SHORT COMMUNICATIONS

Sex Ratio and Egg Sequence in Ring-billed Gulls

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Recently, Ankney (1982) documented a relationship between egg-laying sequence and the sex of newly hatched Lesser Snow Goose (*Chen c. caerulescens*) goslings. In 4-egg clutches more males (64%) than females hatched from the first 2 eggs laid and more females (72%) than males from the last 2 eggs. Investigations of this phenomenon in other species are necessary if we are to appreciate its importance and adaptive significance to sex-ratio dynamics in birds.

During studies of Ring-billed Gulls (*Larus delawarensis*) nesting on Granite Island (48°43′N, 88°29′W) in Black Bay, northern Lake Superior [see Ryder (1976) for a description of the colony] in 1978, 1979, and 1982, I determined the sex of chicks from three-egg clutches in order to record the secondary (hatching) sex ratio. Stimulation for this study arose from the discovery, in 1978, of female-female pairs of Ring-billed Gulls nesting on Granite Island (Ryder and Somppi 1979). My initial objective was to determine whether or not disproportionately more females hatched from three-egg clutches. If so, that might explain an apparent abundance of females in the breeding population; the consequent skewed secondary sex ratio could result in the formation of female-female pairs.

Each season I marked each study nest with a numbered wooden block and the eggs, in order of laying, with either a nontoxic black felt marking pen or brown nail enamel dots representing the egg number. The a-egg, b-egg, and c-egg refer to the 1st, 2nd, and 3rd eggs laid in a clutch, respectively. Only nests that were initiated before or during the peak of egg laying and subsequently contained three eggs were used for analyses, because such clutches are considered to be of normal size for *Larus* gulls (Vermeer 1969, Coulter 1977) and they typically experience the highest hatching success (Ryder and Ryder 1981) relative to clutches of more or fewer eggs. Clutches initiated later are usually smaller and suffer higher egg mortality (Ryder and Ryder 1981). I obtained data from a total of 89 three-egg clutches, but the number of chicks from which I obtained sex and sequence data did not equal 267 (3 × 89). Of the 66 eggs that were not used, 18 embryos died during early incubation, 37 eggs disappeared, and 11 eggs were found destroyed.

From each marked clutch, I retrieved chicks that had died in late incubation, during pipping, or soon after hatching, if their position in the clutch was known, and determined sex by gonadal inspection. I collected newly hatched live chicks under permit, determined their sex, and then deposited them in the ornithological holdings of Lakehead University. Data were analyzed using Chi-square and *G*-tests (Sokal and Rohlf 1981). Significance was set at $P \leq 0.05$.

Significant dependence occurred between chick sex and egg sequence in 1978 and 1979 but not in 1982 (Table 1). The lack of significance in the earliest starting season of 1982 is attributed to a greater proportion of males produced in b-eggs (57%) relative to 1978 (27%) and 1979 (25%). The combined data, however, show a strong statistical relationship. Although the secondary sex ratio for clutches did not differ from unity in any one study season (1978, $\chi^2 = 0.18$; 1979, $\chi^2 = 3.26$; 1982, $\chi^2 = 0.60$), proportionately more females than males were produced in 1979 relative to 1978 and 1982 (Table 2).

The results of this study suggest that the secondary sex ratio of Ring-billed Gulls probably does not contribute to a skewed sex ratio in favor of breeding-age females and, thus, cannot currently be considered an important factor in the origin of female-female pairs in the study population. The data indicate, however, that the allocation of sex by the female to specific eggs in the clutch very probably occurs in Ring-billed Gulls. Although the functional significance of sex allocation is not yet known in birds, it might be adaptive in Ring-billed Gulls for a male to hatch from the a-egg, because potentially it would then be a better-fed, larger, more vigorous son. This would have a

TABLE 1. Number of males and females in relation to egg sequence in Ring-billed Gulls, Granite Island.

		Egg[a]		
Year	Sex	a	b	c
1978	M	11	4	12
	F	3	11	10
	$G = 8.30$, $P < 0.025$, $n = 28$ clutches			
1979	M	15	6	6
	F	11	18	13
	$G = 6.26$, $P < 0.05$, $n = 30$ clutches			
1982	M	18	16	10
	F	11	12	14
	$G = 2.40$, NS, $n = 31$ clutches			
Combined	M	44	26	28
	F	25	41	37
	$G = 9.78$, $P < 0.01$, $n = 89$ clutches			

[a] a, b, and c refer to the 1st, 2nd, and 3rd eggs laid in a clutch.

TABLE 2. Number (percentage) of males and females produced in three-egg Ring-billed Gull clutches in relation to annual timing of nesting, Granite Island.

