

# SEX RATIOS OF RED-WINGED BLACKBIRDS BY EGG SIZE AND LAYING SEQUENCE

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**ABSTRACT.**—Egg sex, size, and laying sequence were determined for 44 three-egg and 129 four-egg Red-winged Blackbird (*Agelaius phoeniceus*) clutches collected in 1982 and 1983. The proportion of males decreased with laying sequence in three-egg clutches and increased with laying sequence in four-egg clutches. In both three- and four-egg clutches, egg size increased with laying sequence. However, egg sex was independent of egg size for both clutch sizes, indicating that the sex-sequence and size-sequence patterns are independent of each other. No support was found for the hypothesis that these patterns represent adaptive strategies associated with hatching asynchrony and clutch reduction or with the predictability of egg infertility. Therefore it remains undetermined whether these patterns represent adaptive strategies or real but nonadaptive artifacts. *Received 10 October 1983, accepted 25 May 1984.*

THE ability to control the sex of one's offspring in response to prevailing environmental conditions would be of unquestionable value (Trivers and Willard 1973). That some species of invertebrates adaptively control offspring sex ratios is well established, but the question is just beginning to be addressed in vertebrates (Clutton-Brock 1982). Avian studies to date have shown that offspring sex ratios vary nonrandomly, and possibly adaptively, through the breeding season in Common Grackles (*Quiscalus quiscula*, Howe 1977) and Red-winged Blackbirds (*Agelaius phoeniceus*, Fiala 1981, Weatherhead 1983). Burley (1981) reported that captive female Zebra Finches (*Poephila guttata*) preferentially produced sons when mated to high-quality males (but see Immelmann et al. 1982, Thissen and Martin 1982), although field studies testing the same hypothesis in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*, Patterson and Emlen 1980) and Red-winged Blackbirds (Fiala 1981, Weatherhead 1983) failed to support the hypothesis.

Ankney (1982) and Ryder (1983) have reported nonrandom sex allocation relative to egg sequence in Lesser Snow Geese (*Chen caerulescens*) and Ring-billed Gulls (*Larus delawarensis*), respectively (but see Cooke and Harmsen 1983). In both studies it was found that, within a clutch, earlier-laid eggs were more often male. In addition, Ankney (1982) reported that in four-egg clutches the first 2 eggs were larger than the last 2 eggs. As a result, males were disproportionately produced from larger eggs.

To date, no parallel data have been reported for a passerine species, although there is reason to expect that some sex-size-sequence relationship may exist. Both Howe (1976) and Fiala (1981) reported that egg size increased significantly with laying sequence in Common Grackles and Red-winged Blackbirds, respectively. Fiala (1981) also found that last-hatching (=last-laid) Red-winged Blackbird eggs from four-egg clutches that he was able to sex were significantly biased in favor of females, suggesting either a bias in the sex ratio or differential mortality by sex during the period between laying and sexing. The methods of Fiala's study did not allow him to sex other eggs by laying sequence. I report here the results of a study to determine whether egg sex-size-sequence relationships exist in Red-winged Blackbirds and, if so, whether the patterns are consistent across clutch sizes and are similar to those found in nonpasserine species.

## METHODS

The study was conducted from May through July 1982 and 1983 on marsh-nesting populations of Red-winged Blackbirds located within 10 km of the Queen's University Biological Station at Lake Opinicon in eastern Ontario, Canada. All study sites were visited daily from the initiation of breeding through the breeding season. Nests were individually numbered when discovered (usually while being constructed) and checked on each subsequent visit. Eggs in each nest were numbered according to order of appearance using a waterproof felt pen. Because one

TABLE 1. Egg sex relative to sequence in three-egg clutches.

