a</sup> See text for explanation of why column totals do not equal 29.

genetic control, i.e. it must be subject to natural selection.

Theories about adaptive sex ratios suggest that somehow sex determination is not (entirely) a random process. For example, Fisher (1930) argued that parents *genetically disposed* to produce the rarer sex in a population will be selectively favored (italics mine). Similarly, Trivers and Willard (1973) argued that under certain conditions natural selection favors deviations away from a 50/50 sex ratio *at conception* (italics mine). Williams (1979), however, concluded that "sex seems to be just another Mendelian unit character" and "deviations from random sex determination are trivial at best." My data suggest that sex determination is not random in snow geese; below I outline three mechanisms whereby this could occur.

*Mechanism 1—nonrandom segregation of sex chromosomes.*—As Howe (1977) pointed out, nonrandom deviations in primary sex ratio of birds must result from maternal control, as the female is the heterogametic sex. The first (sex-determining) meiotic division occurs about 3–4 h before ovulation in domestic chickens and turkeys (Olsen and Fraps 1950). It is unknown when this division occurs in snow geese, but if the timing were similar to that of chickens and turkeys, then nonrandom segregation of sex chromosomes would be a mechanism that could produce the results I observed. Howe (1977) proposed that this was the mechanism that produced seasonal changes in primary sex ratios of Common Grackles and stated that it was "a cytological phenomenon well documented in some insects but hitherto undetected in vertebrates." In any event, if this were the mechanism at work in snow geese, I am puzzled as to why, if the strategy were adaptive, more females do not use it. Although the

relationship I found is statistically significant, there were 3 clutches that produced 2 females from the first 2 eggs (versus 9 that produced 2 males and 12 that produced 1 of each sex) and 2 clutches that produced 2 males from the last 2 eggs (versus 7 that produced 2 females and 8 that produced 1 of each sex). Both of the following mechanisms explain how the sequence-biased sex ratio could occur in snow geese and also why it is only a trend and not an absolute.

*Mechanism 2—earlier and/or faster growth of ovarian follicles that subsequently produce males.*—The developing follicles in a bird's ovary grow in a hierarchical fashion, but the control or regulation of this hierarchy is not understood (Sturkie 1976: 311). Follicular growth is in response to "the endogenous elaboration of follicular stimulating hormone (FSH) and luteinizing hormone (LH)" (Sturkie 1976: 311). Thus, what causes the follicles to grow is known, but why they begin to grow one at a time is unknown and "represents one of the major unanswered questions in reproductive biology" (Norris 1980: 383). Suppose that in snow geese the sex-determining meiotic division occurs much earlier in oogenesis than it does in chickens and turkeys, say just before the phase of rapid yolk synthesis. Suppose also that the follicles that will subsequently produce "male" eggs are stimulated to grow by lower levels of FSH and/or LH. This could explain why the first eggs laid tend to produce males; the last eggs would tend to produce females if meiosis had occurred in a small number of follicles and had been random. This seems possible, because snow geese are determinate layers and only 2–6 follicles undergo rapid yolk development (Ankney and MacInnes 1978). This mechanism would explain why not all females show the general pattern of males first and females last, e.g. random meiosis would result in some females having 4 "female" eggs, some having 3 "female" eggs and 1 "male" egg, etc.

*Mechanisms 3—temperature-influenced sexual differentiation.*—Imagine that genetic sex determination in snow geese can be over-ridden by temperature conditions after the egg is laid. Assume that a snow goose egg that is given a "cold shock," say exposed to 0°C, will produce a male gosling regardless of its sex chromosomes. Also, assume that an egg that is given a "heat shock," say in this case one that is not allowed to cool below 35°C after being laid, will produce a female gosling. Eggs not exposed to

either extreme will produce half males and half females. Under those assumptions, the egg-laying and incubation patterns of snow geese could produce sequence-biased sex ratios. Female snow geese normally lay one egg per day until the clutch is complete, although those laying clutches of four or larger sometimes skip a day after the second or third egg (Cooch 1958, Ankney unpubl. data). Incubation usually begins with the penultimate egg (Cooch 1958, Ankney unpubl. data). Remember, however, that, as in all birds, each egg has been "incubated" for about 24 h before it has been laid; in chickens the embryo has developed to the early stages of endoderm formation (20,000 cells) when the egg is laid (Abbot and Yee 1975: 162). There is variation in the extent to which first-laid eggs are exposed to environmental temperatures before incubation begins. That is so because there is variation among females in how and when they construct nests (Cooch 1958): some females partially bury their first egg in the ground and gradually build a nest as eggs are laid; others begin with an old, built-up nest and add material during egg laying. Finally, as not all females begin laying on the same date, eggs in different nests will subsequently be exposed to different environmental temperatures.