Year	Males	Females	Date of first nest	Dates of peak clutch initiation
1978	27 (52.9)	24 (47.1)	11 May (normal)	17–19 May
1979	27 (39.1)	42 (60.9)	14 May (late)	20–22 May
1982	44 (54.3)	37 (45.7)	8 May (early)	13–18 May
Total	98 (48.8)	103 (51.2)		

selective advantage in terms of the concepts within the Trivers-Willard (1973) hypothesis (see also Ankney 1982). The probability of realizing a 1:1 secondary sex ratio might be increased if sex were allocated to specific eggs rather than determined solely by a random assortment of sex chromosomes in the heterogametic female. Using the a- and b-eggs only from the normal season of 1978, I calculated probability of attaining a 1:1 secondary sex ratio to be 0.64 rather than 0.50, the probability under random assortment (Table 3). The c-egg was not considered in the above calculation, because in *Larus* gulls it is known that chicks from the c-egg typically experience a greater pre-fledging mortality than those from a- and b-eggs (Parsons 1970, Coulter 1977), and thus they contribute less to the adult (tertiary) sex ratio. The c-egg might serve primarily as insurance in case the a- or b-egg fails to hatch or the a- or b-chick fails to fledge (see discussion in Nisbet and Cohen 1975). Therefore, one might predict a 1:1 sex ratio in the c-eggs, because the parents cannot foretell which egg or chick (a or b) might die. The sex ratio of c-eggs did not differ from unity each year (Table 1) and thus supports this prediction. In 1979 and 1982 the expected higher probability of a 1:1 sex ratio in the a- and b-eggs by allocation was confounded by the apparent relationship between timing of nesting and the proportion of males and females produced each year. It is tempting to invoke the Trivers-Willard (1973) hypothesis again, as females entered the nesting season early in 1982, were in good physical condition because of a presumed abundant pre-season food supply, and subsequently produced more male offspring. In the late season of 1979, when food may have been in short supply, females would have begun nesting in relatively poor condition and produced more female offspring. Unfortunately, comparative data are available on neither the prenesting food supply nor on the body condition of females nesting in early, normal, or late starting seasons. Whether or not these are related to any proximate control of the secondary sex ratio is also unknown.

My results suggest that sex determination in Ring-billed Gulls is not random, and they correspond to those of Ankney (1982) for Lesser Snow Geese. How female birds allocate sex to specific eggs in their clutches remains enigmatic (but see Ankney 1982). Confirmation of the phenomenon for other bird species and a mechanistic explanation are required. It is clear, however, that, "with physiological control of sex determination so prominently developed in the insects, the possibility should not be overlooked that it also occurs at least to a limited extent in the vertebrates" (Wilson 1975: 317).

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TABLE 3. Calculation of the probability of a 1:1 secondary-sex ratio by allocation of sex to eggs and by random assortment.

Method	Probability of male in a-egg, female in b-egg	+	Probability of female in a-egg, male in b-egg	=	Probability of 1:1 sex ratio
Allocation:	(11/14)(11/15)[a] (0.79)(0.73)	+ +	(3/14)(4/15) (0.21)(0.27)	=	0.64
Random:	(0.50)(0.50)	+	(0.50)(0.50)	=	0.50

[a] Refer to Table 1 for raw data; a- and b-eggs only, 1978 (see text).

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Mate Changes by Black-bellied Whistling Ducks

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Delacour and Mayr (1945) suspected that whistling ducks (Dendrocygnini) kept the same mate for life. Bolen (1971) confirmed that Black-bellied Whistling Duck (*Dendrocygna autumnalis*) pairs remain together from year to year and reported one pair that had nested together for at least 4 yr. My recapture records of birds banded at nest boxes indicate that Black-bellied Whistling Ducks will pair again when their mate dies; here, I describe two occurrences in which both members of pairs obtained new mates, although their previous mates were still alive.

I studied the nesting ecology of Black-bellied Whistling Ducks by inspecting nest boxes during all or parts of the 1971-1972, 1974, and 1976-1979 nesting seasons in eight south Texas locations. Study areas are described in Meanley and Meanley (1958), Box and Chamrad (1966), Bolen (1967), and Delnicki (1973).

I banded a male Black-bellied Whistling Duck (897-94372) incubating five eggs in Cameron County on 23 July 1971. On 30 July 1971 a female incubating this nest, then containing nine eggs, also was banded (897-94377). This female was also incubating the nest on 6 August 1971. The male was additionally observed incubating on 13 August and brooding four hatchlings and incubating five eggs on 21 August 1971. Ultimately, six of the nine eggs hatched. Female 897-94377 was recaptured incubating 30 eggs on 29 June 1972. Her new mate had been banded 12 days earlier while incubating 25 eggs. Twenty-five of the 30 eggs in this nest hatched between 12 and 19 July 1972. On 27 July 1972 male 897-94372 was recaptured incubating 22 eggs in a nest box 58 m from his 1971 nest and 46 m from the nest box where his 1971 mate had successfully nested 8-15 days earlier. His new mate was banded 3 August 1972. This male was also observed incubating on 14 August, and 18 of the 22 eggs hatched between that date and 25 August 1972.

On 20-21 July 1978 I banded a pair of Black-bellied Whistling Ducks (male 597-64652 and female 597-64653) at Santa Ana National Wildlife Refuge. At that time their nest contained 11 eggs. The female was recaptured at the nest box on 31 July; on 8 August 1978 the male was incubating 11 pipped eggs, all of which hatched. I recaptured male 597-64652 incubating 42 eggs on 8 June 1979, about 1.7 km from the 1978 nest site. On 11 June 1979 his new mate was caught and banded, and I observed this hen on the nest 4 days later. The male was incubating 40 eggs on 21 June, of which 24 hatched between that date and 3 July 1979. Female 597-64653 was recaptured on 19 June 1979 while incubating 32 eggs about 130 m from where her 1978 mate was simultaneously nesting. The following day I caught her new mate, a bird that I had banded in 1977. This hen was incubating 33 eggs on 11 July, 29 of which hatched between that day and 16 July 1979.

During 1971-1979, I banded both members of 106 nesting pairs, 17 pairs of which were recaptured while nesting together one or more years after being banded. One member from each of 26 of these 106 pairs