| Data set and year | Number of nests | Sex    | Sequence |        |       | $\chi^2$ <sup>a</sup> | Significance    |
|-------------------|-----------------|--------|----------|--------|-------|-----------------------|-----------------|
|                   |                 |        | First    | Second | Third |                       |                 |
| Complete          |                 |        |          |        |       |                       |                 |
| 1982              | 18              | Male   | 10       | 6      | 6     | 0.46                  | NS              |
|                   |                 | Female | 8        | 12     | 12    |                       |                 |
| 1983              | 16              | Male   | 8        | 8      | 5     | 1.14                  | NS              |
|                   |                 | Female | 8        | 8      | 11    |                       |                 |
| 1982 and 1983     | 34              | Male   | 18       | 14     | 11    | 2.95                  | 0.05 < P < 0.10 |
|                   |                 | Female | 16       | 20     | 23    |                       |                 |
|                   |                 | % Male | 52.9     | 41.2   | 32.4  |                       |                 |
| All               |                 |        |          |        |       |                       |                 |
| 1982              | 21              | Male   | 10       | 7      | 8     | 1.14                  | NS              |
|                   |                 | Female | 8        | 12     | 13    |                       |                 |
| 1983              | 20              | Male   | 8        | 9      | 6     | 0.45                  | NS              |
|                   |                 | Female | 10       | 9      | 12    |                       |                 |
| 1982 and 1983     | 41              | Male   | 18       | 16     | 14    | 1.52                  | NS              |
|                   |                 | Female | 18       | 21     | 25    |                       |                 |
|                   |                 | % Male | 50.0     | 43.7   | 35.9  |                       |                 |

<sup>a</sup> Cochran rank order  $\chi^2$ ,  $df = 1$  (Cochran 1954).

egg is laid per day in this species, daily visits allowed accurate sequencing of entire clutches. If a nest was discovered after laying was initiated, those eggs already present were marked with a letter and subsequent eggs numbered according to sequence.

At the time a clutch was collected, the maximum length and diameter of each egg were measured using vernier calipers. The product of the length and the square of the diameter was used as an index of egg volume, a value Fiala (1981) reports as being highly correlated with fresh-egg weight in Red-winged Blackbirds.

Because hatching in passerine clutches is quite synchronous, eggs were collected after approximately 10 days of incubation (about 1 day before hatching) to maintain egg sequence data. Collected eggs were preserved in formalin. In 1982, eggs were held to the observer's face during the laying period to detect the onset of incubation based on whether or not the eggs felt warm. Following each breeding season, all embryos were sexed by dissection under a dissecting microscope.

## RESULTS

Data were collected from a total of 23 three-egg clutches and 63 four-egg clutches in 1982 and 21 three-egg clutches and 66 four-egg clutches in 1983. Although several five-egg clutches were collected both years, they were too few to warrant analysis. Due to partial egg loss prior to collection, egg infertility, or nest discovery after the initiation of egg-laying, a

number of clutches provided incomplete sex, size, or sequence data. In the analyses that follow, sample sizes vary according to the number of clutches having complete data for the particular parameters being considered. The criteria for data selection in each analysis are specified.

*Sex and sequence.*—I have defined two types of data sets for this analysis. "Complete" data include all clutches with every egg sexed and sequenced. "All" data include information on every egg that was sexed and sequenced, whether those data were available for every egg in those clutches or not. In both years with both data sets for three-egg clutches, there was a trend toward a decreasing proportion of males with laying sequence, although this pattern approached significance only with the complete data for both years combined (Table 1). A comparison of the sex of first and last eggs for data from both years combined indicates that the tendency of more females in last eggs is more pronounced with complete clutches ( $\chi^2 = 2.94$ ,  $df = 1$ ,  $0.05 < P < 0.01$ ) than for all clutches ( $\chi^2 = 1.48$ ,  $df = 1$ ,  $P > 0.20$ ).

In four-egg clutches the pattern was opposite to that in three-egg clutches, with the proportion of males increasing with laying sequence (Table 2). In all but one within-year analysis this pattern was significant or approached significance at the  $P = 0.05$  level. Using the com-

TABLE 2. Egg sex relative to sequence in four-egg clutches.