Clearly there is considerable variation in the range of temperatures to which the eggs are exposed. The first two eggs in a clutch, especially those in "nests" where the first egg is buried in the ground (sometimes touching the permafrost), will be exposed to cold much more than the last two eggs, especially if the female begins to incubate with the penultimate egg. Consequently, at least some "first" eggs will be exposed to subfreezing temperatures (in 1975, ground temperatures dropped below 0°C every night during the egg-laying period); some "last" eggs may not cool at all after being laid. Thus, the possibility for temperature-influenced sex differentiation exists for snow geese.

If, as outlined above, temperature effects could over-ride genetic sex in snow geese, then it would be predictable that this would occur most often in (1) the smallest "first" eggs because they would cool fastest, and (2) the largest "last" eggs as they would cool slowest. That clearly was the case (Table 2).

I cannot find much evidence for or against Mechanism 3. Genetic sex is not absolute in birds, as there are numerous reports of spon-

TABLE 2. Sex ratio (males : females) versus egg sequence and egg weight in four-egg clutches of Lesser Snow Geese.

Egg sequence	Egg weight category <sup>a</sup>			Total
	Light	Average	Heavy	
First 2 eggs—ratio (% male)	13:4 (76%)	11:8 (58%)	9:7 (56%)	33:19 (64%)
Last 2 eggs—ratio (% female)	4:8 (67%)	6:12 (67%)	2:11 (85%)	12:31 (72%)

<sup>a</sup> See text for definition of categories.

taneous sex reversal in the avian literature (reviewed by Abbot and Yee 1975). Incubating chicken or Japanese Quail (*Coturnix coturnix*) eggs at 40.5°C (versus the optimum 38°C) during mid-incubation results in pseudohyperfeminization, as the Mullerian duct disappears in male embryos and the right Mullerian duct develops into an oviduct in females (Stoll 1945, cited in Romanoff 1960: 859; Lutz-Ostertag 1966). Many researchers have looked at the hatchability of chicken eggs after short- and long-term exposure to cold temperature before incubation (Romanoff 1960), but none reported the sex ratio of those that hatched. There are, however, considerable recent data that show that sex differentiation in some reptiles (5 turtle and 2 lizard families) can be temperature controlled (reviewed by Bull 1980). Generally, cool temperatures during incubation produced males and warm temperatures produced females. That this phenomenon occurs in reptiles suggests that it is possible in birds, because "Birds have been aptly termed 'glorified reptiles'." (Romer 1962: 63).

Clearly, more data are needed to determine the mechanism responsible for the sequence-biased sex ratios in snow geese and to understand the adaptive significance of this phenomenon. Data about sex ratio and egg sequence for other bird species are also needed.

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Unsolicited manuscripts will now be considered for publication in the new journal, *Colonial Waterbirds*. Preference will be given to those authors able to pay page charges but these will not be mandatory. This policy change takes effect immediately, with the next volume (No. 6) expected to be published in the summer or early fall 1983. For details concerning manuscript preparation, consult Volume 5 of *Colonial Waterbirds* or the Editor, Dr. Herbert Kale II, Florida Audubon Society, 1101 Audubon Way, Maitland, Florida 32751.

The **International Conference on Bird Census and Atlas Studies** will be held on **5-9 September 1983** at Newland Park College, Chafont St. Giles, Buckinghamshire, U.K. Papers or posters may be offered on validation and testing of census methods, application of census techniques to bird community studies, description of vegetation and habitats for use in ornithological studies, atlas studies, and data processing methods. Offers of papers or posters should be received by **1 March 1983**; manuscripts should be submitted by **1 July 1983**. The cost of the conference is £120 Sterling, which covers the conference fee, food, and accommodation from 5 to 9 September. All correspondence, including booking, offers of papers, or submission of manuscripts, should be addressed to **R. J. Fuller, British Trust for Ornithology, Beech Grove, Tring, Hertfordshire HP23 5NR, United Kingdom**.

#### SECOND SYMPOSIUM ON AFRICAN PREDATORY BIRDS

The Natal Bird Club, a branch of the Southern African Ornithological Society, will be holding a symposium on African Predatory Birds on 22-26 August 1983. The first symposium on this topic was held in Pretoria in August 1977. Four sessions are planned: The role of captive breeding in conservation; The effects of pesticides, particularly in the Third World; The energetics of large predators; and The biology of rare and poorly known species.

The meeting will be held at the Golden Gate National Park in the Orange Free State. Further information and application forms are obtainable from **Dr. John Mendelsohn, Durban Museum, P.O. Box 4085, Durban, South Africa 4000**.

Proceedings of the conference "Understanding the Goshawk," which was held at Oxford during September 1981 under the sponsorship of the International Association for Falconry and Conservation of Birds of Prey, are now available. The 20 papers in this 200-page volume present recent findings on Goshawk systematics, status, population dynamics, predation, pollution, and domestic breeding and use in falconry. Of particular interest are the discussions of why populations declined during the 1950s and 1960s and how Goshawks recolonized Great Britain. Copies may be obtained for £8.00 (postage included) from **Ian Lindsay, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom**.