| Data set      | Year          | Num-<br>ber of<br>nests | Sex    | Sequence |        |       |        | $\chi^2$ <sup>a</sup> | Significance    |
|---------------|---------------|-------------------------|--------|----------|--------|-------|--------|-----------------------|-----------------|
|               |               |                         |        | First    | Second | Third | Fourth |                       |                 |
| Com-<br>plete | 1982          | 35                      | Male   | 13       | 18     | 22    | 19     | 2.77                  | 0.05 < P < 0.10 |
|               |               |                         | Female | 22       | 17     | 13    | 16     |                       |                 |
|               | 1983          | 50                      | Male   | 19       | 21     | 23    | 28     | 3.39                  | 0.05 < P < 0.10 |
|               |               |                         | Female | 31       | 29     | 27    | 22     |                       |                 |
|               | 1982 and 1983 | 85                      | Male   | 32       | 39     | 45    | 47     | 6.13                  | P < 0.02        |
|               |               |                         | Female | 53       | 46     | 40    | 38     |                       |                 |
| % Male        |               |                         | 37.6   | 45.9     | 52.9   | 55.3  |        |                       |                 |
| All           | 1982          | 57                      | Male   | 15       | 24     | 30    | 29     | 4.32                  | P < 0.05        |
|               |               |                         | Female | 29       | 23     | 25    | 23     |                       |                 |
|               | 1983          | 66                      | Male   | 22       | 28     | 28    | 31     | 1.99                  | NS              |
|               |               |                         | Female | 37       | 34     | 34    | 30     |                       |                 |
|               | 1982 and 1983 | 123                     | Male   | 37       | 52     | 58    | 60     | 6.07                  | P < 0.02        |
|               |               |                         | Female | 66       | 57     | 59    | 53     |                       |                 |
| % Male        |               |                         | 35.9   | 47.7     | 49.6   | 53.1  |        |                       |                 |

<sup>a</sup> Cochran rank order  $\chi^2$ , df = 1 (Cochran 1954).

combined data for both years, there were significantly more males in fourth vs. first eggs for both complete ( $\chi^2 = 5.20$ , df = 1,  $P < 0.05$ ) and all ( $\chi^2 = 6.35$ , df = 1,  $P < 0.02$ ) data. This difference also was found when the sex of the last two eggs was compared with the first two eggs for both the complete data ( $\chi^2 = 5.20$ , df = 1,  $P < 0.05$ ) and all data ( $\chi^2 = 3.87$ , df = 1,  $P < 0.05$ ).

*Size and sequence.*—If egg size is independent of laying sequence, then each of the possible orderings of egg size by laying sequence should be equally likely to occur. For every clutch with complete size and sequence data, the rank order of eggs by size was determined. In three-egg clutches the pattern of smallest first, medium second, and largest third occurred most frequently in both years (Table 3). However, the exact opposite pattern was tied as the second most frequent. Using the combined data for both years, the distribution of size-sequence patterns differed significantly from random ( $\chi^2 = 17.97$ , df = 5,  $P < 0.01$ ).

In four-egg clutches the perfect ordering of egg size from smallest to largest with laying sequence was also the most frequent in both years, with a combined total of 26 of 95 clutches (Table 4). Because expected frequencies are less than 5 in all categories, the data must be grouped for statistical analysis. Logical groupings are clutches showing a monotonic increase, including clutches with two adjacent ranks reversed (i.e. 1234, 2134, 1324, 1243);

monotonically decreasing clutches, including those with two adjacent ranks reversed (i.e. 4321, 3421, 4231, 4312); and those with neither pattern (i.e. all others). The distribution of clutches over these categories differed highly significantly from random ( $\chi^2 = 80.07$ , df = 2,  $P < 0.001$ ). Given the prevalence of clutches in which egg size increases with laying sequence, it is again surprising that the exact opposite pattern (i.e. 1234) was tied as the fourth most frequent of the 24 patterns possible. Fiala (pers. comm.) also found that monotonically increasing and decreasing size-sequence patterns prevailed in three- and four-egg Red-winged Blackbird clutches.

*Egg sex and size.*—From the preceding results it should follow that, on average, females come from larger eggs than males in three-egg clutches while males come from larger eggs in four-egg clutches. A comparison of the mean estimated egg volumes of male and female eggs in the two clutch sizes for both years shows the predicted difference in three of four comparisons (Table 5), but none of the differences approach significance at the 0.05 level by Student's *t*-tests. The lack of significant differences could be due to high between-clutch variation in egg size masking the effect of the within-clutch size-sequence and sex-sequence patterns. To test this possibility the frequencies with which male and female eggs were ranked largest, second largest, etc. in three- and four-egg clutches were computed for clutches with

TABLE 3. Frequency of occurrence of egg size-egg sequence patterns in three-egg clutches. Egg size is ranked from largest (1) to smallest (3).

| Year          | Number of clutches |     |     |     |     |     |
|---------------|--------------------|-----|-----|-----|-----|-----|
|               | Sequence           |     |     |     |     |     |
|               | 123                | 132 | 213 | 312 | 231 | 321 |
| 1982          | 2                  | 2   | 2   | 1   | 2   | 9   |
| 1983          | 3                  | 1   | 1   | 4   | 2   | 6   |
| 1982 and 1983 | 5                  | 3   | 3   | 5   | 4   | 15  |

complete sex and sequence data (Table 6). Contrary to expectation, the sex of eggs was independent of egg size relative to the size of other eggs in the clutch, both in clutches of three ( $\chi^2 = 0.13$ ,  $df = 2$ ,  $P > 0.10$ ) and four ( $\chi^2 = 0.47$ ,  $df = 3$ ,  $P > 0.10$ ), using data for both years combined. The only pattern suggested by the data is for females to occur more frequently in both the largest and smallest eggs in both three- and four-egg clutches, but these differences are not significant when the sex ratio of intermediate-ranked eggs is compared to that of extreme-ranked eggs (three-egg clutches,  $\chi^2 = 0.11$ ,  $df = 1$ ,  $P > 0.10$ ; four-egg clutches,  $\chi^2 = 0.26$ ,  $df = 1$ ,  $P > 0.10$ ). These results indicate that the lack of a relationship between egg size and sex is real. Furthermore, these results show that the sex-sequence pattern is independent of the size-sequence pattern, such that when egg size does not increase with laying sequence, the sex-sequence relationship does not necessarily change in concert.

DISCUSSION

The results of this study can be added to the growing list of studies cited earlier that show some nonrandom pattern of sex allocation in birds. While some of these patterns (e.g. seasonal changes in sex ratio) conform to expectations based on the presumed benefits to be derived from facultative sex-ratio adjustment, egg sex-egg sequence patterns remain more enigmatic. Specifically, what advantage might be realized by an individual laying eggs non-randomly by sex over an individual producing a clutch with an identical sex ratio but in which the sex of eggs is independent of laying order?

An advantage might be realized if the value of offspring to the parent differed by sex while

TABLE 4. Frequency of occurrence of egg size-egg sequence patterns in four-egg clutches. Egg size is ranked from largest (1) to smallest (4).

| Year          | Number of clutches |      |      |      |      |      |
|---------------|--------------------|------|------|------|------|------|
|               | Sequence           |      |      |      |      |      |
|               | 1234               | 1432 | 1324 | 1423 | 1243 | 1342 |
| 1982          | 4                  | 0    | 0    | 0    | 0    | 1    |
| 1983          | 3                  | 1    | 1    | 0    | 1    | 2    |
| 1982 and 1983 | 7                  | 1    | 1    | 0    | 1    | 3    |
|               | 2134               | 2431 | 2314 | 2413 | 2143 | 2341 |
| 1982          | 0                  | 1    | 1    | 1    | 1    | 0    |
| 1983          | 1                  | 0    | 0    | 1    | 0    | 0    |
| 1982 and 1983 | 1                  | 1    | 1    | 2    | 1    | 0    |
|               | 3124               | 3421 | 3214 | 3412 | 3142 | 3241 |
| 1982          | 2                  | 2    | 1    | 1    | 0    | 0    |
| 1983          | 1                  | 0    | 3    | 1    | 1    | 0    |
| 1982 and 1983 | 3                  | 2    | 4    | 2    | 1    | 0    |
|               | 4123               | 4321 | 4213 | 4312 | 4132 | 4231 |
| 1982          | 0                  | 13   | 2    | 7    | 1    | 5    |
| 1983          | 2                  | 13   | 8    | 7    | 4    | 2    |
| 1982 and 1983 | 2                  | 26   | 10   | 14   | 5    | 7    |

at the same time egg or subsequent nestling survival was in some way dependent on laying sequence. The less valuable sex then could be placed disproportionately in the most vulnerable position. Asynchronous hatching and subsequent clutch reduction at the expense of the last-hatching egg would meet the criterion of sequence-dependent mortality. The incubation initiation data from this study indicated that 76.7% of females laying four-egg clutches began incubation on the day the third egg was laid, while 31.3% of females laying three-egg clutches began incubation on the day the second egg was laid. Therefore, asynchronous hatching would be expected in many more four-egg than three-egg clutches. Since asynchronous hatching would be disadvantageous to the last egg laid (Howe 1976), one would expect the sex of the last eggs laid to differ most from that of other eggs in the clutch and for that pattern to be more pronounced in four- than in three-egg clutches. Although the biggest difference in the frequencies of males and females did occur in last eggs in three-egg clutches, in four-egg clutches that difference was greatest in first-laid eggs. Also, because asynchronous hatching only affects the last-laid egg, there was

TABLE 5. Mean ( $\pm$  SD) estimated egg volume (cc) by sex and sequence in three- and four-egg clutches.<sup>a</sup>

| Sex    | Three-egg clutches (1982) |      |                   |      |                   |      |                   |
|--------|---------------------------|------|-------------------|------|-------------------|------|-------------------|
|        | First                     | (n)  | Second            | (n)  | Third             | (n)  | Overall           |
| Male   | 0.765 $\pm$ 0.067         | (10) | 0.753 $\pm$ 0.055 | (5)  | 0.801 $\pm$ 0.044 | (5)  | 0.771 $\pm$ 0.060 |
| Female | 0.711 $\pm$ 0.077         | (6)  | 0.797 $\pm$ 0.056 | (11) | 0.800 $\pm$ 0.090 | (11) | 0.780 $\pm$ 0.075 |
|        |                           |      |                   |      |                   |      |                   |
| Sex    | Four-egg clutches (1982)  |      |                   |      |                   |      |                   |
|        | First                     | (n)  | Second            | (n)  | Third             | (n)  | Overall           |
| Male   | 0.753 $\pm$ 0.066         | (11) | 0.764 $\pm$ 0.087 | (16) | 0.768 $\pm$ 0.076 | (21) | 0.794 $\pm$ 0.104 |
| Female | 0.733 $\pm$ 0.101         | (21) | 0.755 $\pm$ 0.069 | (16) | 0.785 $\pm$ 0.093 | (11) | 0.752 $\pm$ 0.085 |
|        |                           |      |                   |      |                   |      |                   |
| Sex    | Three-egg clutches (1983) |      |                   |      |                   |      |                   |
|        | First                     | (n)  | Second            | (n)  | Third             | (n)  | Overall           |
| Male   | 0.759 $\pm$ 0.062         | (8)  | 0.811 $\pm$ 0.054 | (7)  | 0.771 $\pm$ 0.095 | (5)  | 0.780 $\pm$ 0.073 |
| Female | 0.787 $\pm$ 0.128         | (6)  | 0.749 $\pm$ 0.107 | (7)  | 0.798 $\pm$ 0.070 | (9)  | 0.779 $\pm$ 0.103 |
|        |                           |      |                   |      |                   |      |                   |
| Sex    | Four-egg clutches (1983)  |      |                   |      |                   |      |                   |
|        | First                     | (n)  | Second            | (n)  | Third             | (n)  | Overall           |
| Male   | 0.735 $\pm$ 0.072         | (16) | 0.784 $\pm$ 0.072 | (17) | 0.794 $\pm$ 0.068 | (20) | 0.776 $\pm$ 0.072 |
| Female | 0.747 $\pm$ 0.090         | (28) | 0.757 $\pm$ 0.076 | (27) | 0.782 $\pm$ 0.064 | (24) | 0.757 $\pm$ 0.110 |

<sup>a</sup> Clutches with complete sex-size-sequence data only.

TABLE 6. Within-clutch egg size rank of males and females in clutches of three and four eggs. Size is ranked from largest (1) to smallest (4).

| Year             | Sex    | Number of clutches |    |    |                   |    |    |    |
|------------------|--------|--------------------|----|----|-------------------|----|----|----|
|                  |        | Three-egg clutches |    |    | Four-egg clutches |    |    |    |
|                  |        | 1                  | 2  | 3  | 1                 | 2  | 3  | 4  |
| 1982             | Male   | 6                  | 7  | 7  | 15                | 19 | 19 | 15 |
|                  | Female | 10                 | 9  | 9  | 19                | 15 | 15 | 19 |
| 1983             | Male   | 7                  | 8  | 5  | 20                | 20 | 22 | 16 |
|                  | Female | 7                  | 6  | 9  | 24                | 24 | 22 | 28 |
| 1982 and<br>1983 | Male   | 13                 | 15 | 12 | 35                | 39 | 41 | 31 |
|                  | Female | 17                 | 15 | 18 | 43                | 39 | 37 | 47 |

no reason to expect the observed pattern of a progressive change in sex ratio from the first to last egg. Thus, asynchronous hatching does not appear to provide a satisfactory explanation for the sex-sequence patterns.

If the probability of egg infertility varied with laying sequence and the value of the sexes differed, then it is possible that the sex-sequence patterns are a consequence of placing the more valuable sex disproportionately in eggs least likely to be infertile. In the combined data from four-egg clutches there were 20 infertile eggs in clutches with partial fertility. The distribution of those eggs by laying sequence was 8, 4, 1, and 7, going from first to last. Thus, while these data suggest that egg infertility may not be independent of laying sequence, the pattern does not correspond to the sex-sequence pattern.

The pattern of increasing egg size with laying sequence was the same as the pattern reported by Howe (1976) and Fiala (1981). Howe (1976) suggested that this pattern may increase the relative competitive ability of late-hatching nestlings, thereby improving their survival chances where environmental conditions preclude the necessity for brood reduction. My data do not support this interpretation because egg size increased with laying sequence in both three- and four-egg clutches, although only females laying four eggs widely adopted an incubation pattern that would produce asynchronous hatching. Howe's (1976) hypothesis, therefore, fails to explain why a significant egg size-egg sequence pattern should be found in three-egg clutches when only 31.3% of females laying those clutches incubate them in a fashion that would result in hatching asynchrony. Also, the hypothesis does not account for the

gradual increase in egg size with laying sequence because the expected pattern should simply be that the last-laid egg is larger than the others.

The results of this study, in combination with those of other studies, present a puzzling array of facts. Female Red-winged Blackbirds do not lay eggs randomly with respect to either the sex or the size of those eggs. Lesser Snow Geese also may vary egg sex and size with laying sequence, while Ring-billed Gulls vary at least egg sex with sequence. Within the same population of Red-winged Blackbirds, females laying different-size clutches adopt different sex-sequence patterns. Comparing this study with Fiala's (1981), female Red-winged Blackbirds laying four-egg clutches in the two populations apparently adopt different sex-sequence patterns (unless the excess of females in fourth eggs found by Fiala was due to higher male mortality, which would make the sex-sequence pattern in four-egg clutches apparently maladaptive).

I conclude that it is as plausible that these patterns reflect some adaptive strategy as that they are real but nonadaptive artifacts of some as yet unidentified underlying process. Further research is indicated. It would be important to know if the females of the same species that demonstrate different patterns of egg sex, size, and sequence and clutch size differ in any consistent way, e.g. age, condition. Recently, Blank and Nolan (1983) demonstrated that female age does influence some of the patterns discussed here. In addition to explaining the proximate causes of the nonrandom patterns, it is necessary to understand the consequences for the survival of the eggs and subsequent nestlings from the various combinations of egg sex, size,

and sequence. While this may be a fertile area for further investigation, identification of the mechanism for nonrandom sex allocation may be required before the patterns so produced can be understood.

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The American Ornithologists' Union will hold its 103rd Stated Meeting at Arizona State University in Tempe, Arizona, 7-10 October 1985. All persons interested in the conservation and management of birds are encouraged to attend. In addition to general scientific paper sessions, symposia will be held on the biology and management of Bald Eagles, avian olfaction, and the importance of competition in structuring avian communities. A call for papers to the membership will appear in April, with deadlines for program space being 1 June 1985 for the general scientific programs. Anyone desiring more information should contact Dr. Robert D. Ohmart, Center for Environmental Studies, Arizona State University, Tempe, Arizona 85287.